SYMPOSIUM ON CRUSTACEA

PART II

MARINE BIOLOGICAL ASSOCIATION OF INDIA

MARINE FISHERIES P.O., MANDAPAM CAMP

INDIA

SYMPOSIUM ON CRUSTACEA

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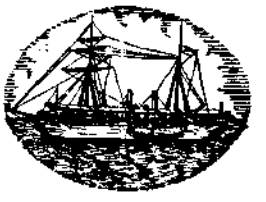


MARINE BIOLOGICAL ASSOCIATION OF INDIA

MARINE FISHERIES P.O., MANDAPAM CAMP

INDIA

PROCEEDINGS

OF THE

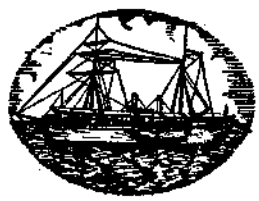
SYMPOSIUM ON CRUSTACEA

HELD AT

ERNAKULAM

FROM JANUARY 12 TO 15 1965

PART II



SYMPOSIUM SERIES 2

MARINE BIOLOGICAL ASSOCIATION OF INDIA

MARINE FISHERIES P.O., MANDAPAM CAMP

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PART II

PAGE

MORPHOLOGY AND TAXONOMY OF FRESHWATER OSTRACODA[1,2]

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ABSTRACT

Representatives of the crustacean subclass Ostracoda are worldwide in distribution, and inhabit both freshwater and marine environments. Some species of ostracods are inhabitants of brackish water, and at least one species lives in a moist land habitat. Freshwater ostracods belong to the order Podocopa and to three families: Cypridae, Cytheridae, and Darwinulidae. The vast majority of ostracod species are free-living. However, members of the genus *Entocythere* live commensally on the gills of crayfish. The known species of the genus *Sphaeromicola* live as commensals on amphipods and isopods. One species of *Cypridopsis* is known to prey upon two different species of snails. Freshwater ostracods are usually oviparous and reproduce either syngamically or by parthenogenesis. Members of the family Darwinulidae are viviparous.

The size, color, and ornamentation of the valves, and the structure of the antennae (second antennae), the maxillae, the mandibles, the third thoracic appendages, the furcae, and of the penis and ejaculatory duct are of taxonomic significance among the Cypridae.

LINNAEUS in the 1748 edition of his *Systema Naturae* applied a scientific name to an ostracod for the first time, designating it *Monoculus concha pedata.* The first significant work on extant Ostracoda was done by O. F. Müller, the results of his investigations were incorporated in a treatise entitled *Entomostrace sva Insecta Testaceae quae in aquis Daniae et Norvegiae reperit, descripsit et iconibus illustravit* that was published in 1785. The genus *Cypris* O. F. Müller, 1776 was established as the type for all Ostracoda. This all-inclusive genus has been divided and subdivided until it is now so restricted that it includes only a few species.

Members of the subclass Ostracoda are bivalved crustaceans and are worldwide in distribution. They occupy every conceivable kind of aquatic habitat. *Mesocypris terrestris* Harding is a land-dwelling species. Freshwater species range in length from 0·35 mm. to 8·0 mm. A member of the marine genus *Gigantocypris* Müller, 1912 reaches a length of 21·0 mm.

The vast majority of ostracods are free-living; however, members of the genus *Entocythere* live as commensals on the gills of crayfish. Two species of the European genus *Sphaeromicola* have been reported as living as commensals on amphipods and isopods. *Cypridopsis hartwigi* Müller preys upon snails of two species, *viz., Bullinus contortus* and *Planorbis glabratus.*

Larval stages of cestodes and acanthocephalans have been found in freshwater ostracods. Ward (1940) discovered that the ostracod *Physocypria globula* Furtos, 1933 [=*Physocypria pustulosa* (Sharpe, 1897)] serves as the intermediate host of the acanthocephalan *Neoechinorhynchus cylindratus* (Van Cleave, 1913), a parasite of the largemouth black bass. Hoff (1942 *a*) observed acanthocephalan parasites of several specimens of freshwater ostracods. I have taken adult nematode parasites from the bodies of individuals belonging to an undescribed species of *Candona* from Canada.

EXTERNAL MORPHOLOGY

According to Kesling (1951) the ostracod shell is composed of two major divisions: (1) a layer of soft sensitive tissue, the epidermis or hypodermis enclosed by chitin, and (2) a layer

[1] This research was supported by National Science Foundation Grant, GB-1534.

[2] The author acknowledges the assistance of Miss Alice Boatright who prepared the drawings.

of hard calcium carbonate coated with chitin. The external surface of the shell may be smooth, reticulated, striated, covered with spines, tuberculated, or pitted. The margins frequently possess one or more flanges. The ostracod shell is without lines of growth. The valves are frequently pigmented. The colors most often observed are white, green, brown, orange, yellow, purple and black.

The two valves are seldom equal, one usually overlapping the other when closed. The valves are connected along the dorsal margin by an elastic band, and are drawn tightly together by a group of adductor muscles (Fig. 1). The muscle scars (Fig. 6) located near the center of the valves are of taxonomic importance. An eye (Fig. 1), either single or double, may be present and is visible through the valves. The inner duplicature may be wide or narrow, and the margins may have a series of pore canals (Fig. 1).

Internal Anatomy

There are seven pairs of appendages in the family Cypridae. There are four pairs of cephalic appendages: first antennae (antennules), second antennae (antennae), the mandibles, and the maxillae. The first antenna is uniramous, and bears from five to seven podomeres; the exopodite has been lost. The second antenna is also uniramous in the Cypridae and possesses four to six podomeres; the exopodite has been reduced to a scale (Fig. 4). The exopodite (flagellum) of the second antenna among members of the family Cytheridae is a long hollow seta forming a duct that carries an adhesive secretion from a gland to aid in locomotion (Fig. 8).

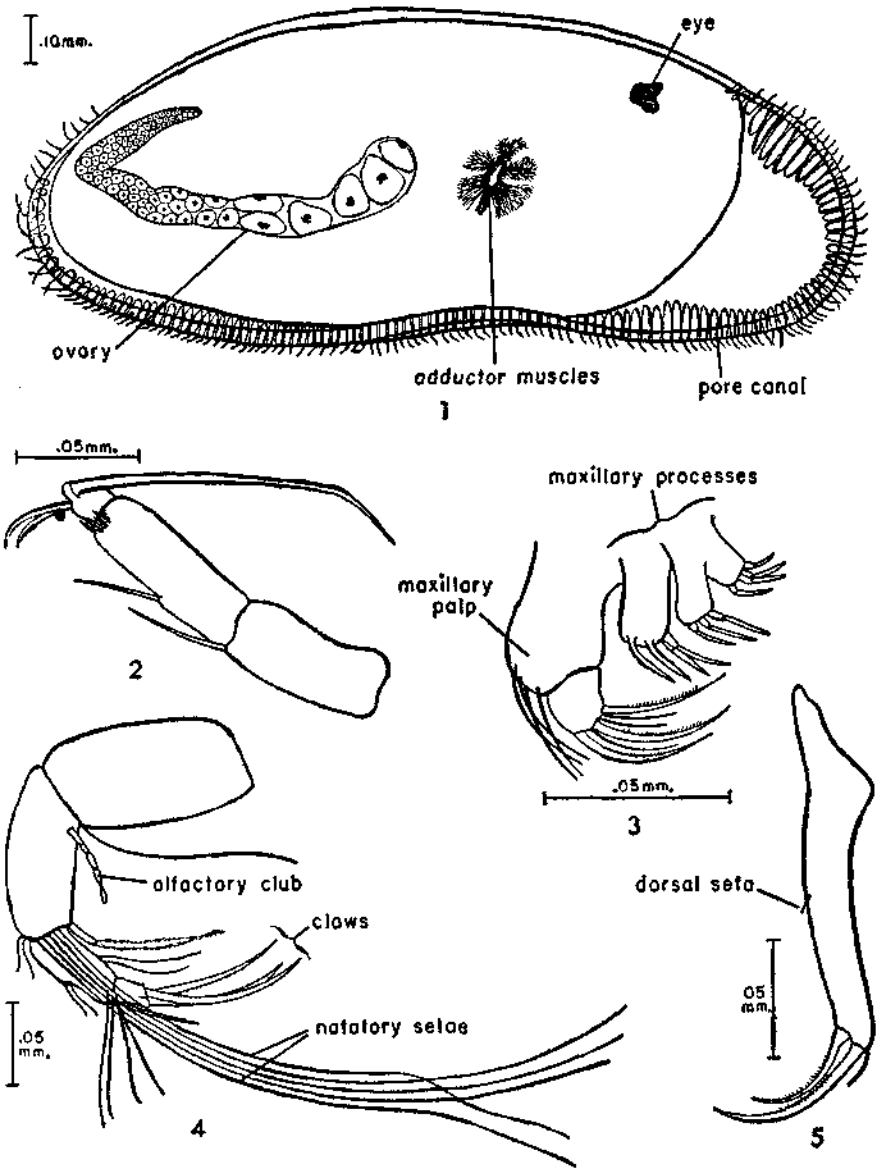
The first antennae have short claw-like structures for climbing and digging, and long natatory setae for swimming. The second antennae are used in feeding and in locomotion; in the male they are also used as clasping organs during copulation. The antepenultimate podomere of the second antenna among the Cypridae bears a club-like sensory seta, the olfactory organ or Leydig's organ (Fig. 4).

The mandibles (Fig. 10) are posterior to the second antennae, located one at each side of the mouth. Each mandible is provided with chitinous teeth at its distal end. The mandibular palp is attached to the lower one-third of the anterior surface of the mandible proper. The base of the mandible is strongly chitinized and is provided with well-developed levator muscles used during mastication. The mandibular palp bears a setiferous branchial plate on its proximal podomere. A number of spine-like setae, some teeth-bearing, are located on the palp. The mandibular palp probably serves as a taste organ and as a tactile organ as well.

The posterior pair of cephalic appendages are the maxillae (Fig. 3). These are the first maxillae of many earlier writers. The base of the maxilla usually has three masticatory processes and a palp of two or three podomeres. The structure and number of setae on the outer masticatory process, the process next to the palp, are of taxonomic value. The exopodite is the setiferous branchial plate. The maxillae are modified as organs for holding and passing food to the mouth. The branchial plate by its vibratory actions maintains a constant flow of water through the shell, and by the same action removes foreign substances from the shell cavity.

The thoracic region bears three pairs of appendages. The first pair of thoracic appendages in the Cypridae have teeth along the distal extremities, and are, therefore, considered by some investigators to be second maxillae. The protopodite ends in a masticatory process which bears spine-like setae. The endopodite is modified as a palp of a single podomere. The exopodite is in the form of a branchial plate. The palp in the male is usually modified as a prehensile structure of one or two podomeres. The prehensile claw is used during copulation. Among the Cytheridae the first thoracic appendage is pediform and ambulatory. The branchial plate is absent.

The sixth pair of appendages have been variously called the first walking legs, and the second walking legs. The second thoracic appendages are uniramous, having a protopodite of one

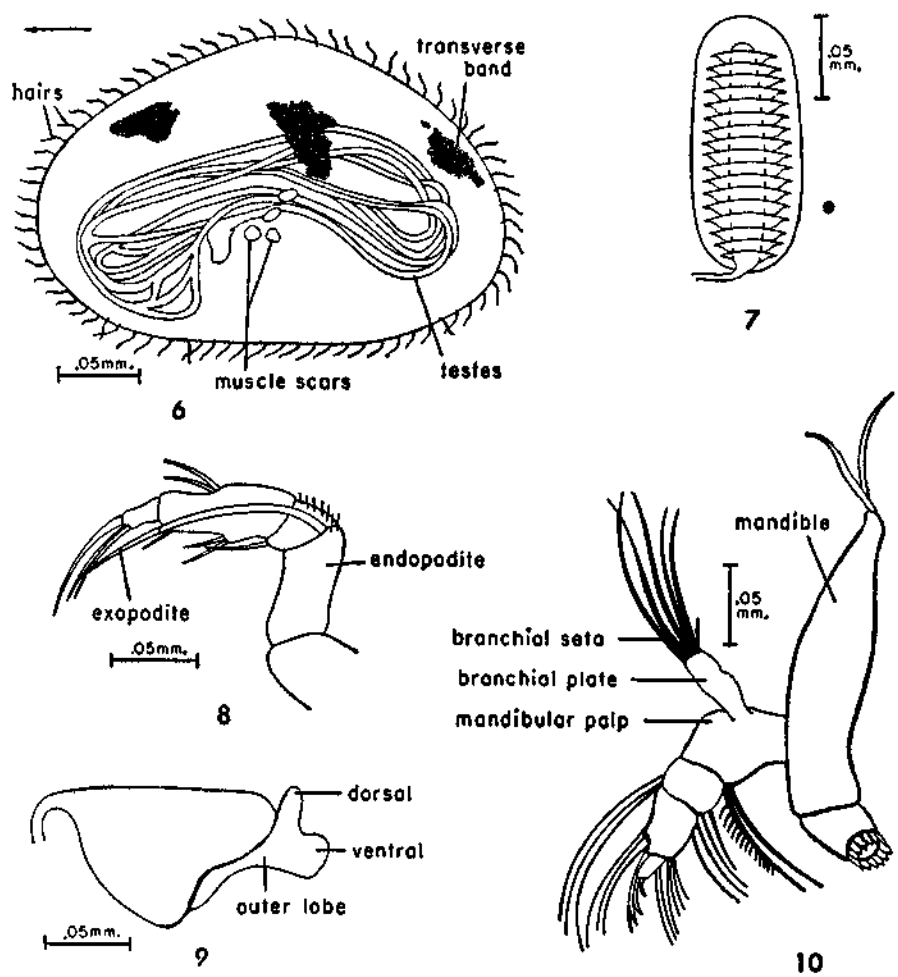


FIGS. 1–5. *Stenocypris bolieki* Ferguson, 1962; female. Fig. 1. Mesial view of left valve (redrawn from Ferguson, 1962). Figs. 2–5. *Cypria petenensis* Ferguson, Hutchinson and Goulden, 1964; female. Fig. 2. Third thoracic appendage. Fig. 3. Right maxilla. Fig. 4. Second antenna. Fig. 5. Furcal ramus. (Redrawn from Ferguson, Hutchinson and Goulden, 1964)

podomere and a backwardly directed endopodite of three or four podomeres; at the distal end of the endopodite is a strongly developed, curved claw.

The last pair of segmented appendages in ostracods are the third thoracic legs (Fig. 2), the "putzfuss" of German investigators. In the Cypridae the third thoracic appendage consists of a basal protopodite of two podomeres and an endopodite of three podomeres. The line of separation between the podomeres of the protopodite is frequently indistinct. When held in its normal position, the protopodite is directed slightly forward and downward, and the endopodite lies in a plane parallel with the long axis of the shell; thus, the third thoracic appendage is usually withdrawn into the shell, and serves to keep the body free of foreign bodies.

In the Cytheridae and the Cypridae the abdomen is represented by an unsegmented pair of appendages, the furcae (Fig. 5) which at rest are carried between the third thoracic legs. Each furca has a basal portion or ramus which ends in two claws, and generally bears two setae, a dorsal one and a terminal one. In some ostracods the furcal rami are greatly reduced and in others they are completely lacking.



FIGS. 6–10. Figs. 6, 7, 9 and 10. *Cypridopsis howei* Ferguson, 1964; male and female. Fig. 6. Lateral view of left valve of male. Fig. 7. Ejaculatory duct. Fig. 9. Penis. Fig. 10. Mandible and mandibular palp of female. Fig. 8. *Limnocythere verrucosa* Hoff, 1942; female. Lateral view of the left second antenna. (Redrawn from Hoff, 1942 *a*)

Reproductive System

The ostracods are dioecious. The reproductive organs follow the bilaterality common to the other organ systems. In many species of freshwater ostracods the reproductive glands may be seen through the transparent or semi-transparent valves.

The female organs of reproduction are: the ovaries (Fig. 1); the oviducts, thin-walled, elongate tubes that pass through the lamellae of the valves; the seminal receptacles, connected by a short tube to the oviducts; and the vaginae located at the posterior end of the body. Kesling (1951) points out that the left half of the female reproductive system in *Cypridopsis vidua* is a mirror image of the right half, but that the two halves are not connected in any portion. This is the basic pattern of the female reproductive organs in all species of freshwater ostracods.

The male organs of reproduction are the testes, which appear as parallel or circuitous bands extending from the postero-ventral region of the valve to the antero-ventral part of the valve cavity (Fig. 6); the vasa deferntia, coiled thread-like structures resembling a watch spring; the ductus ejaculatorius or Zenker's organ (Fig. 7); and the penis (Fig. 9). The male reproductive organs are paired, and are mirror images from side to side.

Digestive, Respiratory, Circulatory, Excretory, Nervous and Muscular Systems

The ostracod alimentary tract starts with the atrium, this is followed by the esophagus, the midgut, and the hindgut. The atrium or mouth lies between the mandibles and is bordered by an unpaired dorsal labium and a paired ventral labrum. The midgut is surrounded by a mesenchymatous layer of tissue. According to Bergold (1910) the secretory cells of the midgut are very large and very numerous. The hindgut opens through the anus. The largest digestive gland is the hepatopancreas or "liver", which discharges its secretions into the midgut.

Among the ostracods the typical respiratory appendages commonly found in most crustacea are absent. Gills have been found in only a few species of the subfamily Asteropinae. Bernecker (1909) found that the inner lamellae of the valves in *Cyprinotus incongruens* are composed of a respiratory epithelium. Kesling (1951) states, "The ostracod has no special structure for obtaining oxygen from the water. At the present time morphological studies have neither confirmed the respiratory role of the epithelium nor cast doubt upon it."

The respiratory process in ostracods is presently in a highly speculative state, and is a problem deserving careful and critical investigation.

There is no heart in freshwater Ostracoda. However, some marine species possess a sac-like pulsating structure. It is not known for certain whether there is an adaptation for circulating body fluids in forms lacking a heart.

Claus (1895) suggests that the shell glands are excretory organs in ostracods. Bergold (1910) gives the following as excretory organs of ostracods: glands of the first antennae, the shell glands, and the maxillary glands.

The central nervous system of cyprid ostracods is made up of a supraesophageal ganglion connected by a pair of circumesophageal commissures to an infraesophageal ganglion. The supraesophageal ganglion represents seven fused ganglia, and the infraesophageal ganglion is composed of three fused ganglia (Turner, 1896). From the supraesophageal ganglion two nerves pass to the antennules and the antennae, and an unpaired optic nerve enters the compound eye. The principal nerves of the Ostracoda are: optic, antennulary, antennary, labial, mandibular, labral, maxillary, thoracic (leg nerves), and the abdominal. The ventral nerve cord shows several variations of a general plan. The number of nerve cord ganglia reported by different investigators varies from three in *Cypris* (Turner) to five in *Cythere* (Lang).

The sense-organs include the eye (Fig. 1), the olfactory club (Fig. 4), tactile receptors, and chemoreceptors. Nowikoff (1908) presents detailed morphological descriptions of the eye. Klie (1926) is of the opinion that the eye is separated from the rest of the body by a partition of connective tissue. When the valves are open, permitting light to enter, the eye is almost transparent; when the shell is closed the dark pigment is visible.

The olfactory organ is located on the antepenultimate podomere of the second antenna in the Cypridae (Fig. 4). Turner (1896) found what he thought to be a positive correlation between the degree of development of the olfactory club and the extent to which the natatory setae of the second antennae had developed. He concluded that members of genera in which the swimming setae are well developed possess relatively larger olfactory organs than individuals belonging to genera with poorly developed natatory setae.

The adductor or closing muscles are attached to the inner surfaces of the valves (Fig. 1). The points of attachment of the adductors are marked by muscle scars (Fig. 6). Kesling (1951) gives a detailed description of the musculature of the appendages of *Cypridopsis vidua*. The appendage muscles are principally of two kinds: one group connects the basal podomere to the dorsal part of the shell and to the endoskeleton, and the other group is composed of two dorsal retractors or deductors and four large and three small muscles connecting the mandible to the endoskeleton. According to Kesling the muscles of the maxillae do not lend themselves to the terms flexor and extensor. The maxillary palp has one flexor and one extensor. The outer and middle masticatory processes are connected by muscles to the basal podomere; the inner process is without muscle attachments.

Reproduction, Development and Seasonal Life-History

Reproduction in freshwater ostracods is always sexual. Some species, *e.g.*, *C. vidua*, are always parthenogenetic. Other species, despite an obvious superiority in numbers of males in some cases and of females in others, always reproduce syngamically. There is no evidence that alternate cycles of syngamic and parthenogenetic reproduction occurs in ostracods. However, some species display a "local parthenogenesis" where males and females are found in some places, and only females in other localities. Klie (1926) reports that males of *Ilyocypris gibba* Ramdohr have not been found in Germany; however, males of this species are known from Algiers, Hungary, Spain, and Russia. Pennak (1953) states that Lowndes (1935) concludes from his investigations that reproduction in ostracods is always parthenogenetic, and "that copulation is merely an instinctive behaviour pattern, a relic of the time when the union of sperm and ovum was probably the sole means of reproduction". If copulation has no reproductive significance in the Ostracoda how do we account for both males and females being produced by impregnated females while virgin females produce only females? *Darwinula stevensoni* is viviparous, apparently other freshwater ostracods are oviparous.

The ostracod egg is capable of withstanding adverse conditions of an extreme kind and still remain viable. Sars found ostracod eggs which he hatched from dried mud to be viable after 24–30 years. There is a common pattern of ontogenetic development among freshwater ostracods. The egg develops into a bivalve nauplius possessing three pairs of cephalic appendages: first antennae, second antennae, and mandibles. Claus (1872) records the developmental stages of *Cypris ovum* = *Cyclocypris ovum* (Jurine, 1820) and *Cypris fasciata* = *Dolerocypris fasciata* (O. F. Müller, 1776). Kesling (1951) discusses at length the ontogeny of *C. vidua*. There are nine instars and eight molts in the developmental history of freshwater ostracods, the ninth instar is the adult.

Freshwater ostracods show seasonal cycles. Ferguson (1944) studied the seasonal life-history of *C. vidua*, *Potamocypris smaragdina* (Vávra, 1891), and of *Physocypria pustulosa* (Sharpe, 1897). *C. vidua* has a seasonal range at the latitude of Saint Louis, Missouri, U.S.A., from March

to December, with a peak of abundance in the July–October period. The range for *P. smaragdina* extends from late March until November, with a peak abundance occurring from late June–September. The peak abundance for *P. pustulosa* at Saint Louis occurs in April. Ferguson (1958 *a*) gives a summary of the life-history of two species that inhabit temporary bodies of water. *Cyprinotus carolinensis* Ferguson 1958 has two broods a year, one appearing during the January–February period, and the other during the March–May period. *Candona orangeburgensis* Ferguson 1958 has a single brood a year; adults live about one hundred days, from early January until late April. Kesling (1951) collected *C. vidua* during every month of the year except January and February from a small pond at Urbana, Illinois. He concludes, that since both young instars and adults occur in all samples collected, reproduction takes place all the year round, but that the survival rate is greater during the spring and summer than during the winter.

Geographical Distribution

Lack of extensive collections of freshwater Ostracoda has resulted in many species being known only from one locality. Some species are cosmopolitan, some have been found only in the Nearctic while others are restricted to the Palearctic, and still others have been recorded only from the Paleotropical.

Active migration of ostracods through a single drainage system accounts for the dispersal of some species. Overland transportation has no doubt been accomplished passively by resistant eggs being carried by wind and on the bodies of birds and insects. Doctor Vernon W. Proctor, of the Texas Technological College, and his students are presently engaged in a series of experiments to determine the extent to which small aquatic organisms are dispersed passively by way of the intestinal tract of birds. They have found that adults of several species of freshwater ostracods are distributed by passage through the alimentary canal of certain species of birds.

Collection and Preservation

"Perhaps the chief reason for the general neglect of American Ostracoda lies in the fact that they are nearly always necessarily collected in debris from which they must be laboriously separated" (Pennak, 1953). This situation is not peculiar to the American ostracod fauna. There are wide areas of the world for which there are no records of collection of freshwater ostracods.

Freshwater ostracods are seldom found in plankton samples because most of them live at or near the bottom. Collections are made with a Birge cone net, a small net to one end of which is attached a heavy wire screen, and to the smaller end is tied a homeopathic vial. The apparatus is dragged through vegetation and over the bottom of a body of water; the small organisms will be concentrated in the homeopathic vial.

The specimens are poured into a Syracuse watch glass. The sample should be examined under a binocular, wide field microscope, and the ostracods removed with a small pipette and placed in a solution of equal parts of water and 95% ethyl alcohol. After the animals are dead, the supernatant fluid should be removed with a pipette. Specimens are preserved in 85% ethyl alcohol. A simple staining procedure is simply to transfer specimens from 85% ethyl alcohol into a 1% alcoholic solution of eosin Y. Overstaining of ostracods is almost impossible, however, if such should occur the excess stain may be removed by several passages through absolute alcohol. Ferguson (1958 *b*) describes the procedure for preparing microscopic mounts using Canada balsam. Specimens stained in lignin pink and dissected and mounted in lactophenol make excellent mounts for microscopic examination.

TAXONOMY

The subclass Ostracoda may be divided into four orders: Podocopa, Myodocopa, Cladocopa and Platycopa. All freshwater ostracods belong to the order Podocopa. The Podocopa also includes marine species. The order Podocopa has the following characteristics: geniculate second antenna with a well-developed endopodite, and an exopodite, when present, in the form of a rudimentary scale, or as a single long seta.

Furtos (1933: 421) states, "G. O. Sars divided the Podocopa into two families, the Cypridae and the Cytheridae, with the division based upon the character of the second antenna and the thoracic legs." Brady and Norman (1889) placed the Bairdiidae and the Darwinulidae in the order Podocopa. The Bairdiidae are exclusively marine, the Cytheridae have a small number of freshwater genera but are otherwise marine, and the Cypridae include both marine and freshwater genera.

Hoff (1942 *b*) established the cytherid subfamily Entocytherinae to receive the genus *Entocythere* Marshall, 1903 and the genus *Sphaeromicola* Paris, 1916. Howe (1961) raised the subfamily Entocytherinae to family rant. Hark (1962) assigned the subfamilies Entocytherinae Hoff, 1942 and Sphaeromicolinae Hart, 1962 to the family Entocytheridae Hoff, 1942. The Entocytherinae include genera that live as commensals on freshwater crayfish, and the Sphaeromicolinae live as commensals on freshwater isopods and marine amphipods.

Howe (1961) elevated the subfamily Limnocytherinae Klie 1938 (= Limnicytherinae Sars, 1925) to family status. The family Limnicytheridae Klie, 1938 includes the following freshwater and brackish-water genera: *Afrocythere* Klie, 1935, *Cytheridella* Daday, 1905, *Elpidium* Müller, 1881, *Gomphocythere* Sars, 1924, *Leucocythere* Kaufmann, 1892, *Metacypris* Brady and Robertson, 1870, *Neolimnocythere* Delachaux, 1928, *Paracythereis* Delachaux, 1928, *Pseudolimnocythere* Klie, 1938, and *Limnocythere* Brady, 1868.

The Cypridae are those ostracods with the hinge line of the valves without teeth; eye simple; second antenna four- or five-segmented, geniculate antepenultimate podomere with a club-like sensory seta; third thoracic appendage modified as a scratch foot. Furcal ramus well developed, sometimes reduced; testes lying partly in the anterior valve chamber; ejaculatory duct cylindrical and possessing a regular pattern of circles of chitinous spines, penis complex; many species without males.

Kaufmann (1900) divided the Cypridae into seven subfamilies: Candoninae, Notodromadinae, Cypridinae, Herpetocypridinae, Cypridopsinae, Cyclocypridinae, and Ilyocypridinae. Müller (1912) recognized five subfamilies of Cypridae: Pontocyprinae and Macrocyprinae both marine and three freshwater subfamilies, *viz.*, Candoninae, Ilyocyprinae, and Cyprinae. Hoff (1942 *a*) with some changes made use of Kaufmann's system and suggested the following cyprid subfamilies: Candoninae, Cyclocyprinae, Ilyocyprinae, Cypridopsinae, Cyprinae, and Notodrominae. Ferguson (1964) proposed the subfamily Stenocyprinae to receive the genus *Stenocypris* Sars, 1889. Pokorny (1958) lists the following families of podocopid ostracods: Macrocyprididae Müller, 1912, Bairdiidae Sars, 1888, Cyprididae Baird, 1845, Cytheridae Baird, 1850, and Darwinulidae Brady and Norman, 1889.

The Darwinulidae have a first antenna of six podomeres that is provided with short clawlike setae. The second antenna has an endopodite of three podomeres and an exopodite of two or three setae, the first podomere bears a sensory seta. First thoracic appendage has a well-developed masticatory process. The second and third thoracic appendages pediform, similar in structure and direction. Furcal ramus absent. Viviparous. Males unknown. The family has a single genus. The genus *Darwinula* includes only freshwater individuals.

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STRUCTURE AND FUNCTION OF THE REPRODUCTIVE SYSTEM OF THE CRAB *PORTUNUS SANGUINOLENTUS* (HERBST) (BRACHYURA: PORTUNIDAE)[1]

I. The Male System

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ABSTRACT

The gross and histological anatomy of the reproductive system of male *Portunus sanguinolentus* (Herbst) were investigated during the molt cycle in pre-adult and the three adult instars. Function of each of the parts of the system was ascertained during the reproductive period and during the process of copulation. The system was studied by vital staining techniques, by the usual histological sectioning techniques and by experimental methods during copulation.

Immotile sperms of the usual brachyuran type were formed in the lobules of the testis without any seasonal cycle. There was also no correlation of sperm formation with the molt cycle of the three mature instars. The vas deferens was divided into six regions of distinctly different structure and function; two of which were associated with formation of spermatophores, three with storage of spermatophores and formation and storage of seminal fluid, and the last region was a muscular ejaculatory duct. Sequential evacuation of the contents of the region of the vas deferens was determined by interruption of copulation at selected intervals during the four hours of the process with the intact spermatophores evacuated last. Several days were required before the system was ready for copulation again.

INTRODUCTION

ALTHOUGH the anatomy and histology of the reproductive systems are described for many brachyurans, there is lack of knowledge concerning the function of the parts of the system, particularly during copulation and ovulation. In order to contribute to the knowledge on these subjects, a study was made on *Portunus sanguinolentus* (Herbst) an important edible crab of the Indo-West Pacific. This research is reported in two parts; the present of which is concerned with the male system and the second with the female system (Ryan, 1967 *b*).

Relatively little is known of the life-history of *P. sanguinolentus*. Its range extends from Hawaii to Japan, India, East Africa and the Eastern Mediterranean (Stephenson and Campbell, 1959). Throughout its range, it is of greater or lesser economic importance, perhaps ranking under two other portunid species, *Portunus pelagicus* and *Scylla serrata*, in the value of its fishery.

Menon (1952) contributed notes on the fishery of *P. sanguinolentus* along the Malabar Coast of India. Breeding and the first larval stage of this species were described by Chhapgar (1956) and Naidu (1955). The present overall study of the reproductive biology included a report of the morphometry, morphology and number of sexually mature instars (Ryan, 1967 *a*). In 1959, Nishioka made a comparative histological study of spermatophore elaboration in three Hawaiian portunid crabs, one of which was *P. sanguinolentus*. His research was initiated at the same time as the present study and they were intended to complement each other.

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Many early papers describe the anatomy of the male reproductive system of crabs but their histological approach was directed toward a specific study such as spermatogenesis. In this manner Fasten (1915, 1917, 1918, 1926) contributed a number of papers on the male reproductive system and on spermatogenesis in several species of crabs. Binford (1913) also studied spermatogenesis and observed fertilization in histological sections of the xanthid species, *Menippe mercenaria*. Formation of the constituents of the sperm plug was the object of a study by Spalding (1942) on *Carcinus maenas*. The first detailed anatomical and histological study of the male reproductive system of a crab was the work of Cronin (1947) on *Callinectes sapidus*, a species of sufficient resemblance to *P. sanguinolentus* to lead Stephenson and Campbell (1959) to question the species being placed in separate genera. In his paper, Cronin reviewed most of the research which appeared in the literature up to 1947. A study of the function of the parts of the male system remained to be done.

Methods of Research

Crabs used in the study were collected from Kaneohe Bay, Island of Oahu, Hawaii, during the period from January, 1962 to June, 1964. Observations were made of the reproductive system during molt and intermolt stages; during all months of the year and, with some experimental methods, during and after copulation.

The reproductive system was studied by the usual histological sectioning techniques and by vital staining. Tissues for sectioning were fixed in Bouin's or Gilson's fixatives, cleared in xylene or toluene and sectioned in paraffin at 8 μ. Harris' hematoxylin counterstained with eosin proved to be satisfactory for general tissue differentiation and was used throughout. Tissues examined *in vivo* were stained with 10% methylene blue in sea water. The testis and most of the vas deferens were examined by lifting the carapace of a live crab, to which these portions would remain attached. The carapace was then immediately inverted and activity of the system observed under a dissecting microscope. The system was separated from surrounding structures and perfused with a fluid suggested by Sawaya (*cf.* Pyle and Cronin, 1950). The remainder of the system was similarly observed by rapid dissection of live crabs.

Parts of the system were measured with an ocular micrometer in a dissecting microscope. Sizes of parts were reported as means of measurements in five males whose carapace lengths were 60–65 mm.

The role of the parts of the system was observed by excision of parts of the copulatory apparatus (first pleopods, second pleopods, penis) on one side of the male prior to copulation and comparison with the intact side of the system at various time intervals after initiation of the process or its completion.

Gross and Histological Anatomy

(Plates I–III)

Testis

As in the gonads of most decapod Crustacea, the paired testes in *P. sanguinolentus* are medially interconnected by a commissure so that they approximate the shape of a letter "H". The testes are a pair of convoluted tubular organs with many lobes about a seminiferous duct as a central axis. Their position is just dorsal to the digestive gland and under the hypodermis of the carapace (Fig. 1). Extending from the middle of the postero-lateral border of the carapace, the testis follows the curve of the antero-lateral border of the carapace and passes lateral to the stomach and ends medial to the tightly coiled anterior vas deferens. The commissure arises on

the medial border of the testis and runs along the testis for several millimeters before passing posterior to the stomach and ventral to the posterior gastric muscles. The portion of the testis posterior to the commissure is tightly bound to the commissure by a connective tissue envelope which also binds all of the loops of the testis together and to surrounding structures. Black chromatophores are seen in this connective tissue and that of the anterior and median vas deferens in freshly dissected material. The vas deferens arises from the posterior end of the testis. Its lumen is confluent with that of the seminiferous duct of the testis.

There is some variation in the dimensions of the testis. Throughout its anterior portion, the testis is 0·4–0·6 mm. wide. However, the tight convolutions (Fig. 2) are about 1·5 mm. wide and this becomes its apparent width. The anterior portion of the testis is 50–70 mm. long but the length of the portion posterior to the commissure is only 4–5 mm.

Lobes of the testis vary in size and degree of subdivision. Many are partially subdivided into two or more lobules for the distal half or so of their length. Lobes measured from 0·2 to 0·4 mm. long and 0·1 to 0·3 mm. wide. Those which show lobulation are as wide, and often wider, than long. As it courses through the loops of the testis, the seminiferous duct may be filled with sperm and visible in freshly dissected material. As its union with the vas deferens, the width of the duct is 0·15 mm. and is progressively narrower in the anterior reaches of the testis.

The wall of the testicular lobes is two-layered (Fig. 3). The outer layer is a connective tissue of a single cell layer with spindle-shaped nuclei, $2 \times 4\,\mu$. The inner wall is slightly stained and without visible cell membranes. Scattered nuclei are present which vary in size from 4 to $7\,\mu$ and are round to oval in shape.

Cells in spermatogenesis completely fill a lobe or lobule from wall to wall. Spermatogonia cells are usually located at the sides or distal borders of the lobes. Occasional lobes seem to be filled with spermatogonia but these apparently are cross-sections through the distal regions of the lobes. Spermatogonia display no cell membranes and have ellipsoidal nuclei, 7 to $10\,\mu$ long, which have a slight chromatin network and often peripheral chromatin granules. These spermatogonia resemble very much the oogonia that are seen in ovary sections.

Primary and secondary spermatocytes have distinct cell membranes. With exceptions of the spermatogonia which line the wall, all of the cells within a lobe in spermatogenesis are usually in the same stage of development. They display meiotic figures. Mature sperm in sections of a testis present a different appearance from living sperm taken from the testis or vas deferens. Sperm in fixed material are truncated cones (Fig. 4). Their basal diameters and heights are 2 to $3\,\mu$. A basophilic layer extends across the base of the cone and another across the top to form a dome-shaped cap. The remainder of the sperm is eosinophilic.

Living sperm taken from either the testis or anterior vas deferens are alike in appearance (Fig. 5). The cells are dome-shaped with a height of $2{\cdot}5\,\mu$ and a basal diameter of $3{\cdot}5$ to $4{\cdot}0\,\mu$. In top or basal view, the sperm appear circular with 7 or 8 immotile rays. In the center of the base, a dark circular area is seen bordered by a clear margin, $0{\cdot}5\,\mu$ wide, which is continuous with the rays. The rays have the same proximal width, $0{\cdot}5\,\mu$, and taper to a fine point. The rays may extend separately or be affixed together in which case it is difficult to distinguish between them. A vesicle is seen in the center of the dark area which, when viewed from the side, is seen to extend from the apex almost to the base. The sperm did not take any of the vital stains used: methylene blue, toluidine blue or neutral red.

More than one cross-section of the seminiferous duct may be observed in histological preparations which are cut through the loops of the testis. Examination of serial sections reveals that these cross-sections do not represent separate branches of the duct but the different portions of the single duct which travels a tortuous route. In preparations which are not cut through loops of the testis, only single sections of the seminiferous duct are observed. The duct at this level does not exhibit branching into lobes or lobules.

The duct in the mid-lateral and distal regions of the testis is a closed "U" or "V" shape in cross-section (Fig. 4). The top of the "U" or "V" is either open into a lobe or closed with a thin tissue of a single-cell layer which resembles the outer wall of the lobes. The "U" or "V" itself is made of thick epithelium with the cuboidal cells resting on a basement membrane. These cells may have protoplasmic projections into the lumen of the duct. Occasional circular and longitudinal striated muscle cells adjoin the basement membrane externally. The thin layer of cells at the "top" is continuous with that covering the outside of the basement membrane and muscular elements. Only mature sperm occupy the lumen of the duct.

Near the posterior end of the testis, the seminiferous duct emerges and runs along the dorsal side of the testis for the last 0·3 to 0·5 mm. Near its juncture with the vas deferens, the epithelial and muscular elements of the duct are continuous around its circumference.

Vas Deferens

The vas deferens extends from the posterior end of the testis through the thoracic cavity and the pereiopodal musculature of the 8th thoracic segment where it ends in the penile papilla on the coxa of the 5th pereiopod (Fig. 1). The vas deferens is divisible into three major portions which differ in form and function. These are termed here anterior, median and posterior vas deferens to conform to the nomenclature of Cronin (1947) and abbreviated AVD, MVD and PVD. Each of these is further subdivided anatomically and/or physiologically into two portions. The major portions are discussed separately below.

Anterior Vas Deferens

Arising from the posterior end of the testis, the AVD is subdivided into a short, more muscular portion (vas efferens in Cronin, 1947) and a tightly coiled, much longer portion which is bound together as one mass. The first part constitutes the efferent duct by which the sperm are evacuated from the testis. It is difficult to locate it in the usual dorsal dissection but when the carapace of a live crab is torn off and inverted under the dissecting microscope, the duct is seen to have an "S" shape. As it leaves the seminiferous duct of the testis, it curves posteriorly and ventrally on the medial surface of the tightly coiled mass of the remainder of the AVD. It then turns laterally and continues as the more extensive second portion of the AVD. When dissected away, the first portion of the AVD tends to curl and is difficult to measure. When straightened, it measures 3 to 7 mm. long and its diameter increases from 0·15 mm. to 0·38 mm. in its mid-region.

As a continuation of the seminiferous duct, this portion of the AVD maintains some of the same characteristics for a distance. More distally, it has a most distinctive structure (Fig. 6). Extending into the lumen are longitudinal typhlosole-like folds which in whole mounts of fresh tissue can be seen to extend most of the length and end at the union with the second portion of the AVD. There appears to be a constriction of the lumen in fresh tissue at the union with the second portion but this is not seen in fixed tissue. Cuboidal epithelial cells, 7 to 9 μ, line the lumen and lie on a basement membrane. The folds may be divided into 2–5 branches. Epithelial cells covering the folds become high columnar, the highest becoming $3 \times 10\mu$. Prominent circular striated muscular fibres completely surround the epithelium. Scattered longitudinal fibers are also present. The duct is covered on the outside by a thick, 10 to 15 μ, connective tissue sheath. In the lumen of some examined, dense masses of sperm were seen but in most sections few sperm were found.

The second portion of the AVD is longer, nearly 80 mm. Its many coils are bound by connective tissue into a compact mass. The AVD is located median to the much larger MVD and antero-ventral to the pericardium. Separation of the coils is most difficult. Almost always the tube ruptures and its contents of sperm and developing spermatophores spill out. At its

beginning, the diameter of the second portion of the AVD is 0·3 mm. This increases to 0·6 mm. in the mid-region and then decreases to 0·45 mm. where the tube changes to the MVD. Although it is a translucent tube, the AVD appears white because it is filled with masses of sperm which are being formed into spermatophores. Separation of spermatozoa into masses destined to become spermatophores is already evident at the beginning of the second portion of the AVD (Fig. 6). In the mid-region, the spermatophores are more discrete and in the form of pointed ovals, 435 × 240 μ. They may be covered with a thick coating which is continuous over many spermatophores. At the end of the AVD, the spermatophores are shorter, more rounded, and have the final dimensions of 275 × 225 μ. Many completed spermatophores fill the end of the AVD.

The first few millimeters of the second portion of the AVD are characterized by having a lining of low columnar cells. These cells are 30 to 40 μ in size with single spindle-shaped nuclei. Along the borders of these cells, a basophilic layer appears to have been secreted into the lumen. A tight aggregate of sperm occupies the center of the lumen. The epithelial lining is surrounded by a circular muscular layer which is, in turn, covered by a thin envelopment of connective tissue. The tube is bound in loops by a thin connective tissue covering. Interstices between the loops are occupied by blood vessels, sinuses, varying amounts of connective tissue and numerous large eosinophilic cells, 20 to 30 μ in diameter. These are probably blood cells. They are so numerous about the testis and first portion of the AVD that they impair visibility in microdissections of fresh material.

In the mid-region of the second portion of the AVD, the increased diameter is associated with an even greater increase in the thickness of the epithelial lining to about 150 μ. The cells become multinucleate with spherical clusters of nuclei that are centrally located. The amount of basophilic material which is secreted into the lumen is trebled and completely surrounds the sperm masses. The external covering and muscle layer remain consistently similar. Near its union with the MVD, the AVD decreases in diameter and the thickness of the columnar epithelium also decreases to 30–50 μ. Two different substances surround the separate sperm masses. Immediately surrounding the sperm masses is a homogeneous lightly basophilic layer, 3–4 μ thick, which is destined to become the capsular wall of the completed spermatophore. Between the capsular layer and the epithelial lining of the duct, there is a strongly basophilic and highly vacuolar layer of secreted material similar to that secreted proximally.

Median Vas Deferens

The MVD, the most massive part of the reproductive system, is a loosely coiled, opaque white tube which consists of major coils in which the tube has a large diameter and minor coils with a lesser diameter. The more prominent major coils are located anterior to the pericardium. The proximal end of the MVD passes posterior to the adductor muscle of the mandible, loops under itself several times, and then passes ventral to the pericardium. The posterior two-thirds of the MVD, the minor coils, lie ventral to the pericardium. Throughout its length, the MVD has a pebbled white appearance because of the spermatophores and sticky white material which fill it. In the minor coils, the white content of the lumen contrasts with the translucent wall.

There is no precise demarcation of the AVD and MVD. However, the former does not have white viscid and granular contents surrounding its spermatophores. As its origin, the diameter of the MVD is about 0·5 mm., after which it increases to 2·5–3·5 mm. The minor coils have a fairly consistent width, number and tubular diameter. There are about 16 loops which are 6·5–7·5 mm. across. The tubular diameter is a consistent 1·2–1·3 mm. Spermatophores are found in the major coils and the most anterior of the minor coils.

The MVD defies either dissection or microtome sectioning with the fixatives used. The constituents of the seminal fluid become hard and brittle and serial sectioning is impossible. The same is also true of the filled seminal receptacle of the female after copulation.

Although macroscopically divisible into two regions according to its tubular diameter and physiologically as evidenced by examination following copulation, there is little difference in the histology of the two regions of the MVD. The epithelial lining of the MVD is composed of columnar cells, 25–35 μ high. These cells are multinucleate with basally arranged spherical clusters of nuclei. Their boundaries may bulge into the lumen. These bulges may accommodate large vacuoles or be filled with a dense eosinophilic granular cytoplasm similar to that which also fills the rest of the cells. Many have vacuoles which appear to have burst into the lumen and to have released eosinophilic material. Whether this is the secretory mechanism or an artifact due to the method of preparation is not clear. Quite prominent circular muscle fibres underlie the epithelial cells. The whole tube is covered by a connective tissue sheath as in the remainder of the male system.

Contents of the lumen include completed spermatophores and an abundance of eosinophilic granules which vary widely in size from 2 to 50 μ. Most are nearly 10 μ, however. The granular material appears white in living material and imparts its color to the whole MVD.

The MVD, throughout its length, is characterized by having a wall that is folded into lateral pouches (Fig. 7). Epithelial cells which line the pouches have larger vacuoles. The pouches are more numerous in the minor coils. Another difference in the minor coils is the increased prominence of the musculature.

Posterior Vas Deferens

Of approximately the same width and diameter as the minor coils of the MVD, the loops of the PVD are easily distinguished by their colorless translucency. They are bound by connective tissue to the ventral surface of the pericardium from which they are distinguished with difficulty. The PVD winds posteriorad, over the posterior part of the digestive gland lateral to the intestine. At the sella turcica, the PVD changes direction passing anteriorly and under a portion of the digestive gland which extends for a short way between the musculature of the 8th thoracic segment. The duct passes up to the bar which joins the sella turcica with the apodeme between the 7th and 8th thoracic segments, passes under the bar, makes a ventrally directed turn, extends ventrally for about 2 mm. and then makes another turn as it passes laterally through the appendicular musculature of the 8th thoracic segment. The duct emerges as the penile papilla on the medial surface of the coxa of the last pereiopod.

There are two distinct portions of the PVD. The first extends from the MVD to the passage under the bar. Posterior to the bar, the duct is no longer looped and secretory, but serves as a muscular ejaculatory duct.

As already noted, the PVD is distinctly different from the MVD in color. Instead of a white granular material, the PVD is filled with a colorless, translucent, viscid fluid. The ejaculatory portion is almost empty in non-copulating crabs. Under the dissecting microscope, the fluid in the live PVD may be seen to be filling pockets, 30–55 μ in diameter, which extend laterally about the duct. The diameter of the PVD is quite consistent being 1·4 mm. up to the bar where the diameter decreases to 0·8–1·0 mm. The PVD is the longest portion of the vas deferens. Its length, including the ejaculatory portion of 30–40 mm., is approximately 90–100 mm.

As its origin, the PVD maintains some of the histological features of the MVD. The lateral outpockets, at first like those of the MVD, become very extensive posteriorly (Fig. 8). Epithelial cells lining the lumen are smaller at the start of the PVD and not as cavernous as those of the MVD, except within the lateral outpockets. The lumen of the duct in sectioned tissue is filled with a light eosinophilic homogeneous mass.

After the first few millimeters, the duct becomes so different from the MVD that sections of it can be instantly recognized at low powers of magnification. A wide border, 10–25 μ, of

connective tissue forms the outer wall of the duct and into this extend the alveoli-like pockets. These are constricted as they open into the lumen of the duct. Between the openings there are typhlosole-like projections which are reminiscent of similar projections in the lumen of the first portion of the AVD. In the PVD, however, they are not bifurcated. A layer of striated circular muscle fibers subtends the typhlosolar projections, interrupted only by the openings of the outpockets. The outpockets measure 65–80 μ in width and are lined by very high narrow columnar cells, 3 × 30–40 μ, which have two or more basal globular nuclei. The distal two-thirds of these cells may be empty vacuoles or their cytoplasm may be moderately eosinophilic.

The epithelial cells which cover the typhlosole projections are even longer, 70–80 μ, than those which line the lumen. They have basal nuclei which may be globular or spindle-shaped. A shaft of connective tissue forms the core of each projection. From one to three longitudinal muscle fibres may be seen in the base of each projection. The epithelial cells of the lumen are not as vacuolar as those of the outpockets but are filled with a dense basophilic cytoplasm. At the distal borders of these cells, spherical structures are seen in the process of being pinched off from the cells (Fig. 9). Some are found separated from the cells. These spherical structures measure 3–5 μ and contain scattered basophilic granules. Beside the spherical structures the lumen contains a homogeneous eosinophilic material, mentioned above, which was secreted by the outpockets.

The ejaculatory portion of the PVD has a more simple circular outline in transverse section (Fig. 10). As the duct passes through the musculature of the 8th thoracic segment, it is adjoined, for 10–20 mm., by large nerves and blood vessels which supply the appendage of this segment, all of which are bound by a common connective tissue covering for this distance. The epithelial lining is made of low columnar cells, 20–25 μ thick, which have centrally-placed spherical nuclei. On the border of the cells lining the lumen, there is a "brush" border, 2–4 μ thick, which may be closely packed cilia or a layer of secreted material. The latter alternative is suggested from the presence of vacuolar epithelial cells in the adjacent portions. The lumen of the duct contains a small amount of eosinophilic substance.

Penis

The penis is a flaccid white tube which arises from the ventro-medial border of the coxopodite of the 5th pereiopod. In adult males, the penis is always found inserted in the proximal foramen of the first pleopod, although it is not fastened there. When the abdomen is flexed, the penis is covered by the terga of the first few abdominal segments. The structure serves mainly as a cover for the gonoduct which passes through it. The penis is 7–9 mm. long and has a diameter of 1–1·5 mm. Its cuticular covering is shed and remains inserted at ecdysis.

The dominant structure in the histological sections of the penis is the prominent muscular ejaculatory duct which passes through it (Fig. 11). Although nearly circular in life, the process of fixing and sectioning cause sections of the penis to appear ellipsoidal or oval. The cuticular covering of the penis is 15–20 μ thick in the proximal region and distally reduced to 9–12 μ. The distal 1·5 mm. of the gonoduct is lined with invaginated cuticle. A hypodermis of one or two cells and 15 μ in thickness underlies the cuticular covering. The space between the gonoduct and the hypodermis is filled with a loose reticulum of connective tissue which contains blood vessels and sinuses.

The diameter of the gonoduct varies from 0·35 mm. in the proximal region to 0·25 mm. in mid-region. Thickness of the prominently striated muscularis varies from 45 to 50 μ. A layer of longitudinal muscle fibres underlies the epithelial lining but these are obscured by the much thicker circular muscle fibers.

Two prominent typhlosolar folds project into the lumen of the duct which is lined by secretory epithelium. Low columnar cells, 10–12 μ high, line the lumen except for the folds which have

narrower columnar cells, that are 25 μ high. A basement membrane underlies the epithelium. The columnar epithelial cells have a "brush" border, about 10 μ thick, which may be empty vacuoles or cilia. A few granules of chromophilic substance are found in the lumen.

The distal 1·5 mm. of the lumen is crescent-shaped and lined with an infolded hypodermis and cuticle. At ecdysis the cuticle of the distal 1·5 mm. of the lumen is shed along with the cuticular coverings of the penis.

Accessory Structures

The paired appendages or pleopods of the first and second abdominal segments are modified for a copulatory function. The first pleopods are curved wand-like structures which, in their normal position, are held in the sternal depression under the flexed abdomen. Their length is 30–35 mm. The first pleopods, or gonopods, are deeply grooved structures in which the edges of the groove are fused to form a tube. In the proximal end of the endopodite, there are two foramina which open into its lumen. The penis is inserted into the proximal foramen and the second pleopod into the distal one. The shaft of the first pleopod is armed with backwardly directed spines near its tip.

The second pleopod is composed of a basi-ischiopodite and an endopodite portion which acts as a plunger in the tube of the first pleopod. Like the first pleopod, there are setae on the basal portion.

Functions of the Reproductive System

Functions of the male reproductive system in the non-copulating crab include formation, transport and storage of spermatozoa, spermatophores and the constituents of the seminal fluid. During copulation, these products are evacuated from the MVD and PVD and introduced by aid of the pleopods into the seminal receptacles of the soft female immediately following her molt. The role of each part of the male reproductive system is discussed in the non-copulatory state and during copulation herewith.

Non-Copulatory Function

Testis

Functional relationships of parts of the testis are difficult to ascertain from histological sections and from micro-dissection of living material. Spermatozoa are produced in testicular lobes and have their origin in the spermatogonia which line the wall in the distal region of each lobe. The presence of spermatogonia in company with completed sperm in the same lobes indicates that more than one mass of sperm is produced in each lobe. However, since almost all of the spermatogenic cells in a testicular lobe are in a similar stage, there is probably some periodicity in the formation of primary spermatocytes by the spermatogonia.

The means by which completed sperm are evacuated from each lobe is not clear. Only those lobes containing completed sperm appear to be open into the seminiferous duct and only completed sperm are found in the duct. No contractile action was observed in any testicular lobes whereas slow periodic contractions were observed in the seminiferous ducts of testes immediately after dissection from a live crab. In the seminiferous ducts of live testes, sperm may be seen to fill the ducts at various locations along their lengths but are collected in the distal region of the duct adjacent to its union with the AVD.

Anterior Vas Deferens

Elaboration of spermatophores is accomplished in the anterior vas deferens. Sperm masses which enter the AVD exit as completed spermatophores. The two portions of the AVD have separate functions in production of spermatophores. The first portion (vas efferens, Cronin, 1947) is more highly muscular than the second and its contractile activity in live material also differs. Activity in the first part was observed in seven males. In these, single peristaltic contractions, several minutes apart, began at the level of the seminiferous duct and continued to the beginning of the second portion of the AVD. In this process, almost all of the sperm were pushed ahead into the second portion of the AVD. The mass of sperm that was pushed ahead appeared to be of the same size as the sperm masses in the beginning of the second portion of the AVD. The single peristaltic wave never continued beyond the first portion, into the second, in the seven observations. Thus, the contraction of the first portion of the AVD appears to determine the size of the sperm mass which will be enclosed in the capsule of the spermatophore.

Weak repetitive contractions are characteristic of the second portion of the AVD. These slowly push the sperm masses ahead through the tube. The amount of secretion in the lumen which surrounds the sperm masses progressively increases distally. In the mid-region, the secreted material surrounds each sperm mass. Thousands of sperm are included in each sperm mass. More posteriorly, each sperm mass is surrounded by two different substances. That immediately surrounding the sperm mass is a compact homogeneous layer which is the capsular covering of the spermatophore. Its thickness is 3–4 μ. The capsular covering is surrounded by granular material like that secreted in more proximal regions of the AVD and which generally fills the lumen. When the vessel in this region is ruptured in live material, the contents flow out in one continuous cylindrical mass with the spermatophores bound together by the granular material. At this location, the spermatophores are sharply pointed ovoids about 425 μ long but at the end of the AVD, they are shortened to 275 μ and are completely separated from each other.

Median Vas Deferens

Like the AVD, the MVD is functionally divisible into two regions: the anterior region of major coils, and the posterior minor coils. The posterior region is completely evacuated at copulation while the anterior region is not.

In addition to storage of spermatophores, the MVD functions in secretion of a white granular material in which the spermatophores are suspended. Rupture of the MVD releases a large amount of this material *plus* many spermatophores. Since after copulation most of the contents of the major coils of the MVD move into the minor coils, the major coils may be the principal source of the white granular material that fills both the major and minor coils. While spermatophores fill the major coils, they are restricted to only the most anterior of the minor coils.

Posterior Vas Deferens

Functions of the two portions of the PVD differ very greatly. The anterior part secretes a viscid gelatinous material which, in addition to the granular material from the MVD, forms a layer of the sperm plug in the seminal receptacle of the female. No muscular activity was observed in the first part of the PVD in a non-copulating crab. In contrast, the second portion or ejaculatory duct is so actively peristaltic that photography of it is only possible an hour or more after its excision. Rupture of the first part of the PVD released much viscid gelatinous material, but rupture of the ejaculatory portion released very little. All efforts to observe ciliary activity in the epithelial lining of freshly dissected material of ejaculatory ducts were unsuccessful.

Penis

The penile papilla was always found inserted into the first pleopod. Despite many efforts to observe reinsertion after it was pulled from the pleopod, no activity in the structure was observed,

In many instances, examination of males 24 hours later showed that the penile papillae were reinserted.

Copulatory Function

General Remarks

In preliminary experiments, it was learned that when the first or second pleopods were excised from one side of a male prior to copulation, only the contents of the vas deferens on the intact side were evacuated. It was further noted that the male always impregnated the female's seminal receptacle on the side facing the intact side *in coitu* and never the other side. For consistency, the parts of the apparatus on the left side of the male were always excised, in which case the right receptacle of the female was always empty, the left inseminated. This not only permitted assessment of the roles of the parts of the copulatory apparatus—first pleopods, second pleopods, penis—but also of the internal parts of the male reproductive system, MVD and PVD, by comparison of the two sides and of the contents of the receptacles of the female partner. When copulation was interrupted at desired time intervals, dissection of the reproductive systems of the male and female permitted observation of the function of the system. There was no evidence that the operation affected the time required for copulation in operated males.

Copulation in *P. sanguinolentus* occurs a few minutes after molt of the female. Prior to ecdysis, the male carries the pre-molt female—with her dorsal side uppermost—for several days. In 143 females that underwent a molt at which copulation would occur, the maximum length of time that a male held a female before molt was eight days. Although copulation of crabs was never observed under natural conditions, the act was observed in laboratory cages in 28 pairs with little variation.

When the actual shedding process of the female began, as evidenced by lifting of the carapace, the male always moved to the bottom of the laboratory cage, released his hold somewhat and backed slightly away so that the female was in front of, instead of under, him. All the while, the second pereiopods of the male were held around the female. In those instances in which the duration of the molting process was observed, the elapsed time from the first lifting of the carapace to completed ecadysis of the female was 74–106 minutes.

After molt, the soft females remained quiet for 2–5 minutes and, in each case, turned themselves over and received the male. As soon as the female turned over, she extended her abdomen. The male straddled the female and inserted the first pleopods into the vulvae. During copulation, there was no body movement by the male. The female, on the other hand, exhibited a slight up and down rocking motion. Copulation lasted from 3·5–4·5 hours, after which the male continued to hold the female for several days in the same manner as before ecdysis.

Physiology of the Male System in Copulation

Examination of the vas deferens when copulation is interrupted at various time intervals reveals that the contents of its regions are evacuated in sequence. Since an insufficient number of males were available for study at these time intervals, no effort is made here to correlate sizes of males with times of the sequence of evacuation of sexual products. Smaller crabs probably evacuate their vasa deferentia in less time than larger ones. The observations recorded here are those of 12 males, carapace lengths 48·5–63·0 mm., whose MVD and PVD were examined after initiation of copulation at: one, two and three hours; completion, and two, seven and 21 days afterwards.

At the end of 1 hour of copulation, only gelatinous material from the distal coils of the first part of the PVD has been evacuated. This material now fills the ejaculatory duct and is in the process of being evacuated through it. The anterior coils of the PVD are still distended to their

original size. In the more posterior coils from which the gelatinous material has been evacuated, many large vacuole-like structures are observed in the lumen of the duct. These apparently are the spherical structures seen in histological sections of the region.

Material was not evacuated from the MVD until examination at two hours after start of copulation. By this time, the PVD has been evacuated of its gelatinous contents and much of the white granular material has been eliminated from the minor coils of the MVD. Despite the emptying of most of the minor coils, the major ones have not released their contents or decreased in diameter. Spermatophores were observed passing single-file through the ejaculatory duct. The row of spermatophores passing through the duct gave the appearance of a string of beads and caused the filled duct to sharply contrast with muscles, nerves and other associated structures which normally are barely distinguishable to the naked eye. There was little change in the system when examined after three hours of copulation; spermatophores were still in the process of traversing the ejaculatory duct.

After cessation of copulation, the minor coils of the MVD have been completely emptied (Fig. 12). The major coils of the MVD have not released their contents into the minor coils and are still of the same diameter as the major coils of the operated side from which none of the contents have been evacuated. Occasional spermatophores may still be found in the ejaculatory duct.

Recovery of the MVD and PVD is not accomplished for several days. The first evidence of this is the movement of the contents of the major coils of the MVD into the most anterior of the minor coils two days after copulation. By the end of seven days, both major and minor coils are filled with white granular material and of nearly equal size. The major coils gradually increase in size compared with the minor coils. The gelatinous material of the PVD is slower to make its appearance in the lumen. At the seventh day after copulation, only the anterior few coils contain an appreciable quantity of the material and the more posterior coils exhibit the vacuoles or spherical bodies. Even 14 days after copulation, the PVD has not been filled and a sufficient amount of gel secreted to mask the vacuoles. By the 21st day, recovery is complete and the MVD and PVD have resumed their original appearance.

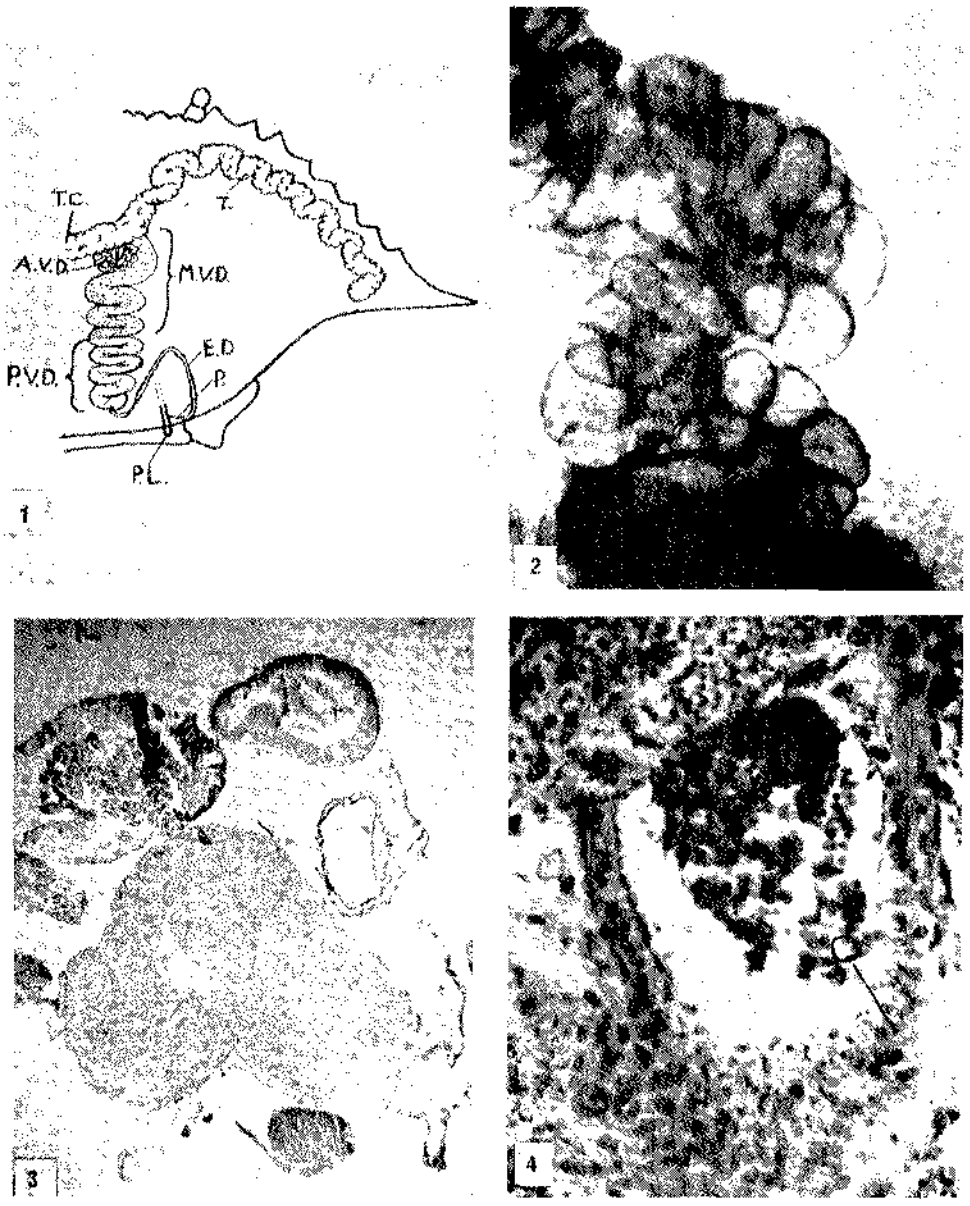
The sequence of evacuation is reflected in the formation of the layers of the sperm plug in the seminal receptacle of the female partners. This is discussed more fully in Part II of this study (Ryan, 1967*b*).

The mechanism by which the spermatophores and seminal fluid are forced out of the vas deferens is complex. Excision of any of the parts of the copulatory apparatus—first and second pleopods, penis—prevents evacuation of any of the materials of the MVD and PVD into the ejaculatory duct. Excision of the penis alone, permitting action of the second pleopod into first, does not cause evacuation of any material whose origin could be in the pleopods themselves, such as the rosette glands, into the seminal receptacle of the female. When the pleopods and penis are left intact and the ejaculatory duct severed, proximal to the base of the penis, prior to copulation, the seminal fluid and spermatophores are forced out of the severed end of the ejaculatory duct into the hemocoel about the muscles. This was observed in seven males, all of which died two days after copulation.

Discussion

Gross and Histological Anatomy

The general organizational plan of the testis and vas deferens in *P. sanguinolentus* is similar to that of other decapod Crustacea. Although the reproductive system shows considerable variation in the Macrura, Anomura and Brachyura, in representatives of each group, spermatogenesis occurs within lobes or sacculi of the testis, masses of spermatozoa are assembled into spermatophores and secretions of the vas deferens contribute to the seminal fluid which usually plays a role of some importance in each species.

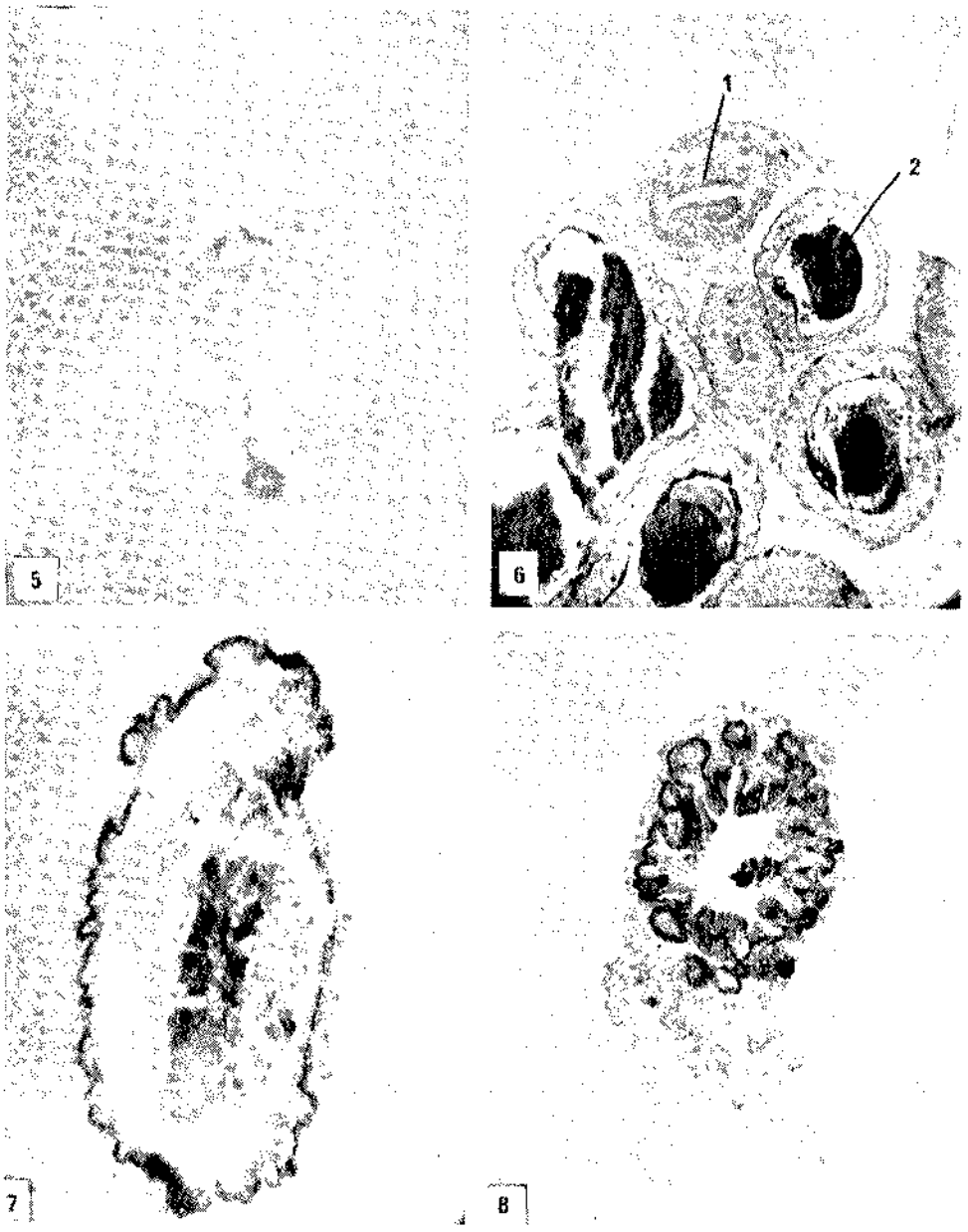


FIGS. 1–4. Fig. 1. Diagram of right side of reproductive system of male *P. sanguinodentus* (system duplicated on left). Testis (T.), testicular commissure (T.C.), anterior vas deferens (A.V.D.), median vas deferens (M.V.D.), posterior vas deferens (P.V.D.), ejaculatory duct (E.D.), penis (P.), first pleopod (P.L.).

Fig. 2. Whole mount, live testis in sea-water showing loops, lobes and lobules. ×43.

Fig. 3. Transverse section of testis at same level as Fig. 2. Showing: lobes, lobules and developing spermatocytes. Bouin's, ×47.

Fig. 4. Transverse section of seminiferous duct, posterior testis. Side view of sperm in circle. Bouin's, ×293.

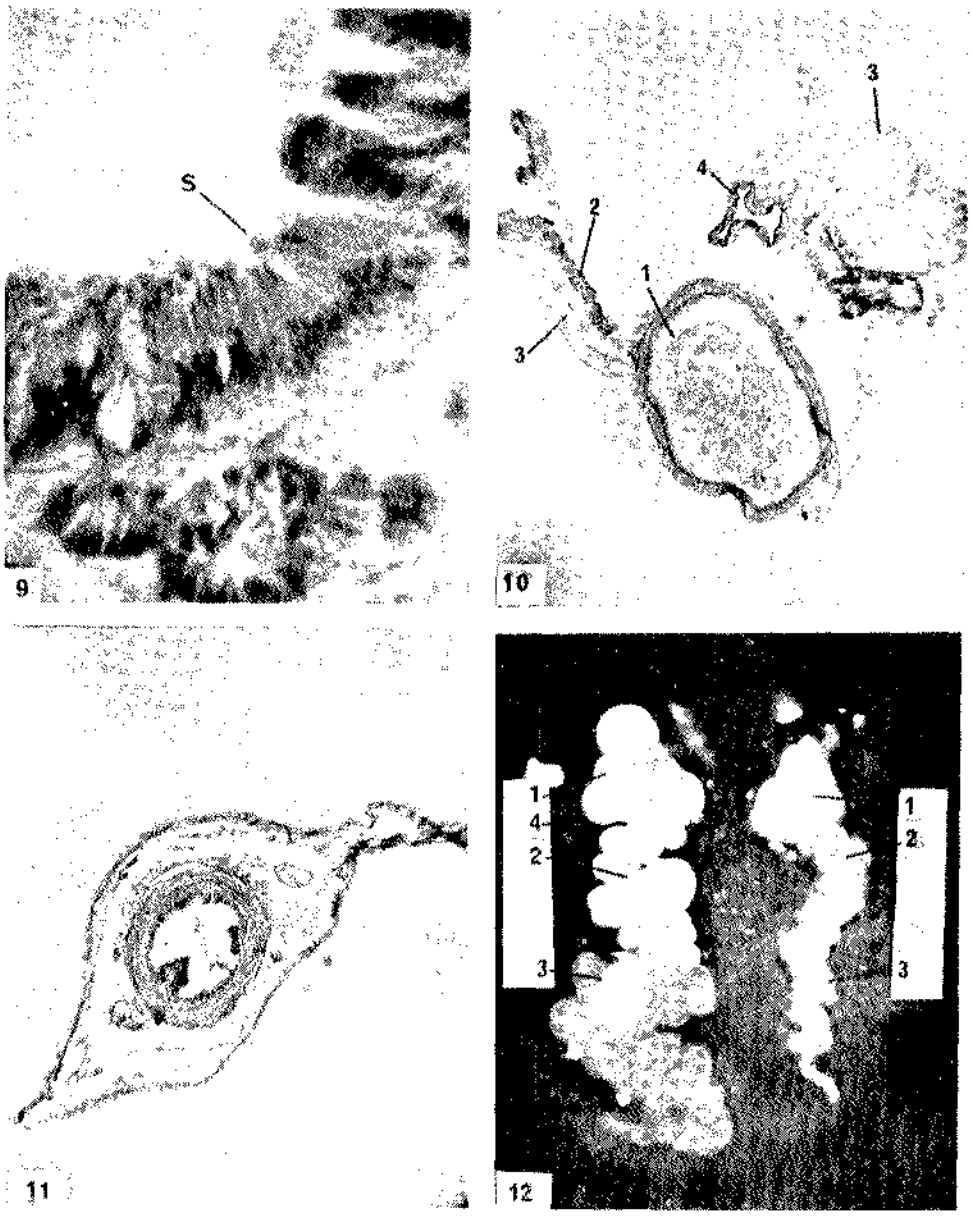


FIGS. 5–8. Fig. 5. Live sperm in sea-water. Side view. Hanging drop slide. 2,333.

Fig. 6. Section through coiled mass of anterior vas deferens. (1) first portion AVD (2) second portion AVD. Bouin's, 50.

Fig. 7. Transverse section of median vas deferens, minor coil. After copulation. Bouin's, 67.

Fig. 8. Transverse section of posterior vas deferens. After copulation. Showing: glandular outpockets. Bouin's, 53.



FIGS. 9–12. Fig. 9. Epithelial lining of posterior vas deferens. Enlarged portion of section in Fig. 8. Showing: spherical structures *pinched off from* epithelial cells (S). Bouin's. ×400.

Fig. 10. Transverse section of ejaculatory duct portion of posterior vas deferens with associated structures. (1) Ejaculatory duct. (2) Androgenic gland. (3) Nerve. (4) Blood vessel. Bouin's. 57.

Fig. 11. Transverse section of penis showing prominent gonoduct. Bouin's. 60.

Fig. 12. Vasa deferentia *un-reduced* after copulation. Copulatory apparatus on left side excised prior to copulation and left vas deferens unemptied.

(1) major coils MVD, (2) minor coils MVD, (3) PVD, (4) loose spermatophores in sea-water. ×2·3.

The results of the anatomical and histological portions of the present study closely approximate those of Nishioka (1959) on the same species and Cronin (1947) on *Callinectes sapidus*. There are certain features which those workers did not observe and discussion of these is necessary in order to understand the function of the parts of the system.

Subdivision of the testicular lobes into lobules was only occasional and, when occurring, was incomplete. In a lobe, or in all lobules of a lobe, all of the spermatogenic cells, except the spermatogonia, were in the same stage of development. Although each lobe adjoined the seminiferous duct only those containing completed sperm were open into the duct. There was no branching of the seminiferous duct as reported by both Cronin (1947) and Nishioka (1959). Whenever more than one portion of the duct appeared in a transverse section of the testis, examination of other sections in the series showed that the two portions were the result of looping of the whole testis.

The circumferential incompleteness of the duct was not mentioned by either Cronin (1947) or Nishioka (1959), although both workers included photomicrographs which show the incomplete epitheliation of the duct. Cronin's observation of epitheliation may be this peculiarly constructed duct. Studies in the development of the testis in juvenile males may clarify the relationships of the parts of the testis. The role of the testis commissure was not investigated. It is not known whether the commissure releases its spermatozoa to one or both of the two testes as occurs in the commissure of the ovary (Ryan, 1967 *b*).

A cytological study of spermatogenesis in *P. sanguinolentus* was not within the scope of this work. The general form and structure of the vesicular sperm in *P. sanguinolentus* resembles the explosive brachyuran sperm described for other species of Brachyura by Koltzoff (1906), Binford (1913), Fasten (1926), Worley (1939) and Yasuzumi (1960). Both exploded and unexploded normal sperm were observed. Examples of the former obtained by subjecting normal sperm to various osmotic conditions as many workers have done, were not the same as exploded sperm observed at fertilization. This subject merits further study and will be discussed in a later paper. The lobes and sperm which Nishioka described as degenerating are actually the completed sperm which he did not describe. A detailed phase and electron microscopical study of mature sperm, both exploded and unexploded, and of spermatogenesis as has been reported for macrurans (Moses, 1961 *a*, 1961 *b*) and anomurans (Barker and Austin, 1963) is needed.

The beginning portion of the vas deferens is termed vas efferens by Cronin (1947) and Nishioka (1959) who followed Cronin's nomenclature. Since the terms vas efferens and vas deferens are used for non-homologous structures in vertebrates and their use based upon differing embryological origins (Patten, 1958) which are not applicable in the Crustacea, the term vas efferens is not used here. The juncture of this specialized part to the proximal end of the AVD undoubtedly indicates that it is merely a specialized part of the AVD. While both Cronin and Nishioka attest to its smallness, the proximal portion of the AVD is visible. It does not penetrate the tangled mass of the second portion of the AVD, but is tightly bound to the medial surface of the tangled mass as indicated in their photomicrographs (Cronin, 1947, Fig. 9, p. 35; Nishioka, 1959, Fig. 36, p. 65). The relationship of this part to the testis and remainder of the AVD is more clearly seen in a ventral dissection.

Portions of the AVD, MVD and PVD contain epithelial linings whose secretions are either associated with elaboration of spermatophores (AVD) or with copulation and formation of the sperm plug in the seminal receptacle of the female (MVD and PVD). Cronin (1947 p. 227) stated that "the function of the massive median vas has not been determined" and Nishioka (1959) showed that the MVD is a site of spermatophore storage and secretion of granular material. Neither demonstrated that the viscid gelatinous material from the PVD (light green in *Callinectes*) and colorless in *P. sanguinolentus* (present author's observations) was associated with copulation. The secretory mechanism by which this gelatinous material is released is unknown. The peripheral pouches undoubtedly play a role in its formation but the contents of the spherical bodies which

arise by constriction of the columnar cells lining the lumen may be precursors of a part of the fluid.

Cronin (1947) was the first to describe a glandular structure associated with the ejaculatory duct. Later studies have demonstrated the presence of the gland in other crustaceans and its role in endocrine control of male secondary sex characters (Charniaux-Cotton, 1960). Since this androgenic gland is not directly associated with the function of the reproductive system, it has not been included here. Its presence and description for *P. sanguinolentus* was noted by Nishioka (1959) and its structure resembles that described by Cronin (1947) and Tcholakian and Reichard (1964) in *Callinectes* and King (1964) in *Pachygrapsus* but is completely unlike that described by Sarojini (1961) for *Portunus pelagicus.*

Muscular elements in the tissue coats of the vas deferens in a number of species of crabs were noted by Fasten (1917) and described more fully by Cronin (1947) and Nishioka (1959). In *P. sanguinolentus,* the degree of development of the musuclar elements is correlated with contractile activity of the different areas of the vas deferens during non-copulatory and copulatory functions.

There were no changes in the histological components of the reproductive system that were associated with the molt cycle in mature males. The only exception to this is the cuticular covering and partial lining of the penis which are shed at molt. As Broekhuysen (1936) has observed in *Carcinus,* there is no seasonal change in the male reproductive system.

Function of the Reproductive System

Non-Copulatory Functions

The results of this study do not offer any evidence of the mechanism by which completed sperm are evacuated from the testicular lobes into the seminiferous duct. Nishioka (1959) suggests that pressure exerted by sperm proliferating from spermatogonial masses may force the completed sperm out of the lobe into the seminiferous duct. Since all of the spermatogenic cells in a lobe, except the spermatogonia, appear to be in the same stage of spermatogenesis, periodicity of spermatocyte production is indicated. Although others (Cronin, 1947; Nishioka, 1959) observed the presence of muscular elements in the wall of the seminiferous duct, the present observations of contractile activity is the only one which suggests evidence of how the sperm move to the posterior end of the duct.

No other workers record a distinctive contractile activity of one part of the anterior vas deferens in the Brachyura which functions to regulate the size of the sperm masses to be incorporated into the spermatophore. Spalding (1942) points out that churning movements of the second portion of the AVD in some way mold the sperm masses into spermatophores. Evidence in the present study indicates that the size of the sperm masses are controlled by single contractions of the first portion of the AVD and that observed churning movements in the second portion of the AVD serve to move the sperm masses along the duct, compacting them as the capsular wall is being secreted about them. A similar observation of the role of muscular activity in molding spermatophores is noted by Matthews (1953) in *Dardanus asper.* Although contractile activity was not observed in the MVD, it probably plays a role there also, as evidence by its action during copulation. The most prominent activity in the non-copulating vas deferens was observed in the ejaculatory duct portion which was as active as a nematode worm after being on a microscope slide for more than an hour.

Copulatory Functions

Perhaps the most distinctive feature of the mechanics of the male reproductive system in copulation is the sequential order of the evacuation of the long coiled vas deferens. The contents

of portions of the PVD are evacuated through the ejaculatory duct, the pumping apparatus of the pleopods and into the spermatheca of the female before the fluid contents of the more proximal portions of the duct are moved into place. There is no extensive mixing of the contents of the MVD and PVD either during ejaculation or afterward in the seminal receptacle. Since spermatophores fill most of the anterior coils of the MVD, they are the last to pass out through the ejaculatory duct. The sequence of evacuation is reflected in the three layers of the sperm plug in the seminal receptacle of the female: a ventral layer of PVD origin; a middle layer of MVD origin and, dorsally, a cap of white spermatophores. When a female is permitted to copulate twice, the three layers of the sperm plug coming from the second male underlie those of the first. There is no evidence of the contribution of the rosette glands of the pleopods to the sperm plug as suggested by Spalding (1942) and Lochhead (1950).

Many theories have been offered as to the mechanics of evacuation of the extensive vas deferens. The principal theories are fluid pressure (Nishioka, 1959; Estampador, 1949), ciliary action (Fasten, 1918; Estampador, 1949) and pumping action of the pleopods (Williamson, 1904; Estampador, 1949). Fasten (1917) emphasized the possibility of the contractile activity of the muscularis of the duct. Observations of this study indicate that contractile activity is the most important mechanism for movement of the contents into the first pleopod where the second pleopod, with its plunger-like action, pushes the material forward. If fluid pressure were responsible, the material of the MVD would gradually move into the PVD as the latter's contents were emptied; but this does not happen. The pumping action of the pleopods cannot be responsible for the movement out of the vas deferens as well as into the female for, if the ejaculatory duct is severed, the contents of the vas deferens pour out of its severed end.

Excision of parts of the copulatory apparatus with resulting evacuation of only one side of the reproductive system indicates that ejaculation is unilaterally controlled. The requirement of the proper action of both pleopods as a sensory role as well as a pumping action is evidenced by the evacuation of the ejaculatory duct when it is surgically severed and the pleopods left intact. Ejaculation in *P. sanguinolentus* may be assumed to be under complex unilateral neuromuscular controls with fluid pressure playing minor roles in each section of the vas deferens.

The constituents of the seminal fluid which form the sperm plug have been suggested as serving a nutritive role for the sperm while in the receptacle (Cronin, 1947; Nishioka, 1959) or to hold the spermatophores within the receptacle (Spalding, 1942). It seems unlikely that the seminal fluid has a nutritive role in *P. sanguinolentus* because the plug begins to disappear, presumably the result of enzyme action, before the capsular wall of the spermatophores does. The sperm remain viable for six months or more after disappearance of the plug (*see* Part II of this study, Ryan, 1967 *b*). Many sperm remain in the receptacle of females that are isolated from males during molt from the first mature instar to the second and, months later, these females laid fertilized eggs without the possibility of any nutritive benefits of the sperm plug since copulation did not occur.

In all probability, the plug does serve to hold the spermatophores within the receptacle, but since the plug disappears in two to three weeks, the effect is short-lived. The materials of the sperm plug have homologous counterparts in other decapod crustaceans where the secretions of the vasa deferentia serve more obvious functions of binding the spermatophores in one mass (Calman, 1909) or of fastening the spermatophoric mass to the sternal surface of the female as in *Panulirus* (Matthews, 1951).

Summary

1. The paired reproductive system of male *Portunus sanguinolentus* (Herbst) consists of testes which are medially interconnected and long vasa deferentia which are anatomically subdivided into three general areas: anterior, median and posterior vasa deferentia. Each have two physiologically distinct regions.

2. The accessory reproductive structures, similar to most brachyurans, consist of the paired abdominal appendages, the first and second pleopods. The first pleopod is modified into a tubular structure at the base of which the penis and second pleopod are inserted. In copulation, the latter acts as a plunger to force seminal fluid outward, into the vulva and seminal receptacle of the female.

3. Non-motile spermatozoa of the usual brachyuran type are formed in the highly lobular and folded testes and evacuated into a singular seminiferous duct which extends the length of each testis. Mature spermatozoa are collected in the posterior portion of the seminiferous duct.

4. The anterior vasa deferentia arise from the posterior ends of the testes and consist of two general areas: a short, more highly muscular portion and a longer, less highly muscular, many-coiled portion. A single contraction of the muscular portion forces a mass of spermatozoa, coming from the seminiferous duct, into the second prortion where churning movements compact the sperm masses and push them along the duct. An epithelial lining of the second portion contributes to the formation of the ovoid spermatophores by secreting a capsular covering about each sperm mass. Completed spermatophores at the end of the AVD measure $275 \times 225\ \mu$.

5. The massive MVD is divided into two sections both anatomically and physiologically. Both function in storage of spermatophores and secretion and storage of a constituent of the seminal fluid. Only the more distal minor coils are evacuated during copulation.

6. The two sections of the PVD differ competely in form and function. A many-looped anterior portion secretes a gelatinous viscid constituent of the seminal fluid, while the second, the ejaculatory portion, does not contribute appreciably to the seminal fluid. The manner of secretion on the viscid fluid in the PVD is unknown and may be first as a pinching off of a part of the epithelial cells lining the lumen of the first portion.

7. During the 3·5–4·5 hours of copulation, the constituents of the MVD and PVD are evacuated in sequential order. The mechanism by which the contents are evacuated is by peristaltic contractions of the duct. Such peristaltic activity is particularly prominent in the ejaculatory duct. The pumping action of the second pleopod into the first forces the seminal fluid and spermatophores through the first pleopod and into the seminal receptacle of the female.

8. There is no extensive mixing of the constituents of the seminal fluid originating in the MVD and PVD. These form distinct layers of the sperm plug in the seminal receptacle of the female. The sperm plug probably does not have a nutritive role but serves to hold the spermatophores in the seminal receptacle, and is homologous to similar secretions in other Decapoda where the spermatophores are fastened to the external surfaces of the female.

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STRUCTURE AND FUNCTION OF THE REPRODUCTIVE SYSTEM OF THE CRAB *PORTUNUS SANGUINOLENTUS* (HERBST) (BRACHYURA: PORTUNIDAE)[1]

II. The Female System

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ABSTRACT

The gross and histological anatomy of the reproductive system of female *Portunus sanguinolentus* (Herbst) were investigated during the molt and reproductive cycle of the pre-adult and two-adult instars. Function of each of the parts of the system was ascertained during the reproductive period and during the process of copulation. The system was studied by vital staining, by the usual histological sectioning techniques and by experimental methods during copulation and ovulation. Captive individuals were reared after breeding to determine the ovarian cycle.

Production of oocytes occurs in the central region of the ovary. These move into the lobes of the ovary where deposition of yolk occurs. The first mass of ova is laid two months after molt, followed by two more batches 40 days apart. The same cycle is repeated in the next instar. Copulation occurs at ecdysis of the female. Dissolution of the spermatophore occurs after that of the sperm plug. Sufficient sperms are stored in the seminal receptacles to fertilize three batches of ova and some sperms may remain in the seminal receptacles during ecdysis to fertilize eggs produced by the second mature instar.

INTRODUCTION

THIS paper is a part of an overall study of the reproductive biology of the Indo-West Pacific species, *Portunus sanguinolentus* (Herbst), and is concerned with the form and function of the female reproductive system. In other sections of this overall study, the morphology, morphometry, and number of sexually mature instars (Ryan, 1967 *a*) and the male reproductive system (Ryan, 1967 *b*) are discussed.

Thus far, there has been no detailed consideration of the anatomy, histology and physiology of the female reproductive system in any brachyuran. This study, therefore, may not only be of value in assessing the reproductive potentialities of a commercially important species, but may also serve as a basis for research into the specialized areas associated with reproduction.

Generalized accounts of the anatomy of the female reproductive system are given by Williamson (1904) and Pearson (1908) for *Cancer pagurus*. Binford (1913) described oogenesis in the stone crab, *Menippe mercenaria*, and fertilization in histological sections of ova. Studies by many workers on the European portunid, *Carcinus maenas*, have contributed much to the knowledge of the intracies of the female reproductive system. Notable among these are the works of Harvey (1929), Shen (1935), Broekhuysen (1936), Spalding (1939) and Demeusy (1958). The important American species, *Callinectes sapidus*, was the object of research by Churchill (1919) in an account of its life-history and by Cronin (1942) who described the anatomical and histological development of the female reproductive system in late juvenile stages. Hard (1942) described some of the histological changes

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[1] The research upon which this paper is based is a part of a thesis submitted to the Graduate School, University of Hawaii, in partial fulfilment of the degree of Doctor of Philosophy. Contribution No. 219, Hawaii Marine Laboratory. (Present name: Institute of Marine Biology).

in the ovary associated with ovulation in *Callinectes*. Oogenesis is described for several species of the portunid genus, *Scylla*, by Estampador (1949).

Fertilization and ova attachment were investigated in detail as a part of the present study of the reproductive biology of *P. sanguinolentus*. These subjects, about which widely conflicting opinions exist, will be discussed in later papers.

Methods of Research

Female crabs used in this study were collected from Kaneohe Bay, Island of Oahu, Hawaii, during the period from January 1962, to June 1964. The crabs were principally collected in galvanized wire traps which resembled Atlantic lobster pots. The traps were placed at selected stations, usually at depths of 5–15 M. over a silty bottom. During the period of this study, the traps were down almost constantly and were emptied and rebaited every second day. Crabs of both sexes were brought back to the laboratory, tagged and kept in floating cages. The crabs were fed every second day with chopped fresh fish.

Premolt females were isolated in special cages just before their molt. In certain cases, males were placed with molting females and, in others, no males were in attendance for at least 14 days after molt. Attending males either had their copulatory apparatus bilaterally intact or one side was excised in such a manner that only one side of the female system was inseminated. This technique is described in Part I of the present study (Ryan, 1967 *b*). Both copulating and non-copulating females were tagged and kept in floating cages until death occurred. Pre-ovulating females or ovigers caught in the field were also tagged and confined in the laboratory cages. All crabs were observed daily and the stage of the ovarian cycle recorded every other day.

The reproductive system was studied during the molt-intermolt cycle and during the ovarian cycle by dissection accompanied by vital staining and by the usual histological sectioning techniques. Tissues for sectioning were fixed in Bouin's fixative, cleared in xylene and sectioned in paraffin at 8 μ. Harris' hematoxylin (Guyer, 1936) counterstained with eosin-Y proved satisfactory for general tissue differentiation and was used throughout. Serial sections of certain regions of the seminal receptacle and oviduct were stained with Mallory's triple stain (Pantin, 1960, modification) to show connective tissue differentiation. Tissues examined *in vivo* were stained with 10 per cent. sea-water dilution of methylene blue in quickly dissected live females and examined under a dissecting microscope.

Parts of the female system were measured with an ocular micrometer in either a compound or a dissecting microscope. Sizes of gross anatomical parts are reported as average measurements in five individuals in the first mature instar (Ryan, 1967 *a*) whose carapace lengths were 50·0–51·5 mm. Since the female system displays cyclic changes with the molt and ovarian cycles, the C_1 stage, within five days after molt, was taken as the basis for a description of the whole system.

In female *P. sanguinolentus*, the imminence of ovulation may be detected. After molt, vitellogenesis proceeds in the oocytes retained within the ovary to such an extent that the orange color of the yolk-filled ovary may be seen through the exoskeleton on the ventral surface at the postero-lateral border. About two weeks prior to ovulation, the color appears first as a faint orange blur and then a few days later as a distinct orange band. Within 24 hours before ovulation, the orange band has a crenulated border and appears pebbled. Within two hours prior to ovulation, the abdomen of the female gapes slightly open. These signs permitted detection of an impending ovulation and the female could be removed to the laboratory for dissection or for observation during the ovulation process and returned to the cages for continuation of the ovarian cycle.

Every attempt was made to keep the detrimental effects of confinement minimal. Nevertheless, few crabs could be confined longer than five months before death occurred. Almost all individuals

became covered with detritus, tube-dwelling annelids, oysters and barnacles. These sessile interlopers and detritus were removed weekly but it was impossible to remove the barnacles which eventually filled the gill chambers.

The research reported in both parts of this paper represent a repetition necessitated after fire destroyed a building of the Hawaii Marine Laboratory. The author wishes to acknowledge the help afforded to redo the research. He is particularly indebted to the following for aid in obtaining scarce references: H. A. Bern, G. J. Broekhuysen, D. G. Cargo, L. E. Cronin, S. Miyake, B. Patel and W. Stephenson. Gratitude is also extended to the University of Hawaii for a grant-in-aid, L. Zukeran for supply of crabs, A. H. Banner and P. B. van Weel for consultation during the research, K. Yamazato and the author's wife for reading the manuscripts. R. Kinzie did the figures.

Gross and Histological Anatomy

(Plates I–III)

Ovary

The paired ovaries with their commissure approximate the shape of the letter "H". Although the ovaries occupy the same location as the testes in the antero-lateral regions, they extend farther posteriorly (Fig. 1). The most anterior part of the ovary is found at the base of the large ninth antero-lateral spine. The ovary curves along the antero-lateral margin and is bound in place by a connective tissue envelope which contains many black chromatophores which are particularly evident in the dissection of a live specimen. As the ovaries curve medially from the lateral spines, they run lateral to the stomach, pass medial to the muscle or tendon of the adductor muscles of the mandibles and are then directed posteriorad. The commissure passes ventral to the posterior adductor muscles of the stomach as does the commissure of the testes. Posterior to the commissure, the ovary passes ventral to the pericardium and extends posteriorly along the medial edges of the endophragmatic skeleton. In the five crabs used for this description, and in most others examined, the right ovary extended farther posteriorly than the left. There may be small lateral protrusions of the ovary near its end at the first abdominal segment.

The appearance of the ovary is the same throughout its length and its commissure. In stage C, the ovary is translucent and light orange in color. Each ovary is divided into many lobes, 0·4–0·7 mm. wide, each containing 50–75 developing oocytes which are about 150 μ in diameter. The ovaries are about 70–80 mm. long; the right one extending 5–7 mm. more posterior than the left. The width, 2–4 mm., of the ovary is consistent throughout its length. In the region of the sixth thoracic segment, the ovary makes a ventrally directed loop. From the ventro-lateral side of this loop, the seminal receptacle portion of the oviduct arises.

The general organizational scheme of the ovary, as revealed by histological sections, is remarkably similar to that of the testis. A central hollow shaft, occasionally with an empty lumen, extends the length of the ovary with lobes projecting outward from this shaft (Fig. 2). Although oocytes undergo vitellogenesis in the lobes, they do not originate there. Unlike spermatogonial cells of the testis, oogonial cells are not located in the lobes. All of the cellular division in the steps of oogenesis occur in generative "zones" which are located along the sides of the central shaft of tissue (Fig. 2). Less cellular division would be expected in the ovary since the eggs are primary oocytes when laid and polar body formation does not occur until after fertilization and ovulation.

The thin wall of the ovary is composed of two layers of connective tissue and all of the lobes are further covered by a thin connective tissue layer, one cell in thickness. The outer walls of the lobes are about 3 μ thick. Cell boundaries are indistinct but long, 7–8 μ, spindle-shaped nuclei lie with their axes parallel to that of the wall. Cell boundaries in the inner layer are also obscure. Their spherical nuclei are 3–4 μ long and resemble the follicular nuclei.

Cells within the lobes of the ovary are of two general types: developing oocytes and follicular cells. Those of the latter type may in reality be of two types but this is not clear (Fig. 6). The developing oocytes in the C_1 crab are in various stages of vitellogenesis. They have large, 15–20 μ, vesicular nuclei with prominently stained nucleoli. Cytoplasm in the oocytes is compact and basophilic. In many oocytes, basophilic cytoplasmic granules, 4–10 μ, are surrounded by a clear area; these may be the "yolk" nuclei" described by many authors. Usually there is one of these per oocyte but, in some cases, there are more. Cell membranes are distinct in the oocytes at this stage.

Cells designated as follicular cells are disposed in two ways. Some are arranged in a single layer around each oocyte. These comprise the ovarian follicle and eventually form the chorionic membrane. Others are arranged, several cells thick, as septa which subdivide the lobes into compartments, each containing several oocytes. Larger groups of these cells are seen where the septa join with the wall of the lobe. The follicular cells have thin, oval or spherical, 3–5 μ, nuclei which are prominently stained. Their cell membranes are not always distinct at this stage. In the clusters of these cells along the walls of the lobes, some are undergoing division.

The central shaft of tissue running through the ovary in C_1 crabs has a thin wall similar to that of the lobes. Most of the shaft is filled with an amorphous basophilic granular mass. At the angles of the shaft and along its wall are, as apparent from longitudinal sections, generative zones or disjointed groups of oogonia in various stages of division (Fig. 2). These oogonia consist of large nuclei, 8–15 μ long. Those within the generative zone which are undergoing division have no nuclear membrane present. The generative zone is subdivided into three distinct areas: the area against the wall of the central shaft composed of the syncytial oogonia, the middle area composed of dividing oogonia, and the inward comprised newly formed oocytes. Even in the generative zone, a thin but densely stained cytoplasm is formed around the nucleus of the newly formed oocytes. The oocytes extend in a procession from the generative zones along the wall of the central shaft and into the lobes. These oocytes are of various sizes but have nuclei which are almost identical with those of the more advanced oocytes within the lobes. Cell lengths are 20–30 μ.

Interstices between the lobes may be filled with parenchymatous connective tissue, blood vessels or sinuses. Although waves of contraction were observed in the ovary of an ovulating crab, no definite muscular elements were evident in the walls of the lobes in a C_1 crab.

The organizational scheme of the histological elements is essentially the same throughout the length of the ovary and its commissure. In sections cut through the union of the latter with the ovary, the hollow central shafts of both are seen to be confluent and to contain generative zones.

A few differences characterize the ovary of a C_1 crab in the second mature instar. These are differences associated with a recent ovulation. As discussed below, a female may molt to the second mature instar 30–50 days after spawning. In such females, there are many empty spaces in the lobes from which ova have been released. Although the lobes contain oocytes in advanced stages of vitellogenesis, there are larger numbers of newly formed oocytes extending in rows from the generative zones. Some degenerating ova which were not spawned are present in the lobes and there are many loose granules present between the oocytes. These granules have similar size, shape and staining properties as the large granules of yolk in the ripe ova. In the ovary of the C_1 crab of either instar, there is no opening from the ovary into the seminal receptacle.

Seminal Receptacle and Oviduct

The seminal receptacle and oviduct adjoin the ovary and open to the exterior on the sternite of the 6th thoracic segment (Fig. 1, 11). The seminal receptacle or spermatheca is an enlarged portion of the oviduct. Although there is no opening between the seminal receptacle and ovary in the

C_1 crab, the anlagen of a short tube is present as a convoluted sheet of cells in the medial wall of the seminal receptacle. Both the ovary and the seminal receptacle undergo cyclic changes, but the cyclic changes of the seminal receptacle are co-ordinated with the molt cycle.

In the C_1 female, the seminal receptacle would be distended with the sperm plug. The empty receptacle is described here. The seminal receptacle is oriented in an almost straight dorso-ventral line. When empty, the ovoid receptacle measures 9 mm. high, 7 mm. wide (antero-posterior axis) and 3 mm. thick (medial to lateral axis). The ventral part of the seminal receptacle narrows to the small oviduct which leads from it and passes through the pereiopodal musculature of the sixth thoracic segment. The narrowed ventral end of the receptacle is bound very tightly to the medial faces of the endophragmatic skeleton.

The oviduct passes through a small crook of the endophragm between the sixth and seventh thoracic segments. The duct is so tightly bound to this endophragm at the crook that it cannot be dissected out without either destroying the endophragm or the duct. The width of the duct is 1 mm. and it is barely distinguishable from the musculature through which it curves medially and ventrally to the opening on the sternite of the sixth thoracic segment. The duct and lower portion of the receptacle are lined with soft chitin which is continuous with the soft chitin surrounding the opening. The openings, whose axes are transverse, are two soft ovals in the sternal exoskeleton. In the first mature instar, the ovals are about 3 mm. wide, whereas in the second mature instar the width is 5 mm. In the center of the oval is the transvere slit-like aperture of the oviduct. Its width is about 1·5 mm. Normally the slightly thickened lips of the aperture are held tightly closed.

Greatest tissue development of the seminal receptacle occurs at the time of molt when copulation would normally take place. In females which copulated at molt where the receptacle is distended with the male products which form the sperm plug (Fig. 12), paraffin sectioning is impossible since the sperm plug becomes very hard and brittle. This difficulty was overcome by using females which were isolated from males at molt or by excising parts of the copulatory apparatus from one side of the male. The non-inseminated side could then be sectioned.

The seminal receptacle is divided into a dorsal glandular portion and a ventral portion which has a chitinous lining continuous with that of the oviduct. The anlagen of the opening between the ovary and receptacle is located at approximately the level of the separation of the dorsal and ventral portions of the seminal receptacle.

In transverse sections, the empty receptacle has a characteristic outline similar to the Greek letter epsilon. Its lumen has the same general shape. The three folds of the receptacle are directed laterally and the interstices between them are filled with blood sinuses, blood vessels and loose connective tissue.

In the upper, glandular half of the receptacle, the sequence of tissue elements from the outside-inward is everywhere similar but with varying thickness. The wall consists of two stratified layers, the inner of which eventually sloughs off. The outer stratified layer very closely resembles the classic text-book illustrations of stratified epithelium of vertebrates. Externally, a compact fibrous coating, possibly containing muscular elements, merges with a fibrous parenchymatous tissue, each having scattered lightly stained nuclei that are 5–6 μ long. These overlie a compact stratum of cells of varying shapes but without intercellular material. The nuclei of this compact layer are similar to the outer two.

Extending from this compacted layer to the lumen is the inner stratified layer. In this series from the compacted layer toward the lumen, the cells are in various stages of degeneration. The nuclei, at first similar to those of the outside layer, become completely basophilic and then next to the lumen, the entire cells become basophilic spindles. Many of these cells are dislodged and loose in the lumen. The lumen contains a dark amorphous granular mass and, also, in its center, a number of large oval granules, 5–50 μ, which stain similarly to the amorphous mass. The inner

stratified layer is often separated from the outside stratified layer in fixation. In freshly dissected tissue, the inner stratified layer may easily be scraped off. At molt, the lumen of the receptacle contains a small amount of amber fluid which probably contributes to the amorphous and granular contents of the lumen.

At the juncture of the granular upper half with the chitinous lower half of the receptacle, a convoluted cord of columnar epithelium extends from the ovary through the external stratified layer of the receptacle (Fig. 3). Cells in this cord are columnar with their long axes transverse to that of the cord. Beginning at the ovary with a width of 13 μ, the cord decreases in width at its distal end. Nuclei in the cells are all approximately of the same size, 10–12 μ, and most are centrally located. Occasional cells are binucleate. This cord later becomes the tube through which the ova are released from the ovary. There is no indication of further division of these cells to form a tube in the C_1 crab. In some specimens, there is an invagination of the lining of the lumen of the receptacle at the level of the cord. Although in transverse sections this appears as a cord of cells, it is in reality a sheet of cells since, in serial sections, it is seen to extend vertically through approximately 2 mm. of sections.

The chitinous portion of the seminal receptacle begins at the level of the tube which connects the ovary with the seminal receptacle. It makes its appearance as a large typhlosolar projection into the lumen of the receptacle at the lateral fold opposite the ovary. A convoluted chitinous lining, 25–30 μ thick, covers the fold. This is secreted by a layer of very high, 5 × 100 μ, columnar epithelial cells. These have central ovoid nuclei, 7–10 μ long. Fibrous connective tissue fills much of the central portion of the fold. More ventrally, the fold splits into two, each of which extends vertically on the edges of the lumen. Between the folds, a single rugose layer of chitin-secreting high columnar cells lines the lumen. These are similar to those of the periphery of the fold but are only 55–65 μ long. The chitinous folds gradually extend wider to include all of the lumen of the receptacle and the lumen loses its regular outline. At the level of the oviduct, the lumen of the receptacle is nearly circular.

The oviduct which leads from the receptacle to the exterior is a highly muscular tube. Its lumen is lined with a rugose chitinous lining that is continuous with that of the receptacle. A layer of high columnar epithelium, similar to that of the seminal receptacle, secretes the lining of the duct. A prominent layer of circular and longitudinal striated muscle which is encased by a connective tissue envelope, completes the duct. The chitinous lining of the oviduct is continuous with that of the soft oval which surrounds the opening to the exterior.

There is very little difference in the oviduct and seminal receptacle in crabs of the first and second mature instars at stage C_1. In the first mature instar, some of the chitinous lining is broken off and not shed with the rest at molt. Thus, pieces of loose chitin may be found in the lumen of the seminal receptacle in the second mature instar. Many sperms may also be found there. These were inseminated into the receptacle several months previously, after the pubertal molt.

Accessory Structures

Four pairs of abdominal appendages or pleopods function as accessory reproductive structures (Fig. 11). These are located on the second through the fifth abdominal segments. Each biramous pleopod is constructed in essentially the same manner. It consists of a basal protopodite from which arise the medial endopodite and the lateral exopodite. The exopodite bears a large number of pinnate setae on its anterior and posterior borders. The endopodite on the other hand is segmented and bears a cluster of long, very smooth setae on the distal border of each segment. The number of segments, and hence number of clusters of setae, decreases progressively in more posterior pleopods. The long setae of the endopodites are the setae to which the ova are fastened after ovulation.

Functions of the Female Reproductive System

Functions of the female reproductive system are essentially cyclic in nature. Following the pubertal molt, the ovary enters into a cycle of the production and release of ova. Changes in the seminal receptacle are co-ordinated with the molt cycle. The histological changes and role of the ovary and seminal receptacle during their respective cycles are discussed separately herewith.

Ovary

Structural Changes

Last Juvenile Instar—As females of the last juvenile instar enter the premolt stage, the ovary is extended to its full length at the postero-lateral border. The width of the ovary in early pre-molt stage is about 1·1 mm. Individual lobes measure 0·05–0·10 mm. Although some oocytes are found within the lobes of the ovary, many newly formed oocytes are found in the lumen of the ovary. The generative zones in the ovary at this stage are longer and extend almost continuously along the walls of the ovary lumen. The lumen contains considerable chromophilic granular substance which possibly is blood. Oocytes within the lobes are of various sizes and shapes, usually measuring 15–30 μ. Some lobes, however, contain all smaller oocytes of the same size, 10–15 μ, as the newly formed ones which are found in the lumen. Accessory or follicular cells within the lobes of the ovary divide the lobes into compartments. The follicular cells have not yet clustered about the oocytes.

Post-Molt to First Ovulation—At the molt to the first mature instar, there is little change in the ovary from that of the pre-molt juvenile. The ovary is slightly wider, measuring 1·5–2·0 mm. in width. Oocytes within the lobes measure 30–45 μ and are nearly spherical in shape. Follicle cells now are arranged in a single layer about each oocyte. The ovary lumen contains many newly formed oocytes. Generative zones are present with oogonia in stages of cell division, but the zones are disjointed masses.

Between ecdysis and the first ovulation, there is a tremendous increase in width of the ovary due to the deposition of yolk within the oocytes. From a diameter of 30–45 μ at ecdysis, the oocytes increase to a diameter of 145–200 μ (in histological preparations). Each lobe of the ovary increases in size as the yolk distends its contained oocytes. The ovary becomes more prominently orange and opaque and fills all available space. Midway through the cycle, follicle cells completely and tightly surround each oocyte. When oocytes from the lobes of a freshly dissected ovary are vitally stained, the follicle cells are seen to cover each oocyte like thin tiles. Prior to ovulation, however, the nuclei of the follicle cells disappear and the cells probably form the chorionic membrane about each oocyte.

At ovulation, the nuclei of the oocytes are so changed that they are not visible with the histological preparations used. The oocytes, now fully formed ova ready for release, are filled with yolk granules which measure 10–15 μ in diameter. A chorionic membrane, 0·5 μ thick, tightly surrounds the cell membrane of each ovum. The ova are retained in the lobes and lumen of the ovary until the process of ovulation actually starts. At this time, the ovary is so distended with ova that it is plainly seen through the exoskeleton of the crab. About 24 hours prior to ovulation, the lobes of the ovary are distinct when viewed through the exoskeleton at the ventral side of the postero-lateral border. In crabs which have not ovulated before, no sperm are present in the lumen of the ovary prior to ovulation.

Immediately following ovulation, almost all of the ova have been evacuated from the ovary. Occasional unexpelled ova are present in the lobes and lumen of the ovary (Fig. 8). Most distinctive are the empty spaces separated by septal walls. It is not apparent how these spaces (Fig. 7), from which ova have been expelled, are confluent with the lumen of the ovary. Germinative zones are present in the lumen and their oogonia are in the process of cellular division. Newly formed oocytes are of two distinct sizes. Those in the central region of each lobe of the ovary measure 35–50 μ and have prominent cytoplasm. Those along the border of the ovary lumen measure

8–10 μ. Sections of ovary lobes fixed within 30 minutes after ovulation already contain at least 20–30 oocytes and processions of the smaller oocytes extend from the germinative zones to the lobes. A few sperm are present near the opening of the ovary into the seminal receptacle but none are in the distal reaches of the ovary.

After First Ovulation—Following the first ovulation, oocytes moved into the positions recently occupied by ova which were expelled at the first ovulation. It was not determined how the oocytes move from the site of origin in the germinative zones to the lobes. Immediately after ovulation, the lobes of the ovary are seen to be divided by septa which are several cells thick (Fig. 7). When near-term oocytes fill these spaces prior to ovulation, the septa are not distinguishable. Obviously, the spaces must be confluent with the lumen of the ovary, at least at ovulation, or the eggs would not be released into the lumen.

In sections of ovaries one and two weeks after ovulation, the thick septa are still present and the oocytes do not quite fill the space in them. One week after ovulation, most of the oocytes of the larger size were already in the spaces and processions of smaller, newly formed oocytes extended from the generative zones into the lobes. By the second week, oocytes within the spaces have increased from 30–50 μ to 70–110 μ. Their nuclei are still vesicular and measure 20–30 μ. In the lumen of the ovary at the second week following ovulation, there are very few processions of oocytes extending into the lobes although newly formed oocytes are seen on the borders of the generative zones which are now decreased in size.

Occasional ova which were not released remain in the lobes and are in various stages of degeneration. There are very few spaces not occupied by either degenerating ova (of the immediate preceding ovulation) or oocytes undergoing vitellogenesis. At the second week, granules of yolk are seen in the cytoplasm of the oocytes within the lobes. Follicle cells could not be distinguished from other accessory cells forming the septa.

There is little difference in the ovaries of females of the first and second mature instars following the first ovulation. Ovaries of crabs in the second mature instar had a few spaces filled with granular material which appeared to be degenerating ova from an ovulation preceding the molt.

Changes at the third week following the first ovulation are associated with the increased size of the oocytes and the deposit of yolk within them. Oocytes measure 150–200 μ. Most have large vesicular nuclei, 25–35 μ in diameter, but a few have smaller nuclei which are spherical and chromophilic. Follicle cells are displaced around each oocyte. These are thin cells different in shape from the almost spherical nuclei of the accessory cells. There are no empty spaces between the compartmental oocytes. Large numbers of newly formed oocytes, 15–25 μ, fill the lumen of the ovary. The germinative zone in crabs of the first mature instar are larger than those of the second. But in both instars, meiotic figures are present in the germinative zones.

There is little change at the fourth week from that of the third. Although some captive crabs ovulated in less than four weeks after the first, in those whose ovaries were examined, the eggs were not ready for ovulation. The nuclei were approximately the same size, 25–35 μ, and were more darkly stained. Ovary lobes contain a few centrally-placed oocytes of nearly the same size as those which remain in the lobe after ovulation. The germinative zones are small, but there are still many newly formed oocytes in the lumen. The nuclei of follicle cells are still present around each ovum but no chorionic membrane is observable.

Examination of the ovaries of crabs in the first mature instar and the second mature instar at the second ovulation reveals few striking differences from ovaries of these two instars at the first ovulation. At the second ovulation, in crabs of the second mature instar, there is a reduction in the size of the germinative zones to small clusters, 100 μ in diameter. These do not extend lengthwise in the lumen. Fewer newly formed oocytes are present in the lumen.

Changes in the oocytes within the ovary lobes during the interval between the second and third ovulations were essentially identical to those during the interval between the first and second

(Fig. 5). The number of unexpelled degenerating eggs is cumulative and those in various stages of degeneration were observed. This was particularly evident in crabs of the second mature instar in which as many as five to six degenerating eggs were present in each lobe.

Only one female in each instar survived long enough after the third ovulation for histological examination of the ovaries. One was a laboratory molted female of the first mature instar which was dissected three weeks after the third ovulation. The ovary was transparent and light orange in colour as in pre-molt. Oocytes within the lobes did not fill the spaces and measured 50–70 μ in diameter. The germinative zones were small and few newly formed oocytes extended from them. Many lobes were filled with smaller-sized oocytes. No yolk granules were present in the cytoplasm.

The ovary in only one second mature instar was sectioned after the third ovulation. The crab was caught while ovigerous and ovulated twice more in captivity. Upon dissection 11 days after the third ovulation, the ovary was tan in color. The same tan color was observed in the ovaries of two other field ovigers which ovulated a third time in captivity and three which ovulated a second time in captivity. Morphological evidence in each of these indicated that they were in the second mature instar. Lobes of the ovary contained oocytes which were of the normal size but whose cytoplasm contained many clear vacuoles. Nuclei were vesicular and not unusual in appearance. In each lobe, many of the oocytes contained large, 30–50 μ, black bodies which appear to be products in the degeneration of the oocytes. No germinative zones were observed in any of the sections of the ovary in the single female which ovulated a third time while in the second mature instar.

Ovulation Cycle

From observations of ovigerous crabs or crabs from which eggs had recently hatched, it was evident that female *P. sanguinolentus* ovulate more than once in each mature instar. In an attempt to estimate the number of ovulations and time intervals between ovulations, 108 females were reared in laboratory cages until their death and the periods of time determined between ovulations. Of these, 67 were caught in pre-molt stages and reared after molt until death; 39 of these had molted from the last juvenile to the first mature instar and 28 from the first to the second mature instar. The results of these observations are summarized in Table I. To complement the experiments summarized in Table I, 41 females which had molted in the field before capture were also reared in the same laboratory cages. Of these, 25 were ovigerous when caught and had ovulated at least once. The remainder, 16 females, were caught in a stage when the expanded ovary could be seen through the exoskeleton and these formed a sponge, or egg mass, in the laboratory. Tables II A and II B summarize the observations of the field-molted females.

These molts and ovulations occurred in all months of the year in Kaneohe Bay where the mean monthly water temperature varies 4° C. during the year. Since there were so many individuals whose period of captivity overlapped months of varying temperatures, splitting them into groups according to the water temperatures to which they were exposed proved to be impractical.

As shown in Table I, 21 of the females of the first mature instar and 13 of those in the second mature instar survived long enough to ovulate at least once in the cages. The mean lengths of time between ecdysis and ovulation, in each instar, approximated the other: 59·4 days in the first mature instar and 63·1 days in the second. Those crabs which died before ovulating at least once yield negative evidence in the sense that their deaths occurred in less than the mean length of time between ecdysis and ovulation. On autopsy, 19 crabs had ovaries which were in preparation for ovulation and 12 were cannabalized to such an extent that ovary examination was not possible. Two of the females in the first mature instar died in molt without ovulating after ecdysis.

A second ovulation in these laboratory-molting females is recorded in Table I. The mean length of time between the first and second ovulation is 32·5 days in the first mature instar, and 34·7 days in the second mature instar. Only one crab, of the first mature instar, survived long enough

to ovulate a third time, 31 days after the second, and, upon its death, 28 days after the third ovulation, was in pre-molt condition. Each of the crabs which died after a second ovulation had ovaries which were in preparation for a third ovulation.

To complement the above observations on crabs which molted in captivity, the lengths of time between ovulations in females which molted in the field are shown in Tables II A and II B. Similar lengths of time between ovulations were observed. Date of first ovulation in field ovigers was estimated as hatching date *minus* 12 days, the mean time required for hatching of all eggs of *P. sanguinolentus* observed in this study. It was not known whether the field ovigers were bearing an egg mass for the first or later time. A second ovulation occurred in 16 individuals and a third ovulation in four individuals. The time intervals between ovulations, as shown in Table II A, approximate those of crabs which molted in captivity. Mean time between ovulation-1 and ovulation-2 was 34·5 days and between ovulation-2 and ovulation-3 was 30·8 days.

TABLE I

Ovulation cycle in laboratory-molting females

Ovulation cycle	No. crabs	Time	
		Range	Mean
First Mature Instar			
		days	days
Ecdysis to Ovul-1	21*	35–92	59·4
Ovul-1 to Ovul-2	9	27–49	32·5
Ovul-2 to Ovul-3	1	31	...
Second Mature Instar			
		days	days
Ecdysis to Ovul-1	13*	35–88	63·1
Ovul-1 to Ovul-2	5	27–40	34·7
Ovul-2 to Ovul-3	0	...	...

* Laboratory molts which died before ovulation-1 (Both Instars), not included in Table I.

Preparation for ovul-1	.. 19 crabs
Unknown, cannabalized, etc.	.. 12
Molted (First mature instar)	.. 2
Total	.. 33

Since the crabs whose data are summarized in Table II A, were collected a year prior to the determination of a morphological basis of distinguishing the mature female instars (Ryan, 1967 *a*), the data include both instars. Nevertheless, the sample included four individuals which molted a mean of 43 days after the first ovulation in captivity and one which displayed evidence of being in premolt condition 34 days after the second ovulation. Four of the field ovigers ovulated a third time. Upon dissection, three had ovaries which gave evidence of being fully expended and each had a carapace length well within the size range of the second mature instar.

Results similar to those obtained with field ovigers were also obtained in females caught just prior to an ovulation and which formed at least one sponge in captivity. The data for these labo-

ratory ovigers are summarized in Table II B. Of 16 crabs which formed a sponge in the laboratory nine ovulated a second time, mean 35·7 days, and one a third time, 36 days after the second. Only one laboratory oviger molted after ovulating in captitvity. Each of the nine crabs which ovulated for the second time had ovaries which, upon autopsy, indicated that the ovaries were in preparation for a third ovulation.

TABLE II

Ovulation cycle in field-molting crabs

(Instars combined)

A. Field Ovigers

(ovigerous when caught)

Ovulation cycle	No. crabs	Time	
		Range	Mean
1	25*	(est. date ovul-1 = hatch date *minus* 12 days)	
		days	days
2	16†	25–41	34·5
3	4	28–37	30·8

* Crabs not ovulating second time in laboratory:

Died, prep. for ovul-2	5
Molted after ovul-1	4 (mean 43 days)

† Crabs molting after ovul-2 1

B. Laboratory Ovigers

(Egg mass formed after capture)

Ovulation cycle	No. crabs	Time	
		Range	Mean
1	16*	..	..
2	9	25–54	35·7
3	1	36	..

* Crabs not ovulating second time in laboratory:

Molted after ovul-1	1 (37 days)
Died, prep. for ovul-2	3
Unknown, cannabilized	3

The above data provide an estimate of the number and time intervals of ovulations and molt in both sexually mature instars. From these data, it is estimated that female *P. sanguinolentus* in each mature instar ovulate at least three times. The first ovulation occurs approximately 60 days

after ecdysis, the second 40 days after the first, and the third 40 days after the second. It is also estimated that crabs of the first mature instar molt approximately 40 days after the third ovulation. Accordingly then, the life-span of each mature instar would be approximately six months. Such an estimate based upon laboratory rearings must be treated with caution since it may not reflect what actually occurs under field conditions. Until more accurate field studies can be made, this estimate provides a working hypothesis.

Mechanics of the Ovary at Ovulation

At the start of the process of ovulation, the ova are, for the most part, still within the lobes where they had undergone vitellogenesis. Some have moved into the lumen of the ovary. The change (24 hours prior to ovulation) in appearance of the ovary, when viewed through the branchiostegite, probably indicates the time of movement of these eggs from the lobes into the ovary lumen.

The process of ovulation in *P. sanguinolentus* is very rapid. In nine females, the duration of the process was 45–60 minutes. Ova from the lateral extensions of the ovary were extruded last and were visible through the branchiostegite 10–15 minutes before the end of the process. After ovulation, the orange mark of the ovary was not seen until the mid-point of the next ovulation cycle.

The number of eggs produced by each ovulation is very large and varies from female to female. The number of eggs produced may be estimated by calculating the number of eggs attached in an egg mass. In four field ovigers, the number of eggs in their sponge was estimated by determining the average number of eggs attached to each seta, the number of setae per cluster, the number of clusters per pleopod and doubling to account for pleopods on the opposite side. The estimated numbers of eggs in these four sponges varied from 960,000 to 2,250,000. However, an estimate calculated in this way does not account for any eggs which may have been lost in the attachment process.

The mechanical forces which cause nearly 2 million eggs to be evacuated from the two ovaries and to pass through the seminal receptacles and oviducts in 45–60 minutes are intriguing. As reported above, no definite muscular elements were seen in the walls of the ovary. A more thorough examination would undoubtedly disclose their existence for in two crabs which were dissected at the height of their ovulation, contractile waves were observed in the ovary and seminal receptacle. Although excessive handling of the female appeared to delay the start of ovulation after its first signs are noticed, once the process starts, the flow of eggs from the oviducts (Fig. 9) did not cease in approximately 40 crabs which were handled in one way or another during the process.

In a series of experiments to determine the site of fertilization and the mechanism of ova attachment, the oviduct on the left side of the female was blocked prior to ovulation. Three methods of blocking were used: heat cautery destroying the opening, capping with molten paraffin, and inserting a plug in the oviduct. Blocking of the oviduct disclosed a noteworthy fact about the mechanics of ovulation. Upon dissection following ovulation in 11 females whose oviducts were blocked prior to ovulation, it was observed that the eggs were completely evacuated from the portions of the ovary on the blocked side, anterior to the commissure. The number of eggs remaining in the ovary and seminal receptacle posterior to the commissure was not large enough to include those eggs which came from the anterior portions of the ovary. Furthermore, when such individuals formed a sponge, the sponge appeared to be larger than half-size. It is assumed that the eggs passed from the left anterior ovary, across the commissure and out of the oviduct on the opposite side.

Seminal Receptacle and Oviduct

Structural Changes

Last Juvenile Instar.—Extensive thickening of the seminal receptacle begins in early pre-molt stage. At first, only the outer stratified layer is present. Many of the cells of the compacted zone

of the outer stratified layer exhibit mitotic figures, probably in production of the inner stratified layer. There are some granules of lightly staining material in the lumen. The convoluted cord of cells, destined to become the opening of the oviduct, extends from the ovary to the compacted zone of the outer stratified layer. Its length is approximately 0·6 mm. The secretory epithelial cells of the ventral portion of the receptacle have not yet secreted the new chitinous layer.

In late pre-molt stage, the inner stratified layer is present. None of the cells of the compact zone of the outer stratified layer display mitotic figures. At this stage, the cells of the inner stratified layer have distinct membranes which outline the slender cells. The convoluted cord of cells begins at the wall of the ovary and does not pass through the inner stratified layer but ends at its border (Fig. 3). In the lumen of the ovary, opposite the cord, there is a germinative zone in some sections but it is separated from the cord by the wall of the ovary.

Post-Molt to First Ovulation.—Following ecdysis, the seminal receptacle gradually decreases in size and shape. The size increase prior to molt occurs primarily in the dorsal glandular half of the receptacle and, similarly, after ecdysis, the greatest decrease is in this portion. The change in the receptacle includes a change in shape as well as size. At molt, the enlargement of the grandular portion occurs primarily in the lateral area with the result that the ovary is in a position medial to the mid-region of the enlarged receptacle. Whereas after molt and subsequent decrease in size, the ovary occupies a position dorsal to the receptacle.

Decrease in the thickness of the wall of the receptacle is accompanied by two differences in the histology of the glandular portion. Most significant is the disappearance of the inner stratified layer. The parenchymous portion of the outer stratified layer no longer has spaces between its cells but becomes compacted. Within two weeks after molt, the thickness of the entire wall is 0·3 mm. which is approximately the thickness of the parenchymatous layer, alone, at molt.

The convoluted cord of cells which will form the opening between the receptacle and the ovary remains closed until some time prior to ovulation. By the fourth week after ecdysis, the width of the cord has increased. The cells are now binucleate with the nuclei occupying opposite ends of the cells. It could not be determined whether this actually was a double row of cells or not.

At the time of first ovulation, the seminal receptacle is reduced in diameter and there is a slight thickening of the walls. Great masses of sperm fill the lumen, particularly at the upper level of the chitinous-lined portion. The opening of the ovary into the receptacle is surprisingly large and is large enough to permit four eggs at once to pass through it (Fig. 7). It appears as if the whole wall of the ovary gives way and the lining of the ovary lumen is everted outward toward the lumen of the receptacle. The width of the opening in a section of the ovary fixed while in the act of ovulation was 0·7–0·9 mm. The opening is lined with low columnar cells which measure $3 \times 40 \mu$. In some sections, a few sperm are present in the lumen of the ovary in close proximity to the opening of the receptacle. The eggs contained within the lumen of the receptacle have many sperm adherent to the chorionic membrane, but none of the sperms are in the "exploded" condition. At ovulation, the ventral half of the seminal receptacle and oviduct have a continuous chitinous lining. There is no change in this lining at ovulation.

After First Ovulation.—There is little change in the histology of the seminal receptacle from the first ovulation to the second or third ovulations. The opening into the ovary remains as a tube, 50μ wide and 400μ long, which remains open into the lumen of the ovary. The upper glandular portion of the receptacle maintains a lining of columnar epithelium whose cells measure 6×20–35μ (Fig. 8).

At onset of pre-molt in females of the first mature instar, the opening into the ovary closes. In early pre-molt, as the wall of the glandular portions thickens, the opening tube is already closed and the tube appears as in the convoluted cord prior to the puberty molt. The chitinous lining of the ventral half of the seminal receptacle and oviduct become separated from their underlying

epithelial layers as molt progresses. Much of the chitinous lining of the receptacle, and all of that lining the oviduct, is shed at molt and is observed, in microscopic examination, attached to the exuvia.

Following molt from the first to the second mature instar, the histology of the seminal receptacle and oviduct is essentially the same as that of the first mature instar mentioned above. The opening from the receptacle to the ovary remains closed until just prior to the first ovulation (Figs. 3, 4). After the third, and probably final ovulation, the seminal receptacle still contains sufficient sperm for subsequent ovulations.

Copulatory Functions

During copulation, the first pleopods of the male are introduced into the oviducts and seminal receptacles of the female. In 28 copulating pairs, the process was observed from start to finish and, in each pair, the copulation was continued without interruption until its end 3·5–4·5 hours later. After once inserting the first pleopods, the male does not exhibit any movement of them. The female, on the other hand, exhibits a side-to-side rocking motion. In three females, the depth to which the first pleopods were inserted was observed in side view. The pleopods were excised from the respective males and the intact oviduct and seminal receptacles dissected from the females. When the male pleopods were inserted to a depth equivalent to that observed before interruption of copulation, the distal end of the pleopod was seen to extend to the dorsal portion of the seminal receptacle.

After copulation is completed, a firm mass, the sperm plug, fills each seminal receptacle. The sperm plug has the consistency of paraffin wax. It is composed of three layers: a ventral translucent, sometimes amber, layer; a middle opaque white layer, and a dorsal white cap of spermatophores (Fig. 12). As described in the first part of this study (Ryan, 1967 *a*) the ventral and middle layers of the sperm plug are shown to have their origin in the posterior and median vasa deferentia, respectively, of the male. Just prior to ovulation, the receptacle contains an amber fluid which may cause the male products to harden. Duplication of the three layers of the sperm plug was obtained in two females by removing the male at the end of the process of copulation and substituting a second male. The females then copulated a second time, producing a second plug ventral to the first. The transverse lips of the oviduct openings are normally held tightly closed (Fig. 11) but, following copulation, they may remain gaping open for as long as four days.

Following copulation, the sperm plug gradually disappears. Individuals examined during the first two weeks copulation showed little change in the sperm plug. After 15 days, the edges of the sperm plugs were softened and the spermatophores were intact. At 25 days, the sperm plug was in a semi-solid state and spermatophores were still intact. In examination at 30 days, all of the sperm plug material was softened, some had disappeared and spermatophores were intact in some individuals and not in others. The sperm remain in the mid-region of the receptacle. With examination by the light microscope, sperm taken from the seminal receptacle have the same appearance as those taken from the vas deferens prior to their being incorporated into the spermatophore.

Ovulatory Function

At ovulation, eggs pass through the seminal receptacle, where sperm may adhere to the adhesive chorionic membrane, and to the outside through the oviducts. Since each ovary may produce approximately one million eggs which are ovulated in 45 minutes, each egg passes through the seminal receptacle rather quickly. As reported above, contractile waves were observed in the ovary and seminal receptacle of two individuals which were dissected at the heights of their spawning. Presumably, this is the mechanism for the release of such a large number of eggs in a short time. No muscular activity was ever observed in the seminal receptacle or oviduct at any other time. The lumen of the oviduct is wide enough to permit only two or three eggs to pass a point at one time.

Although the oviducts were not examined in the dissections of the two individuals mentioned above, contractile activity was observed in the oviduct openings of other females at ovulation. In these, the lips of the oviduct openings were rhythmically pushed outwards, extruding a few eggs at each time.

Sperm can remain in the seminal receptacle during molt, even though the female be isolated from males, and remain viable for an ovulation three months later. One first mature instar female caught while ovigerous, molted 48 days after capture and ovulated twice, at normal intervals, after molt. Fertilized eggs were observed in the egg mass of each ovulation.

Ovulation Behavior

As mentioned previously, the morphological indication of an impending ovulation is first apparent as the change in the configuration of the ovary as seen through the exoskeleton. In each case after this change was observed, ovulation occurred within 24 hours in over 50 individuals. Onset of the actual process of ovulation is detected two hours in advance by a relaxing of the abdomen which is normally tightly held against the sternum. At first the abdomen gapes open to an extent of 2–3 mm. It is not necessary to view the crab from its lateral aspect in order to detect the slight gaping of the abdomen or even to remove it from the water. When viewed dorsally, the tergites of the second and third segments of a normally posed female abdomen are seen to fit tightly against the coxae of the fifth pereiopods. As the abdomen is extended, a space can be seen between these tergites and the coxae of the fifth pereiopods.

A second behavioral change is noted in the abdominal appendages. Normally the exopodites and endopodites of the pleopods are held together and fold into the sternal grooves as the abdomen is fixed against the sternum (Fig. 11). When the abdomen gapes open preceding ovulation, the exopodites and endopodites are separated; the exopodites being extended outward (Fig. 9). After the sponge is formed, the outwardly extending exopodites encircle it.

In crabs held in small laboratory containers, the female is active at the surface of the container, apparently seeking escape. Quite suddenly at the time of extrusion, the female settles to the bottom of the container, elevates the cephalothorax from the bottom and extends her abdomen backward to its full extent, sometimes at almost a 180° angle. As the ova stream from the sternal openings of the oviducts, the pleopods are moved forward and backward with the endopodites passing under the two orange streams of ova. However, under these conditions the eggs do not become fastened to the pleopods but are spewed out onto the bottom of the container.

Following a suggestion of Broekhuysen (1936), it was determined that successful fastening of the large number of ova could only occur when the female had an opportunity to bury herself in the soft substratum. This fact was particularly well demonstrated in the females retained in the floating laboratory cages. In 73 ovulations in the laboratory cages, attachment of eggs did not occur, except for a few hundred attached to the terminal setae of the first two pleopods. When females were moved from the floating cages (after the change in the orange mark was detected) to a large well-aerated sea-water aquarium tank which had 7–10 cm. of fine sand in the bottom, sponge formation occurred in 35 out of 37 individuals. Attachments of eggs to form the egg mass takes place quickly, within one to two hours. In Fig. 9 streams of eggs are seen being extruded from the oviduct openings. Immediately after this picture was taken, the crab was forcefully buried in the bottom sand of the aquarium. Figure 10 shows the same crab with a fully formed sponge 1½ hours later.

No satisfactory explanation has yet been given for the attachment of eggs in any brachyuran. This subject was studied in great detail in *P. sanguinolentus* and a more detailed discussion of this will be presented in another paper.

Many authors (Churchill, 1919, etc.) note that the large mass of eggs in an ovigerous crab forces the abdomen backward. It is mentioned above that the abdomen is extended backward just prior

to egg extrusion. In the laboratory caged females which ovulated and in which no egg attachment occurred, the abdomen open gaped for several days following ovulation. In those individuals for which the event was observed daily, the abdomen was held open and the exopodites of the pleopods held outward an average of 9·3 days in 31 females. This is almost as long as the average time, 12 days, required for carrying and hatching of eggs in the water conditions of Kaneohe Bay.

Discussion

Gross and Histological Anatomy

While the general organizational plan of the ovary in *P. sanguinolentus* is similar to other decapod Crustacea, the modifications of the oviduct in the form of the seminal receptacle are similar to only those of the Brachyura in which internal insemination occurs. In addition, the seminal receptacle of those brachyurans which copulate after ecdysis of the female exhibits changes which are co-ordinated with the molt cycle.

The results of the anatomical and histological portions of the present study include certain features unnoticed in considerations of the female reproductive system in other species or features about which there are conflicting statements. Discussion of these is pertinent.

Ovary

Details of the anatomy and histology of the ovary have been presented for *Callinectes sapidus* in the works of Hard (1942) and Cronin (1942) and the structure has been described in lesser detail for a number of other species by other workers with many conflicting opinions, some of which were founded upon peculiarities limited to the species in question.

The ovary may be considered as a single structure with paired gonoducts (Demeusy, 1958) or as paired gonads which are medially interconnected (Calman, 1909). The latter point of view has been taken in this study. Evidence for this point of view may be taken from the observation that the early beginnings of the gonadal tissue are a pair of masses of germinal tissue which later interconnect medially (Dawdyoff, 1928).

In general, the ovary in *P. sanguinolentus* is constructed much like the testis. That is, a central tubular shaft of tissue gives off lateral lobes in which the completion of the gametes occurs. A striking difference is that the oogonial cells are located on the wall of the central tubular shaft and not in the lateral lobes as the spermatogonia of the testis. Both however are found in syncytial masses.

Nomenclature of parts in the ovary is somewhat confused in the literature. Hard (1942) uses the term follicle for the lateral diverticula of the ovary in which oocytes undergo vitellogenesis. In the present study, the diverticula are considered ovary lobes. Other workers (*e.g.*, Herrick, 1896; Block, 1935; Suko, 1954; Demeusy, 1958) who studied brachyurans or other decapods reserve the use of the term follicle for a group of specialized accessory cells which surround each ovum in the lobe and probably contribute to the formation of the chorionic membrane. In spite of the denial of their existence by Yonge (1938), Cronin (1942), and Burkenroad (1947), oocytes in *P. sanguinolentus* are surrounded by a distinct follicle of thin-walled, squamous-like cells which may be seen both in sections of fixed material and in vitally stained oocytes. Since the follicle cells are reported for macrurans, anomurans and brachyurans, it seems unlikely that they would be present in one brachyuran species and not another.

A very striking difference in the ovary of *P. sanguinolentus* and *Callinectes sapidus* is its relative size after molt to the first mature instar. In *Callinectes*, Hard (1942) and Cronin (1942) report that the ovaries are white and very short while in the former species, the present study has shown that the ovaries extend their full length to the postero-lateral border and to be already tinted with yolk deposits long before the molt to the first mature instar.

Seminal Receptacle and Oviduct

Structure of the seminal receptacle and oviduct is almost identical with that reported for *Callinectes sapidus* (Churchill, 1919; Hard, 1942; Cronin, 1942; Lochhead, 1950). The principal difference lies in consideration of what appears as a convoluted cord of cells in the medial wall of the seminal receptacle. Hard (1942) and Cronin (1942) term this the "germinal cord" and consider it to be the source of all oocytes produced in the ovary. In *P. sanguinolentus*, the cord lies entirely within the thickened wall of the seminal receptacle. Although appearing as a convoluted cord in histological sections of the receptacle, the structure is in reality a convoluted sheet of cells, one or two cells in thickness and 2·0–3·0 mm. deep. The cord stops at the wall of the ovary.

Stratification in the tissues forming the wall of the receptacle was previously noted by Spalding (1939) and Cronin (1942). Little difference was noted in the general structures of the receptacle except for the absence of a ridge of ciliated columnar cells between the dorsal and ventral halves as reported by Cronin (1942).

Function of the Reproductive System

Ovary

Structural Changes

Post-Molt to First Ovulation.—After molt to the first mature instar, oocytes within the lobes of the ovary undergo vitellogenesis. Oogonia in the process of oogenesis with meiotic figures are only observed in the germinative zones as Binford (1913) and Demeusy (1958) have described. No division of primary oocytes with extrusion of polar bodies was ever observed in any section of the ovary of *P. sanguinolentus* from the last juvenile instar to the end of the second mature instar as has been reported by others (Estampador, 1949; Block, 1935, etc.). Polar bodies were only observed in extruded eggs 30–60 minutes after ovulation. Broekhuysen (1936, Pl. V, Fig. 1) also shows polar bodies in eggs after ovulation in *Carcinus*.

The follicle cells disappear prior to ovulation, after which time the oocytes possess a chorionic membrane. At the time of ovulation, eggs taken from the ovary, eggs taken from the seminal receptacle and extruded eggs possess the prominent chorionic membrane in addition to the cell membrane. This differs from the findings of Yonge (1938, 1947, 1955) and Burkenroad (1947) who concluded that additional membranes were added after release of the eggs from the ovary.

After First Ovulation.—Following ovulation and release of most ova from the ovary lobes, newly formed oocytes move from the areas of their formation into the ovary lobes. Although several workers (Binford, 1913; Harvey, 1929; Demeusy, 1958) have described the origin of the oocytes from the syncytial oogonial areas, none have suggested how the newly formed oocytes actually moved into the recently emptied lobes. Hard (1942) and Cronin (1942) indicate that in *Callinectes*, oocytes originate in the convoluted cord of cells which actually comprises the very proximal end of the oviduct. Hard (1942) acknowledges that some oocyte production may occur within the ovary but considers these to be immature lobes, although he figures (Hard, 1942, p. 17, Fig. 9) a region comparable to a germinative zone in *P. sanguinolentus*.

Whether, after ovulation, the oocytes move into the same spaces recently occupied by ova was not directly observed in the present study. This is indicated, however, by the absence of the individual empty spaces in ovaries sectioned one week or more after ovulation. Another possibility is that the accessory cells forming the septal walls could be rearranged to form new septa. Hard's (1942) observation of immature lobes following ovulation is not apparent in *P. sanguinolentus* since there is no evidence of degeneration of old lobes after ovulation or evidence of other than oogonial and oocyte cells in the germinative zones which he believed to be the immature lobes. Furthermore,

the presence of degenerating unexpelled eggs within the ovary lobes indicates that the same lobes are participating in the production of a future batch of eggs.

Binford (1913) and Estampador (1949) report that fertilization occurs within the ovary. Careful examination both of ovary dissections and of sectioned material failed to reveal any sperm within the ovary except in that portion of the lumen just at the oviduct opening in individuals which had ovulated at least once. Estampador's (1949) figure of an ovary section has more the appearance of a tubule of the digestive gland and is not comparable with *P. sanguinolentus*. Binford (1913) suggests that the glandular part of the seminal receptacle may force the sperm into the ovary. This could not be concluded from the present study since no quantity of sperm was observed in the ovary and great quantities of sperm were observed in the seminal receptacle, even after the crab had spawned several times.

There is little difference in the ovary between ovulations. As Herrick (1911) and Hard (1942) have observed, the presence of degenerating eggs within the lobes of the ovary indicate a previous spawning but it cannot be determined if the crab is preparing for the second or third ovulation.

As the crab of the first mature instar enters pre-molt, probably after its third ovulation, vitellogenesis is suspended and the ovary has about the same appearance as in a juvenile female that is about to enter the pubertal molt. In crabs of the second mature instar, the ovary is tan in color following the third ovulation and all of the ova remaining within the lobes show signs of degeneration. This is similar to Hard's (1942) observation in *Callinectes* following a second ovulation.

Ovulation Cycle

The results of the present study indicate that female *P. sanguinolentus* may spawn year-round with a peak season from October to February. However, the evidence for this conclusion is circumstantial. Only 28 ovigers were collected in the traps in the two-year period out of a total number of approximately 1,500 individuals. The 28 ovigers were all collected between the months of October and February. Year-round spawning with a peak season during the colder months was similarly reported for *P. sanguinolentus* by Menon (1952) and Chhapgar (1956).

In the absence of ovigerous females in the field collections at all months, confirmation of the possibility of year-round spawning in Kaneohe Bay exists in other lines of evidence. Mature females caught at all months of the year showed the prominent orange ovary which could be seen through the exoskeleton. Many of these crabs were caught during summer months and spawned a day or two later. Not included in the present report were the results of seinings for post-larval crabs. Crabs of the probable sizes of the first and second crab instars (2·5–4·0 mm. carapace length; Miss K. G. Rajabai, personal communication) were caught along the shore of Kaneohe Bay at all months of the year which indicated a year-round hatching.

In addition to these lines of evidence, cage rearing studies of females which molted just after capture included individuals ovulating after molt regardless of the time of the year when molt took place. Only two out of 67 individuals, as shown in Table I, were exceptions; they molted from the first to the second mature instar without ovulating. In one of these, vitellogenesis proceeded to such an extent that the ovary could be seen through the exoskeleton and then the orange color gradually disappeared as the female began pre-molt. Of the 12 unknowns shown in Table I, all died in less than 19 days which is less than the usual time for the orangeness of the ovary to be apparent through the exoskeleton.

The usual length of time from ecdysis to first ovulation in *P. sanguinolentus* is quite similar to minimal lengths of time from ecdysis to first ovulation in a number of species of crabs from temperate regions. Reporting a near two-month minimum are Churchill (1919) and Van Engel (1958) for *Callinectes sapidus*, Broekhuysen (1936) and Veillet (1945) for *Carcinus maenas*, Binford (1913) for *Menippe mercenaria* and Knudsen (1964) for several species of *Cancer*. Although more

than one ovulation in a spawning season was reported, none of the above workers showed a regularity of subsequent spawnings.

In the laboratory rearings of females after the first ovulation, the cycle leading to the second and third ovulations occurred without exception. Each individual ovulated a second or third time, within the times shown, or, upon its death, autopsy revealed an expanding ovary in a stage of vitellogenesis. Similar time intervals between ovulations were noted for females which had molted in the field prior to capture. These individuals were ones which were caught as ovigers (Table II A) or showed impending ovulation when caught (Table II B). In crabs of either group, it was not known whether the first observed ovulation was actually the first, second or third ovulation. Some in each category would be expected, and it was found that some molted after the first and second ovulation in captivity. In *P. sanguinolentus*, empty egg cases do not usually remain attached to the pleopodal setae and there is no way of estimating whether a crab had spawned before capture.

Many of the individuals listed in Tables I and II A ovulated in the holding cages without attachment of ova. Those listed in Table II B all formed a sponge and carried the eggs until hatching. Hiatt (1948) reported that in *Pachygrapsus*, ovigerous females undergo an "abnormally prolonged intermolt interval". Similarly, Scudamore (1948) concluded from questionable data that removal of eggs from ovigerous female crayfish hastened onset of molt. There was no evidence that the attachment of eggs in *P. sanguinolentus* extended the molt or had any bearing on the onset of vitellogenesis in preparation for another ovulation.

The significant conclusions from the above observations are that in *P. sanguinolentus*, ovulation is effected by rhythmic controls during intermolt which are probably extrinsic to the ovary itself and possibly hormonal. The above data also permit an estimate of the minimum of three ovulations per mature instar and of molt following the third ovulation of the first mature instar. When the time intervals required for all of these are added, an estimate of the life-span of approximately six months for each mature instar or 12 months for the mature life of the crab, is obtained. Such an approximation remains only a working hypothesis until more accurate field studies can be conducted.

Mechanics of the Ovary at Ovulation

The only explanation of the mechanism which causes ova to be evacuated from the ovary in a decapod crustacean was given by Herrick (1911) for *Homarus* stated that ova were released from the ovary "by contraction of their muscular walls". Such contractile activity was observed in the ovary and seminal receptacle of *P. sanguinolentus* which were dissected during the ovulation process. At the onset of ovulation, the eggs are confined within the lobes and lumen of the ovary but during the period of vitellogenesis, the eggs are only found within the lobes of the ovary. After the change in the configuration of the ovary was observed 24 hours prior to ovulation, many of the eggs have moved into the lumen of the ovary and each lobe is definitely open into the lumen.

No reference could be found to this change in the configuration just prior to ovulation. Arriola (1940) and Matthews (1959) report seeing the gravid ovary through the exosekleton in other species. A change in the configuration of the ovary just prior to ovulation was also observed, during the present study, in *Podophthalmus vigil*, another portunid species of similar size also inhabiting Kaneohe Bay.

Seminal Receptacle and Oviduct

Structural Changes

Many workers report thickening of the glandular portion of the seminal receptacle at a molt in which copulation would take place (Churchill, 1919; Binford, 1913; Broekhuysen, 1936; William-

son, 1904; Spalding, 1939; Cronin, 1942; Estampador, 1949, etc.). Utilization of this thickening as an indicator of pre-molt has not been made. This would be of particular value in those forms in which the females molt several times after reaching sexual maturity. Heretofore, the mitotic activity of the stratified layer as a factor in the pre-molt thickening of the seminal receptacle has not been noted.

If the thickening of the seminal receptacle at molt is an adaptation enabling the receptacle to accommodate the male sexual products received at copulation immediately after molt of the female, some similar modification would seem to exist in those brachyurans which copulate when the female is hard, *i.e.*, in intermolt, or perhaps the male products may not form a plug of appreciable size. Broekhuysen (1941) and Knudsen (1960, 1964) who studied species which copulate when the female is hard, make no mention of modifications of the seminal receptacle at the time of copulation.

Spalding (1939), Hard (1942), Cronin (1942) and Lochhead (1950) considered the anterior portion of the oviduct to be located inside of the ovary. The anterior portion of the oviduct in *P. sanguinolentus* lies entirely within the thickened wall of the seminal receptacle. From the photomicrographs in Hard's paper, it is apparent that the same would be true in *Callinectes sapidus*, if the appropriate structures were re-examined. The closing of the anterior portion of the oviduct at molt from the first to second mature instar in *P. sanguinolentus* is apparently due to a constriction of that portion of the oviduct caused by the extreme enlargement of the glandular portion of the seminal receptacle.

Examination of the seminal receptacle and oviduct of *P. sanguinolentus* failed to reveal any histological changes during the ovulation cycle. Herrick (1896) and Yonge (1938) report a cyclic secretory activity of the wall of the oviduct in *Homarus*. In view of the chitinous lining of the receptacle and oviduct in the brachyurans, it seems unlikely that any secretory activity, other than the secretion of the chitinous lining itself just prior to molt, would exist. It is suggested that the secretory cells of the oviduct in *Homarus* may be homologous with those secreting the chitinous lining in *P. sanguinolentus*.

Copulatory Function

The seminal receptacle functions in the receipt and storage of the male sexual products at copulation. These products are evacuated in sequential order from the posterior and median vasa deferentia of the male during copulation (Ryan, 1967 *b*). Spalding (1939) points out the dual nature of the sperm plug and suggests that the ventral portion of the plug has its source in secretions of the rosette glands of the male pleopods which Cronin (1947) also found in the male pleopods in *Callinectes*. The results of the present study (Ryan, 1967 *b*) show that no part of the sperm plug could be ascribed to the pleopods.

After copulation, the male materials form a hard plug, the sperm plug, which is gradually softened and has almost disappeared at the time the capsular wall of the spermatophore disappears 25–30 days after copulation. Spalding (1939) points out the probable cause of its disappearance in enzyme-like secretions of lining of the receptacle itself. The role of the plug has been suggested as providing a nutrient medium for the sperm. In view of the rapid disappearance of the plug compared with the many months that the sperm remain viable in the receptacle (even through a molt, Broekhuysen, 1941 and 1955 and the present study), a nutritive role seems unlikely. A more logical function of the sperm plug is given by Spalding (1939), that of holding the spermatophores within the receptacle.

Ovulatory Function

The opening of the seminal receptacle is complete at ovulation and eggs pass quickly through the receptacle and oviduct. Observed contractile activity probably accounts for the rapid evacua-

tion of the eggs in *P. sanguinolentus*. Nearly one million eggs are moved through each receptacle in 40–45 minutes at each ovulation.

The seminal receptacle and oviduct are widely credited with being the site of fertilization in the Brachyura. In spite of the numerous references, no conclusive evidence has been presented that fertilization actually occurs there or even inside of the female. Yonge (1938) suggests a very probable alternative. The actual process of fertilization may occur externally as in the Macrura and Anomura and the seminal receptacle merely serve as a site where sperm may come in contact with the adhesive surface of the chorionic membrane, penetration taking place after extrusion.

The modification of the sexually mature seminal receptacle is apparently not necessary for ovulation to occur. Demeusy (1958), in an experiment on the hormonal controls of vitellogenesis, obtained successful ovulations in juvenile females which were several instars preceding the first sexually mature one. Similar results were obtained in the juveniles on *P. sanguinolentus* by the present author after implant of certain endocrine structures.

Summary

1. The paired reproductive system of female *Portunus sanguinolentus* (Herbst) consists of ovaries which are medially interconnected to oviducts, a part of which is enlarged to form a seminal receptacle. The oviducts open to the exterior on the sternite of the sixth thoracic segment.

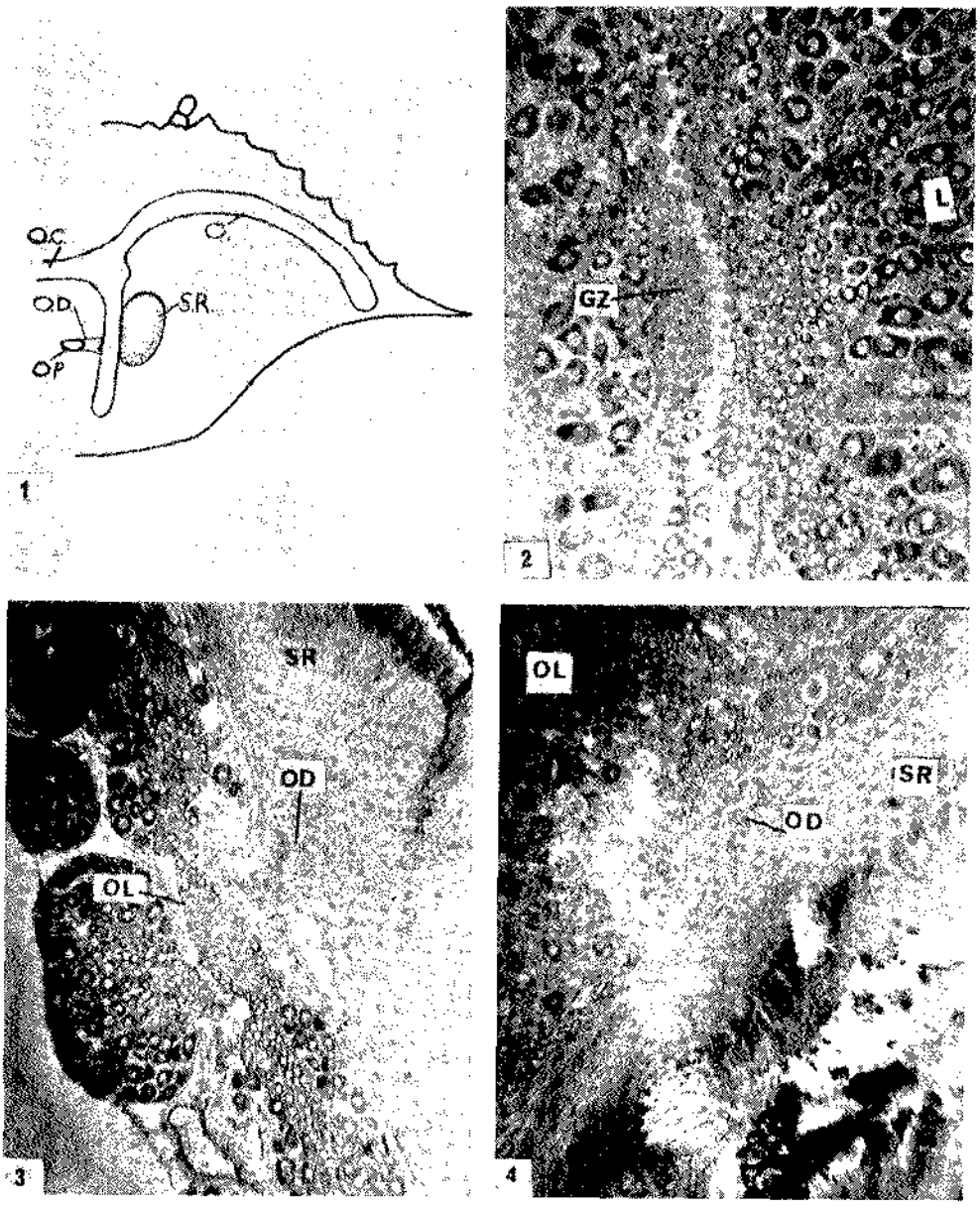
2. Accessory reproductive structures, similar to most decapods, consist of four pairs of biramous pleopods on the second to fifth abdominal segments. The endopodites bear long setae to which the eggs are attached at ovulation.

3. The ovaries consist of a central hollow shaft and lateral lobes. Syncytial germinative zones with meiotic figures extend along the wall of the lumen. Primary oocytes are found in processions from the germinative zones and fill each lobe where they are surrounded by follicle cells and other accessory cells.

4. The oviduct begins as a tiny portion folded in the wall of the thicker seminal receptacle. The seminal receptacle consists of a glandular dorsal portion and chitin-lined ventral portion. The wall of the glandular portion is stratified. A short narrowed portion or vulva extends from the receptable through the appendicular musculature to open to the exterior. Its chitinous lining is continuous with that of the receptacle and is shed at molt.

5. Functions of the ovary follow two cycles: molt and ovulation cycles. Oocytes move from the germinative zones to the lobes prior to the pubertal molt. Vitellogenesis occurs in the lobes, principally after the pubertal molt. In the first and second mature instars, molt is followed by ovulation, approximately 60 days later. The eggs remain in the ovary lobes until 24 hours prior to ovulation when some move into the ovary lumen. All eggs remain in the ovary until the process of ovulation begins. Ovulation lasts approximately 45 minutes. Contractile action forces the 900,000–2,000,000 eggs from the two ovaries in each ovulation. A second and third ovulation follows, approximately 40 days apart. In the first mature instar, molt occurs approximately 45 days after the third ovulation. Attached eggs measure 0·28 mm. and are surrounded by a single extra-cellular membrane, the chorion, in the ovary. No further extra-cellular membrane is added.

6. The seminal receptacle stores the male products at copulation. The products form a three-layered firm plug; the dorsal layer is a cap of spermatophores. The plug gradually softens and disappears, presumably by enzyme action, about 30 days after copulation. Loose sperm are stored in the glandular half of the receptacle. The receptacle displays a single cycle of change with a thickening of the glandular half at molt. At ovulation, contractile action forces the eggs outward. Fertilization was not observed in the receptacle and the structure probably functions

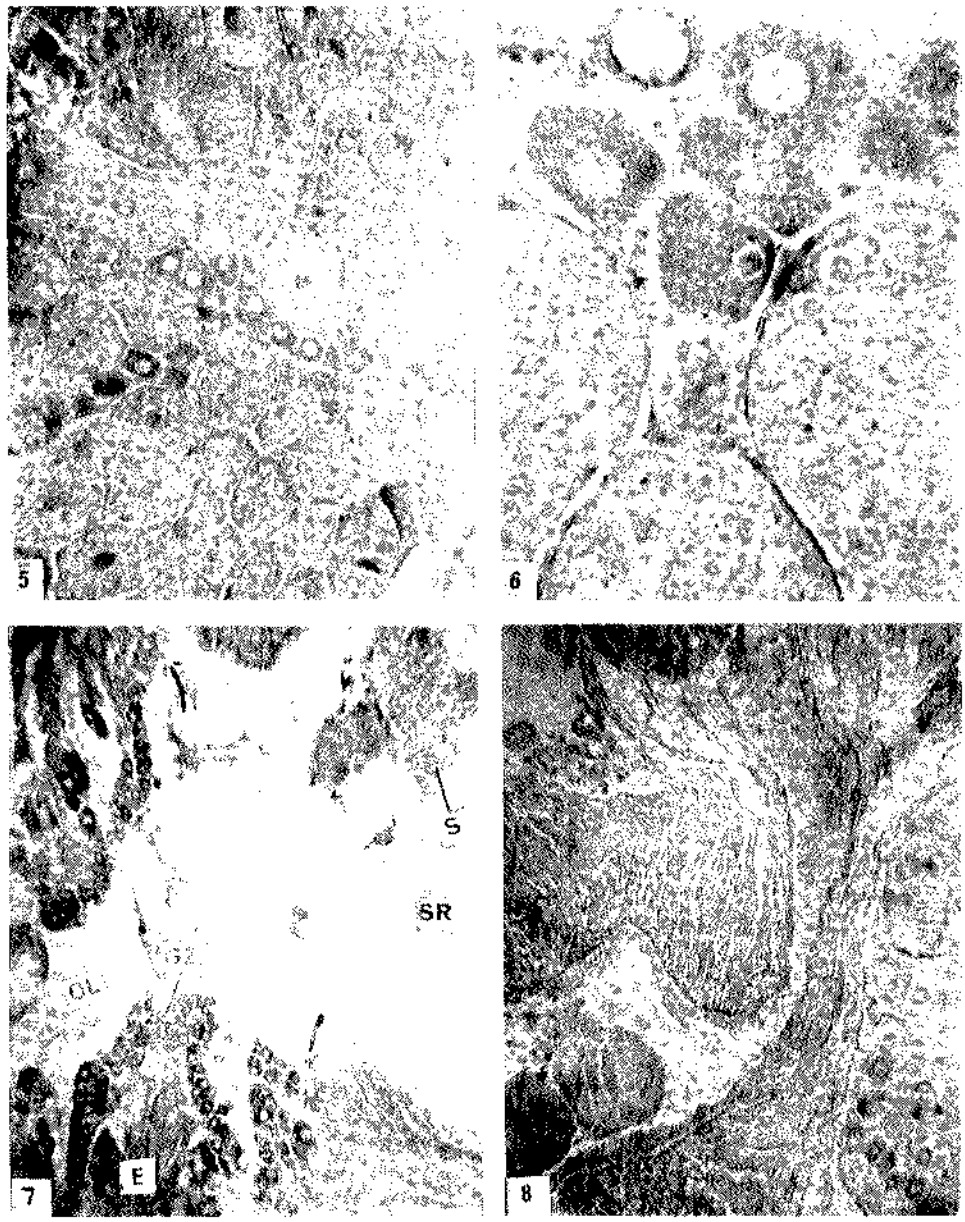


FIGS. 1–4. Fig. 1. Diagram of right side of reproductive system of female *P. sanguinolentus* (system duplicated on left): ovary (O), ovary commissure (OC), seminal receptacle (SR), oviduct (OD), oviduct opening (OP).

Fig. 2. Longitudinal section of ovary at molt to first mature instar: central lumen of ovary with germinative zones (GZ), lobes of ovary with developing oocytes (L). Bouin's, 80.

Fig. 3. Section through ovary and seminal receptacle at molt to first mature instar showing: convoluted proximal portion of oviduct (OD), wall of seminal receptacle (SR), central shaft of ovary with *lumen* filled with newly formed oocytes (OL). Bouin's, 100.

Fig. 4. Section through ovary and seminal receptacle at molt to second mature instar showing: convoluted proximal portion of oviduct (OD), wall of seminal receptacle (SR), central shaft of ovary with newly formed oocytes (OL). Bouins', 100.

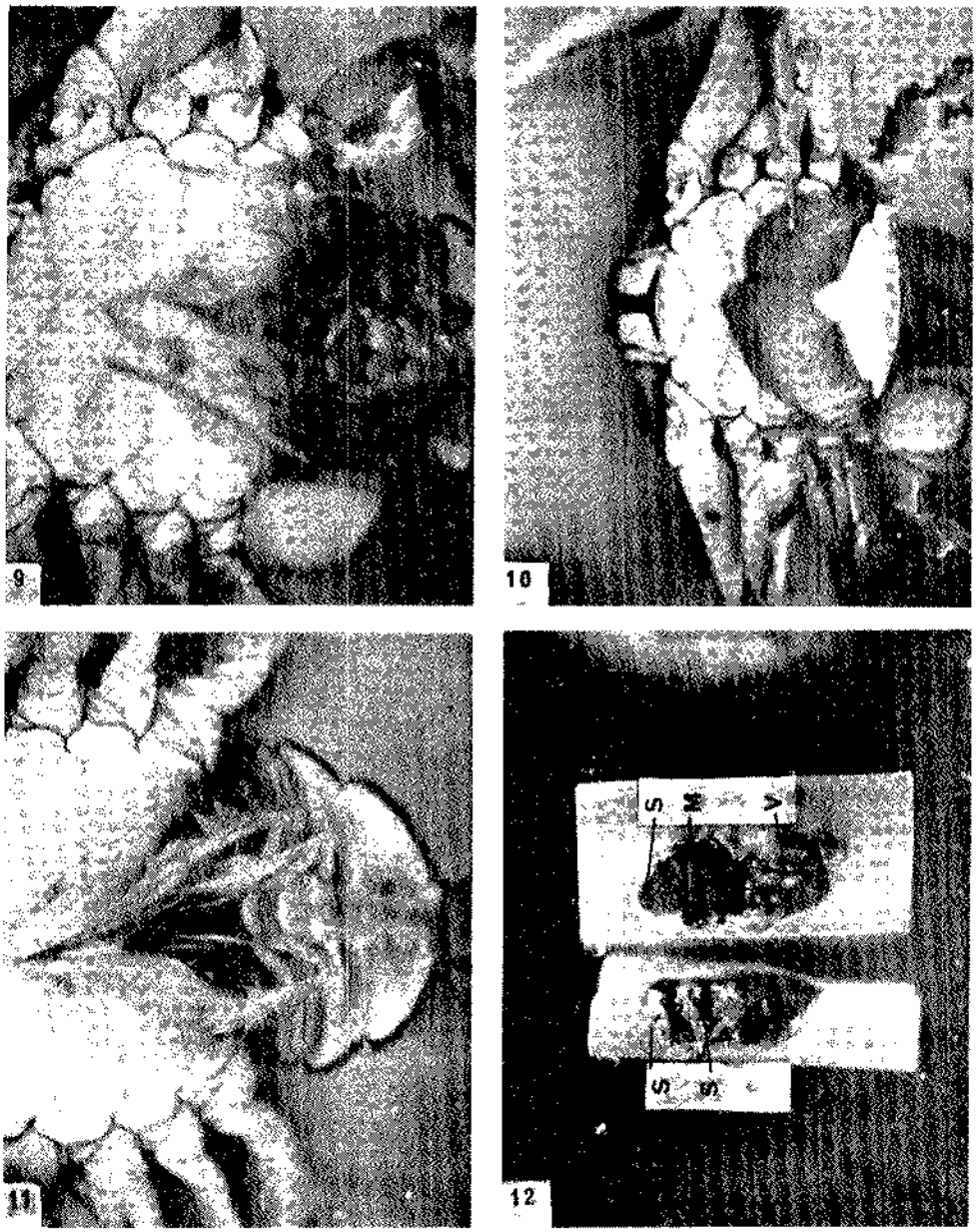


FIGS. 5–8. Fig. 5. Section of ovary in second mature instar 21 days after second ovulation. Note maturing yolk-filled oocytes with nuclei in company with younger oocytes having vesicular nuclei. Bouin's, ×133.

Fig. 6. Higher magnification of section in Fig. 5. Showing thin follicle cells surrounding maturing oocytes and oval nuclei of accessory cells. Bouin's, ×609.

Fig. 7. Section of ovary at opening to seminal receptacle 30 minutes after ovulation showing ovary lumen (OL), seminal receptacle lumen (SR), spermatozoa (S), spaces in emptied lobes (L), germinative zone (GZ). Arrows denote boundary between ovary and seminal receptacle. Note processions of newly formed oocytes. Bouin's, ×93.

Fig. 8. Section of ovary and seminal receptacle of first mature instar seven days after second ovulation showing proximal portion of oviduct open into ovary. Note two unexpelled eggs in receptacle. Bouin's, ×80.



FIGS. 9–12. Fig. 9. Ventral view of female at onset of ovulan. Material being extruded from each oviduct is a fluid mass of eggs. Note laterally extended exopodites of pleopods. ×0·9.

Fig. 10. Attached egg mass of same female in Fig. 9. Female buried in sand immediately after first photograph, second photograph taken 1·5 hours later. 0·7.

Fig. 11. Extended abdomen of non-ovulating female to show normal position of exopodites of pleopods. Note soft ovals in sixth thoracic sternites with transverse openings of oviducts. ×0·9.

Fig. 12. Sperm plugs in seminal receptacles after copulation (four days). Sagittal halves. Right: female copulated once; note middle (M) and ventral (V) layers of sperm plug and dorsal cap of spermatophores (Sp). Left: female copulated twice; note two layers of spermatophores (S). Males of different size produced differing amounts of plug material. Bouin's. 2·1.

as a site where sperm come in contact with the adhesive chorionic membrane. External fertilization is indicated.

7. Approximately two hours prior to ovulation, the abdomen is relaxed and the exopodites of the pleopods are extended laterally. Successful attachment of eggs was only obtained in females which were allowed to bury themselves in sand. Attachment was effected in less than 1·5 hours.

8. Summation of the period required for the usual cycles indicate an estimate of six months as a life-span for each of the two sexually mature instars.

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THE FEEDING HABIT AND THE DIGESTIVE SYSTEM OF *HYPERIA GALBA*

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ABSTRACT

Hyperia galba (Family Hyperiidae: Order Amphipoda) are found crowding in the sub-genital pouches of medusae which provide excellent shelter. According to Edward (1868), they are parasitical in nature. However, they can also survive independently outside the body of the medusa. The feeding appendages of *Hyperia*, especially the mandibles and maxillae, are strongly built and are provided with teeth and spines which suggest that the animal, perhaps, gets its nutriment by scrapping off the body of the medusa. The oesophagus of *Hyperia* is thickly chitinous. The stomach, unlike in other amphipods, is not divisible into cardiac and pyloric parts. The inner wall of the stomach is produced into paired dorso-laterals, lateral and ventro-lateral ridges. The lateral ridges are beset with fine bristles while the ventro-lateral are provided with thick spines and teeth for the trituration of food. The absence of the pyloric stomach which acts as a filter apparatus in other amphipods is also suggestive of its parasitic habit. The wide midgut is produced into a pair of anterior dorsal and two pairs of ventral caeca. The small rectum opens to the exterior through a narrow anus.

Hyperia galba Montagu (Family Hyperiidae; Suborder Hyperiidea) is an amphipod, commonly found to exist in the sub-umbrellar space of medusae. According to Edward (1868), they are also occasionally found living on fishes. Gould (1841) and Gosse (1853) reported that the animal is found in the sub-genital pouches of medusae. According to Hollowday (1948), they are present in the umbrella of jelly fishes, being visible through the semi-transparent tissue. They are found crowding in the sub-genital pouches which provide excellent shelter for them. Edward (1868) has given the parasitic nature of the animal. Hollowday (1948) has also described the habitat of *Hyperia* in some details.

However, the digestive system of no member of this family has been described. In this present account an attempt is made to discuss the feeding habit, mouth parts and alimentary canal of *Hyperia galba*.

MATERIAL AND METHODS

A few specimens of *Hyperia galba* were collected at Plymouth while some others were procured from the Marine Biological Station, Plymouth.

For studying the feeding appendages, the different mouth parts were directly mounted in a mixture of polyvenyl lactophenol and indigo carmine. It was found that in these preparations all the muscles had dissolved after some time and the appendages had taken a light pink colour.

For the detailed study of the alimentary canal, reconstruction drawings were prepared. A diagram of the entire animal was drawn on a sheet of graph paper with the help of a squared eye piece. The transverse sections of the same animal were set, according to the calculations, on the predrawn diagram of the animal. The different sections were also critically studied and the diagrams were drawn with the help of the camera lucida.

Different fixatives such as Bouin's fluid, Duboscq-Brasil, Zenker and Gilson's fixatives were employed. The sections, 8 microns thick, were stained with Mallory's triple stain, Heidenhain's

Azan stain, Mann's Methyl blue eosin and Heidenhain's iron-alum haematoxylin counterstained with orange G.

The Digestive System

The food is captured with the help of the mouth parts and antennae of the animal. The large mandibles help in the mastication of the food. Each mandible consists of the masticatory part, which is beset with a large number of chitinous teeth, the molar expansion with a few rows of tooth-like structures and the tri-articulatd palp. The two pairs of maxillae also help in the trituration of large food particles.

The alimentary canal of Crustacea has been studied by many workers but the gut of an amphipod has not been studied in detail. Sars (1867) was one of the earliest workers to refer to the armature of the foregut. Ide (1892) described briefly the gut of *Gammarus pulex*. Cussan (1904) in his memoir also described the alimentary canal of *Gammarus* only briefly.

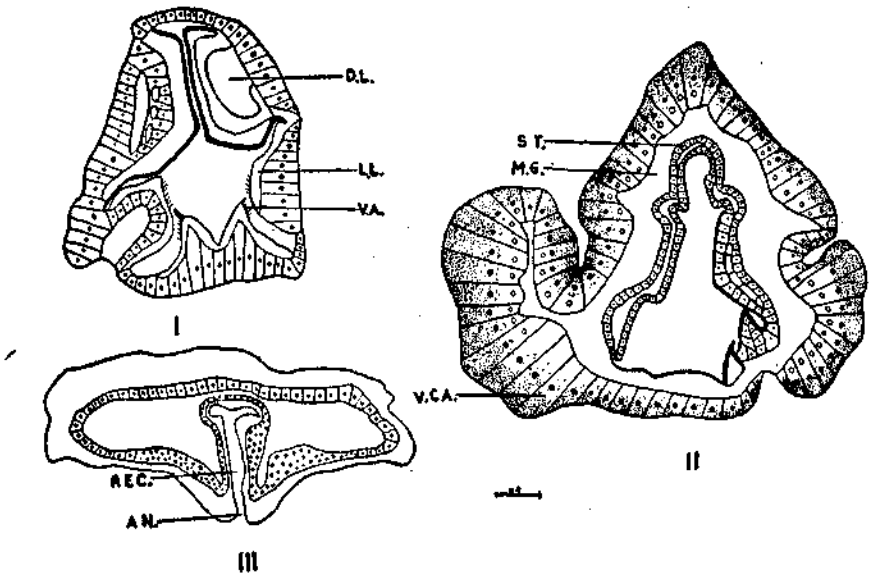

Fig. 1. Alimentary canal of *Hyperia galba*. (I) T.S. through stomach; (II) T.S. through midgut; (III) T.S. through anus. AN, anus; D.L., dorso-lateral ridges; L.L., latero-lateral ridges; M.G., midgut; REC., rectum; ST., stomach; V.A., ventral ridge; V.C.A., ventral caeca.

The alimentary canal of *Hyperia* consists of the foregut, midgut with hepatopancreatic caeca and the hindgut. The foregut and hindgut constitute the stomodaeum and proctodaeum respectively and are lined internally with a chitinous cuticle, while the midgut forms the mesenteron.

The foregut includes the mouth, oesophagus and stomach. The ventral mouth opens into the long, thickly chitinous oesophagus which opens dorsally into the stomach which does not extend forwards beyond the mouth. At the junction of the oesophagus and stomach are to be found a pair of very small ridges.

From the ventro-lateral wall of the stomach arise a pair of well-developed ridges (Fig. I) which are about 0·26 mm. long and 0·16 mm. high and extend backwards into the midgut upto the second thoracic segment. In the middle region of the stomach, these ridges shift more ventrally so that the central chamber of the stomach is divisible into a pair of narrow lateral and a single

broad ventral cavity. Each ridge is produced distally into a single long serrated tooth and a few fine bristles. The stomach of *Hyperia* unlike that of other amphipods such as *Orchestia* (Agrawal, 1964) is not divisible into cardiac and pyloric portions. The dorso-lateral wall of the stomach is produced into paired thickly chitinous dorso-lateral ridges (D.L.) which extend deep into the lumen so that the dorsal cavity of the stomach is reduced to a narrow streak. The cavity of the stomach is thus divided into a narrow dorsal chamber, the ventral chamber divided into three portions and a wide middle portion which is produced laterally into lateral ridges (L.L.) which also extend backward along the midgut. The lateral ridges bear a few fine bristles.

In the region of the second thoracic segment, the stomach passes into the midgut which in *Hyperia* is a very broad duct extending backwards upto the fifth abdominal segment. From the antero-dorsal margin of the midgut arise a pair of wide anterior dorsal ceaca which run forwards on either side of the stomach to end blindly opposite the mouth. From the antero-ventral margin of the midgut arise a pair of ventral caeca (Fig. I, II) which extend a short way forwards. They run backwards as very wide tubes which are lined with tall, vacuolated cells. In the region of the third thoracic segment, the ventral caeca divide into two pairs, a long narrow upper pair which extends as far as the middle of the first abdominal segment and a very small lower pair.

The small rectum is lined internally with the cuticle. It is dorso-ventrally flattened and opens to the exterior by a narrow ventral anus (Fig. 1, III).

Discussion

It is a well-established fact that the nature of the feeding mechanism and the character of structures concerned with the capture, manipulation and sorting of food are related to the kind of food taken. Many authors like Yonge (1928), Dennell (1933), Manton (1937) and Agrawal (1964) have examined crustacean feeding mechanism with this point of view.

The structure of the feeding appendages and the form of the gut may be expected to be related to the nature of the food taken. The size of the food is probably the most important single factor, when one seeks for correlation between structure and function of mouth parts and gut organisation.

Although *Hyperia* usually lives within the medusae, it is not certain if it is truly parasitic. Edward (1868) states, "I have seen that in the medusae they move their swimming feet and I have seen mandible and other mouth parts also opening and so were in the act of feeding." All the same, it can survive independently outside the body of the medusae. The guts of the animals examined by the author were found to be almost empty. The structure of the stomach of *Hyperia* is also in favour of the view that it is a partial parasite as the armature of the stomach is not so strongly built and is not produced into very strong plates as in other amphipods. Moreover, the fact that the stomach is not divisible into triturating cardiac and filtering pyloric stomach also points to its parasitic nature.

The ventral caeca in *Hyperia*, which are mainly concerned with the digestion of food (Agrawal, 1962), are not so well developed as in *Orchestia* (Agrawal, 1964) as they are parasitic in habit and feed on digested food material.

It can now be concluded that the character of the food governs to a great extent the construction of the mouth parts and the gut organisation.

Acknowledgement

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THE FEEDING APPENDAGES AND THE ALIMENTARY CANAL OF *CYAMUS OVALIS* (L.)

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ABSTRACT

Cyamus ovalis or whale louse (Family Cyamidae; Order Amphipoda) is an ectoparasite; its dorso-ventrally flattened body is fixed on the skin of whale by means of its strong appendages. It has been found that the mouth parts of the animal are very small in comparison to the body size. However, the mandibles and maxillae are strongly built with teeth and spines. The alimentary canal consists of the mouth, oesophagus, cardiac stomach, pyloric stomach, intestine and the rectum. The internal lining of oesophagus is thickly chitinous and is produced ventrally into a few very fine bristles. The chitinous inner wall of the cardiac stomach is provided with a median dorsal, paired lateral and a median ventral ridges. However, unlike other amphipods, the ridges are not provided with any teeth. The pyloric stomach is produced into a mid-ventral piece and paired ventro-lateral ridges. The midgut or intestine is provided with a single dorsal caecum and 2 pairs of ventral caeca. The hindgut or rectum of *Cyamus* opens to the exterior by a narrow ventral anus. The mucosa of the rectum is produced into a large number of villi. It seems probable that the parasite feeds on a liquid diet. As such the armature of the stomach is much simplified as compared to other amphipods such as *Orchestia, Corophium*, etc.

Cymaus ovalis, the whale louse (Family: Cyamidae; Order Amphipoda) is an ectoparasite; its dorso-ventrally flattened body is fixed on to the skin of whales by means of its strong legs. The animal is ectoparasitic on whale and is supposed to exist on a liquid diet by sucking the food through the mouth. The gut of a few specimens, when examined, was found to be empty.

For the present study, a few specimens of *Cyamus* were procured from the Natural History Museum, London. The different methods employed are the same as given in an earlier paper on *Hyperia*.

FEEDING APPENDAGES

The mouth parts of *Cyamus* are very small in comparison to its body size.

The paired mandibles (Fig. 1, MAND.) of *Cyamus* are poorly developed and are pyramidal in shape. The protopodite of the mandible includes the coxa and the basis. The masticatory part or coxal segment of the mandible includes the cutting edge or the incisor process which is provided with two sets of strong chitinous teeth and the molar expansion which is only slightly developed. In between the incisor and the molar expansion are present a few feathered spines. The palp is not present.

There are two pairs of maxillae. The first maxilla (Fig. 1, F.MAX.) which is tri-partite in most of the amphipods (Agrawal, 1962) does not have the basal lobe. The masticatory lobe is strongly built and bears seven teeth and a few fine spines. The uni-articulate palp is comparatively small and bears only a few small setae distally. The second maxilla (Fig. 1, S.MAX.) has a large outer lobe and a small inner lobe. The inner lobes of the two sides are united in the centre. Each inner lobe bears 2 long spines while the outer lobe bears a few long spines distally.

The two maxillipeds (Fig. 1, MAX.PD.) are fused by their protopodites to form a sort of lower lip. The protopodite consists of a large basal lobe which is provided with a few small spines,

The endopodite or palp is very well developed and has five joints. The last joint is claw-shaped. The palp is produced into a very large number of fine, tooth-like structures arranged in rows.

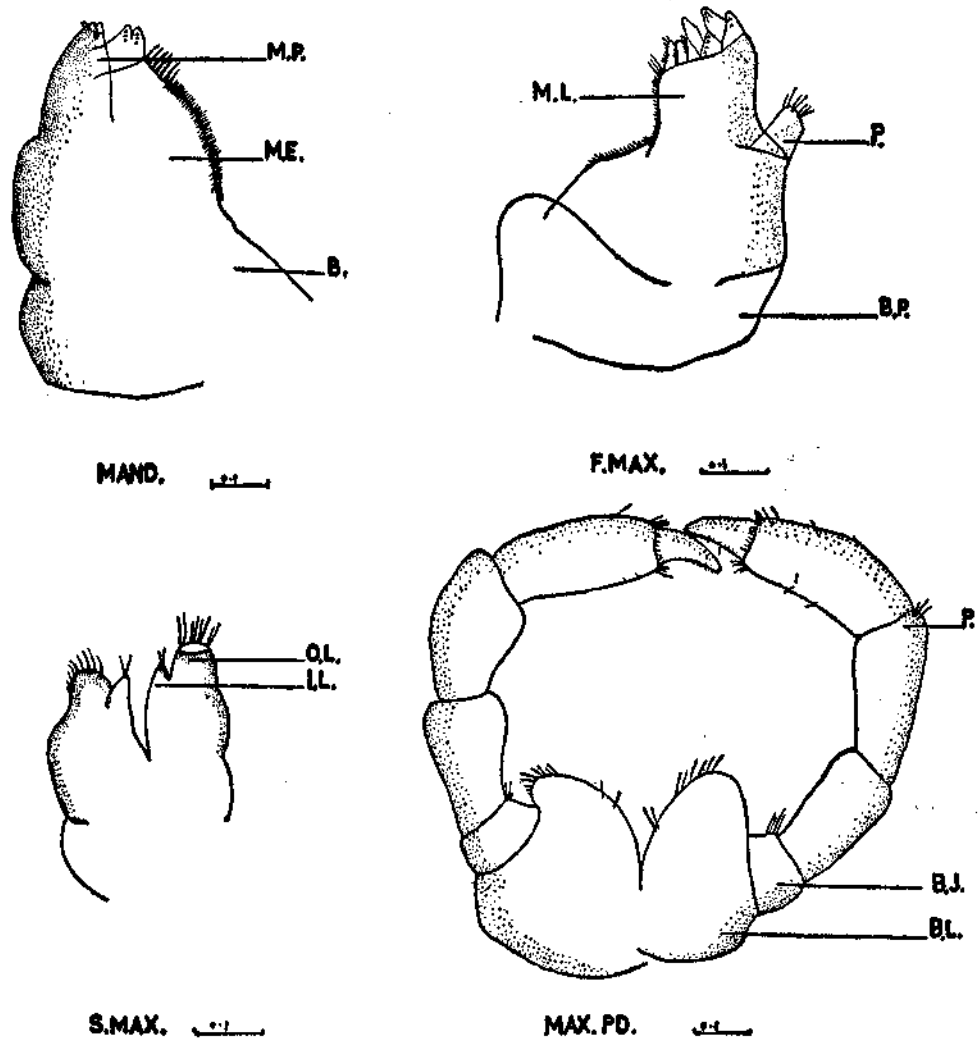

FIG 1. *Cyamus ovalis*. Mouth parts; B, body; B.J., basal joint; B.L., basal lobe; B.P., basal part; F. MAX., first maxilla; I.L., inner lobe; MAND., mandible; MAX. P.D, Maxillipeds; M.E., molar expansion; M.P., masticatory part; O.L., outer lobe; P., palp; S.MAX., second maxilla.

THE ALIMENTARY CANAL

The alimentary canal of *Cyamus* is simple in its internal armature due to its parasitic habit. The gut is a straight tube consisting of the foregut, midgut and hindgut.

The foregut consists of the mouth, oesophagus and stomach. The ventral mouth is a wide opening leading into a small oesophagus. The inner wall of the oesophagus is thickly chitinous

and is produced into a few very long bristles (Fig. 2, I, OE). Dorsally, the oesophagus opens into the wide stomach which does not extend forwards beyond the mouth. At the junction of the oesophagus and stomach are to be found well-developed oesophageal ridges (OE.A.) which are directed upwards into the stomach.

The stomach of *Cyamus* is not clearly marked off into the cardiac and pyloric chambers. The roof of the anterior part of the stomach is produced into a well-developed median dorsal ridge which is about 80 microns high. It projects upwards into the lumen of the stomach. A pair of thickly chitinous lateral ridges, about 9·35 mm. long and 90 μ wide also develop, which soon shift to the ventral side (Fig. 2, II) and divide the ventral cavity of the stomach into two grooves. Beyond the cephalothorax, the cardiac stomach passes into the pyloric stomach. From the floor of the pyloric stomach arises a mid-ventral piece (Fig. 2, III, M.V.P.), from the lateral borders of which arise paired wing-like processes, the ventro-lateral ridges (V.L.). Shortly, the mid-veentral piece (Fig. 2, III) is lost while the ventro-lateral ridges persist.

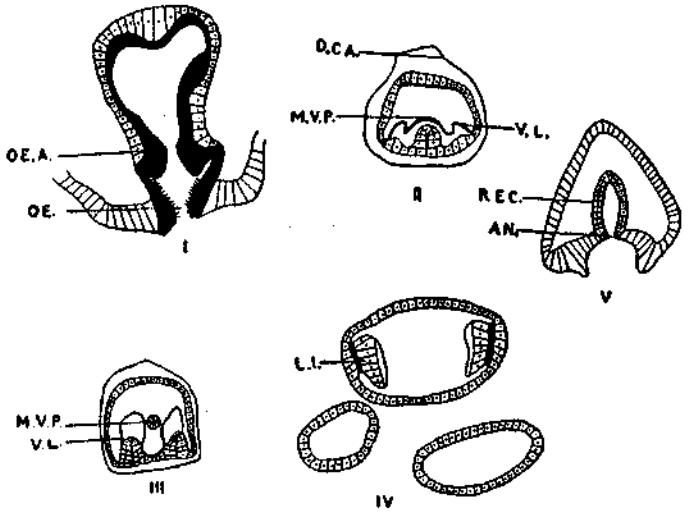

FIG. 2. *Cymins ovalis*. Alimentary canal. (I) T.S. through oesophagus; (II) and (III) T.S. through stomach; (IV) T.S. through rectum and (V) T.S. through anus.

AN, anus; D.CA., Dorsal caecum; L.I., lateral inpushing; M.G., midgut; M.V.P., mid-ventral piece; OE., oesophagus; OE.A., oesophageal ridge; RCC., rectum; V.L., ventro-lateral ridge.

The midgut is a long tube and bears a few caeca. The stomach extends a long way into the midgut, in the form of a horse shoe. The median dorsal caecum, arising from the roof of the midgut, runs forwards above the stomach as a narrow tube. The paired ventral caeca do not arise from the anteriormost part of the midgut as in other amphipods but from the middle of the midgut. Towards the beginning of the fifth segment, they divide into two pairs of caeca, an upper and a lower. The lower pair is comparatively small while the upper pair extends almost upto the end of the midgut.

The rectum is comparatively large; its inner wall is highly complicated. Anteriorly it gives off a pair of small pouches which are soon separated off and lost. In the same region, the inner wall produces a pair of cushion-like inpushings (Fig. 2, IV, L.I.). Posteriorly the inner wall of the rectum is produced into a larger number of villi. Ultimately, the rectum opens to the exterior by means of a ventral anus (Fig. 2, V, AN.).

Discussion

In *Cyamus ovalis* which lives on whales and perhaps lives on a liquid diet, the mouth parts are very small as compared to the body size, while in macrophagus forms like *Orchestia* (Agrawal, 1963), the mouth parts are well developed. However, the mandibles and maxillae are strongly built perhaps to scrape off the food from the body of the whale.

The functions of the crustacean stomach have been described by various authors. Huxley (1880) described the cardiac stomach as a filtering organ. Ide (1892) and Gelderd (1907) also credited the different plates of the cardiac stomach as auxiliaries to the mandibles. According to Tait (1917) and Nicholls (1931), the stomach of crustaceans has nothing to do with the mastication of food. However, the author is convinced that in the amphipods studied, the cardiac stomach is mainly concerned with the mastication of food while the pyloric stomach filters the food particles.

As circumstantial evidence in favour of this view, it may be noted that the internal armature of the stomach of *Cyamus* which is an ectoparasite is very simple. It has only poorly developed plates and ridges which are without any spines or teeth, while in the macrophagous forms like *Orchestia* (Agrawal, 1963), the stomach is provided with well-developed ridges which bear hooks and teeth. The oesophagus of *Cyamus* is very wide so as to suck the liquid food. The pyloric stomach which serves for filtering the food particles is also very simple in *Cyamus*. The ventral caeca which secrete the different digestive enzymes (Agrawal, 1963) are much smaller as the animal feeds on liquid and almost digested food.

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PRELIMINARY RESULTS OF THE AGE AND GROWTH STUDY OF THE MARKET CRAB (*CANCER MAGISTER*) IN CALIFORNIA: THE AGE AND GROWTH OF *CANCER MAGISTER* IN BODEGA BAY

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ABSTRACT

Age and growth of the market crab, *Cancer magister*, were determined from collections made in Bodega Bay, California, from June 1961 to December 1964. Instar sizes were also calculated from molting increments obtained from 91 crabs that molted in traps, suture-tagged crabs that molted and retained the tag, and trawl caught individuals obviously near molting which were held in live tanks until molting was complete. One year from metamorphosis the 1961 year-class was observed to be in the 8th, 9th, and 10th instars at an average size of 63·1, 81·6 and 94·2 mm. respectively. After 2 years instars 11 and 12 were observed with an average shoulder width of 133·1 and 151·9 mm. respectively; and after 3 years instars 11, 12 and 13 were observed with an average width of 134·7, 152·4 and 169·9 mm. respectively. Legal size (160 mm.) was attained by some of the crabs in the 12th instar after 2½ years; most of the crabs reached legal size in the 13th instar after 3½ years. Females grew at the same rate as the males from instars 1 through 11. Growth observed was faster than growth calculated; width-frequencies showed the crabs reached legal size in the 13th instar and calculations showed the crabs reached legal size in the 14th instar.

DETERMINATION of the age and growth of the market crab, *Cancer magister*, is complicated by the unusual process of molting. Because the animals are enclosed in a rigid external skeleton they are unable to increase gradually in size as most organisms do and growth is accomplished by a series of instars, each corresponding to a molt.

Tags attached to the exoskeleton are lost during molting. To eliminate this type of tag loss, a suture tag has been developed and tried on the blue crab *Callinectes sapidus*, the edible crab *Cancer pagurus* (Edwards, 1962), and the market crab *Cancer magister* (Butler, 1957). Initial tagging was with stainless steel wire, which was inserted in the line of separation of the carapace. A Peterson disc tag was attached to the wire. Growth data were provided, but returns were low from crabs that actually completed the molt with the tag attached. Recently Oregon and California biologists have attached plastic spaghetti tags in the same manner. Returns have again been low.

Market crab growth data have therefore been obtained from other sources, particularly by measuring molted crabs taken in traps, trawls, and beach collections. Width frequencies are also useful for determining the frequency of molting and the number of instars.

The first growth study of the market crab based on width frequencies and molting increment showed that, off British Columbia, Canada, male crabs attain maturity at 4–5 years and reach 165 mm. in width after 7–8 years, passing through 17 instars (MacKay and Weymouth, 1935). Sixteen instars were required for maturity of females, which mature at about the same age as males but rarely reach legal size.

Butler (1961) determined that British Columbia crabs reach instars 5 or 6 a year after hatching; after 2 years, instar 11 or 12; after 3 years most crabs are in the 13th; after 4 years instar 14 is reached; and generally at the end of 5 years crabs are in the 15th instar. British Columbia crabs enter the market at widths of 165 mm. in stage 14 after 4 years. Both sexes attain maturity in the

11th or 12th stages after 2 years. The maximum size and age of British Columbia crabs is 235 mm. and 8 years.

In Washington, Cleaver (1949) determined that sexes mature after 3 years and males attain a width of 169 mm. at the 14th or 15th instar after 4 years. Growth of females for the first 2 years was similar but subsequently the rate was uncertain.

In California, I have determined age and growth of the market crab from data obtained during 1961–64.

Methods

Monthly sampling was conducted in Bodega Bay using a 10 foot beam trawl with 1-inch mesh net. A ¼-inch liner was added to the cod end during May and June to collect the first instar. Twenty-minute tows were made in depths of 4 to 70 fathoms. All early instars were taken on sand bottom in water shallower than 12 fathoms (Fig. 1). Bodega Bay is open to the sea and data collected are assumed to represent ocean growth.

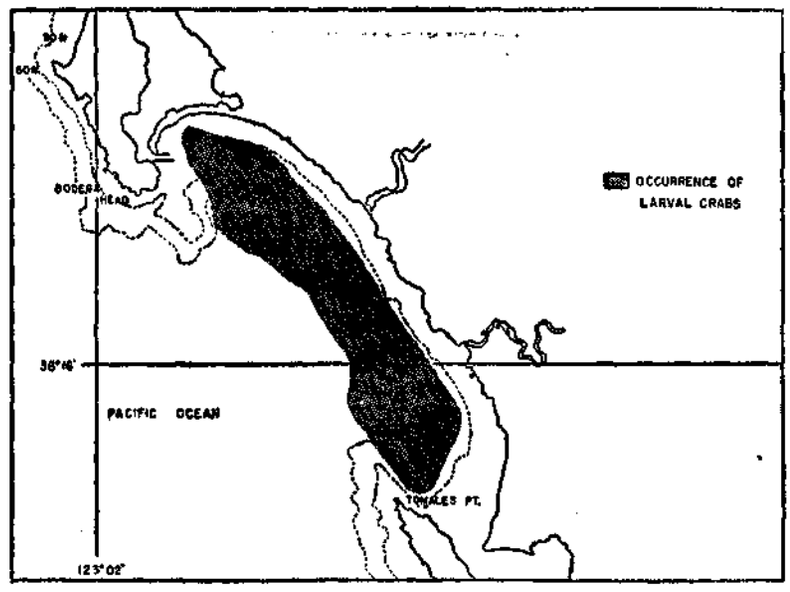

Fig. 1. Map of Bodega Bay showing the distribution of the early instars

Escapement from the small beam trawl increased as the crabs reached a larger size, and a gulf shrimp trawl with a 60-foot head rope was used beginning in January 1963. Crab traps with 1-inch stainless steel mesh were also used to collect crabs. Traps were baited with squid (*Loligo opalescens*) and rockfish (*Sebastodes*) carcasses and allowed to fish overnight at selected stations.

Sex was determined for crabs collected and width (caliper measurement in front of the 10th antero-lateral spine) was measured to the nearest millimeter. Width frequencies were summarized and plotted for each cruise. Sexes of the early instars were not recorded during our first cruise in Bodega Bay, but subsequently we determined sex for all crabs in the second instar and larger.

RESULTS

Calculation of Instar Sizes

Instar sizes were calculated from molting records of 91 crabs obtained in the San Francisco area from 1951–64: trapped soft-shelled crabs matched with molted shells; trawl-caught crabs obviously near molting (these were placed in tanks where ecdysis occurred within a day or two); and tagged crabs which had molted while at freedom and retained the tag. Instar sizes were also determined by width frequency samples as a comparison to the instar calculations. Insufficient data on females prevent calculation of female instar sizes.

TABLE I

Increase in size of male market crabs upon molting and percentage increase : Measurements include the 10th lateral spine and are in millimeters

Size	Numbers	Carapace width		Increment	
		Old	New	Absolute	Per cent.
5– 9	1	7·5	10·7	3·2	42·7
10– 14	5	12·4	16·3	3·9	31·5
15– 19	6	18·4	23·7	5·3	28·8
20– 24	4	21·4	27·8	6·4	29·9
25– 29	9	26·4	33·1	6·7	25·4
30– 34	2	31·9	39·1	7·2	22·6
35– 39	1	35·3	41·8	6·5	18·4
40– 44	..	..	..	..	..
45– 49	..	..	..	..	..
50– 54	2	51·4	65·9	14·5	28·2
55– 59	..	..	..	..	..
60– 64	..	..	..	..	..
65– 69	1	63·2	81·4	18·2	28·8
70– 74	..	..	..	..	..
75– 79	2	77·6	97·0	19·4	25·0
80– 84	..	..	..	..	..
85– 89	2	85·7	107·6	21·9	25·6
90– 94	1	90·0	113·6	23·6	26·2
95– 99	..	..	..	..	..
100–104	1	102·8	126·4	23·6	23·0
105–109	..	..	..	..	..
110–114	1	110·5	128·3	17·8	16·1
115–119	..	..	..	..	..
120–124	..	..	..	..	..
125–129	..	..	..	..	..
130–134	2	132·5	154·5	22·0	16·6
135–139	1	137·7	164·9	27·2	19·8
140–144	7	141·1	169·5	28·4	20·1
145–149	8	147·0	173·5	26·5	18·0
150–154	3	154·1	184·4	30·3	19·7
155–159	9	157·2	183·0	25·8	16·4
160–164	5	161·1	187·9	26·8	16·6
165–169	12	166·7	191·9	25·2	15·1
170–174	4	172·5	196·5	24·0	13·9
180–184	..	..	..	..	..
185–189	1	186·9	214·1	27·2	14·6

Molting records were obtained for almost all sizes and grouped by 5 mm. intervals (Table 1). Absolute growth-per-molt in the San Francisco area increased until the male crab reached a width of approximately 135 mm., after which, the growth increment remained relatively constant. The

smallest crabs exhibited high percentage of size increase, 42·7% after the first molt. Percentage of increment at molting decreased as the crabs grew larger (Fig. 2).

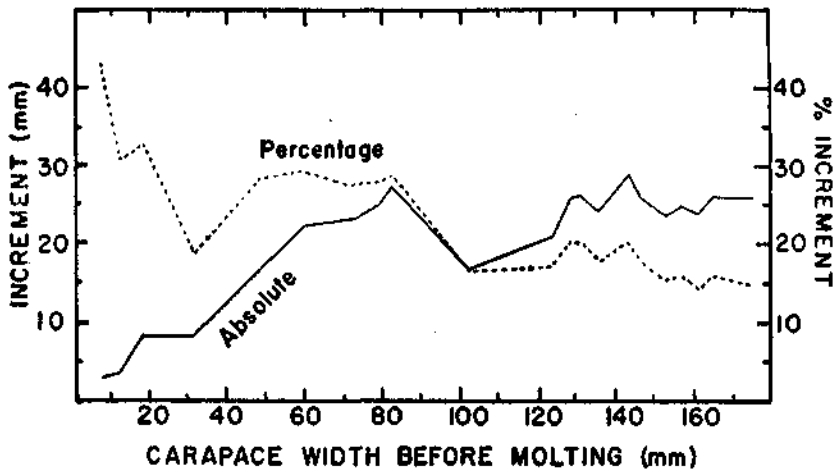

FIG. 2. Absolute and percentage increments at molting of male crabs

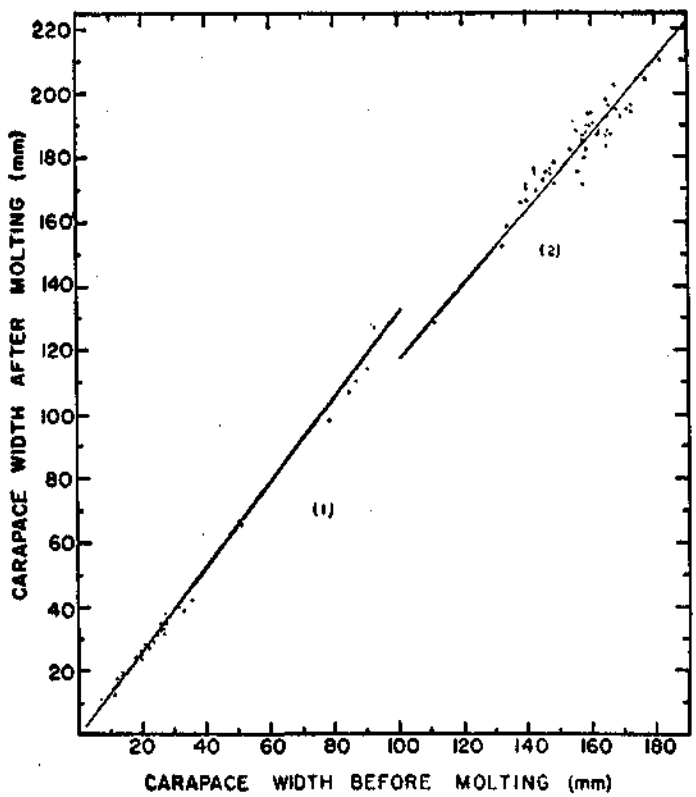

FIG. 3. Growth per molt of male market crabs with lines fitted by least squares

Butler (1961) showed that by plotting carapace width before molting against carapace width after molting and fitting two lines by least squares a point of intersection results that represents abrupt changes in growth rate. Butler concluded that the abrupt change in growth rate agrees well with size at maturity, and hence the change in growth rate is associated with sexual maturity. The intercept of 115·9 mm. obtained by Butler agrees well with an intercept of 102 obtained from Cleaver's data (1949). In every case, growth rate does change at or near sexual maturity.

In California, no male crab less than 93 mm. had mature spermatophores, but all males over 122 mm. did contain spermatophores. Straight lines were fitted by least squares for crabs up to the time of maturity, 7·5 to 102·8 mm. and during and after maturity, 110·5–186·9 mm. (Fig. 3). Carapace widths after molting were computed from the following formulas:

$$\text{For males } 7{\cdot}5\text{–}102{\cdot}8\text{ mm.:} \quad Y = 1{\cdot}284X - 0{\cdot}027 \tag{1}$$

$$\text{For males } 110{\cdot}5\text{–}186{\cdot}9\text{ mm.:} \quad Y = 1{\cdot}167X + 0{\cdot}059 \tag{2}$$

The point of intersect of these two lines was calculated to be ·72 by the method of Kurata (1960). No change in growth rate is indicated by this intersect as was noted by other investigators.

Instar sizes were calculated using these formulas. Starting with the 2nd post-larval stage at a carapace width of 12·2 mm. (observed size of the 2nd instar) equation (1) was used to calculate sizes through the 11th instar and equation (2) was used to calculate instar sizes 12–16. Calculated carapace widths are given in Table II. Instar growth in the Queen Charlotte Islands, British Columbia and off Central California is approximately equal. Instars 11 and 12 are slightly larger in California but subsequent growth is slower according to the calculations.

TABLE II

Comparison of computed widths of male Cancer magister *instars. Measurements include the 10th antero-lateral spines. Data for Washington, Southern B.C. and the Queen Charlotte Island from Butler* (1961). *Measurements in millimeters*

Instar Number	Central California	Washington	Queen Charlotte Isl.	Southern B.C.
1	7·5	5·7	6·9	5·2
2	12·2	9·4	10·0	7·4
3	15·6	12·5	13·8	9·7
4	20·0	16·8	18·5	13·4
5	25·7	23·5	24·2	18·2
6	33·0	30·4	31·1	24·0
7	42·3	37·2	39·6	31·5
8	54·3	47·2	49·9	41·0
9	69·7	59·8	62·5	52·5
10	89·5	72·8	77·9	65·7
11	114·9	90·6	96·6	80·5
12	134·1	113·4	119·5	95·8
13	156·6	138·4	146·9	112·6
14	182·8	165·9	176·2	130·0
15	213·9	(188)?	207·5	149·6
16	249·1	..	241·0	170·8

Age from Width-Frequency Data

To check growth calculations, determine frequency of molting, and to determine time spent in various instars, monthly sea cruises were made aboard the department research vessel *Nautilus*. Data from crab tagging cruises and pre-season surveys were also incorporated in the width-frequency graph. In all, 11,803 crabs were used in this study; these were collected by traps and trawl from March 1961 to October 1964.

Growth of Early Instars

The mating season of the market crab in California extends from late February to August. The eggs are spawned and carried by the female from October to February; females have been taken as late as May with eggs. Hatching occurs mainly in December, January and early February. Since the hatching period covers a considerable length of time, I have assumed January 1 as the mean birth date after having examined females for evidence of hatching eggs. The larval life extends over four months and consists of five zoeal stages and one megalop stage (Poole, 1966).

Megalops, taken on May 3, 1962, and May 9, 1962 from trap bouy lines, molted soon thereafter into first post-larval crabs. Four first instar crabs were obtained from these molts were 6·8–7·0 mm. wide, exclusive of spines. First post-larval crabs were also taken in trawl nets in May 1962. They were 6–8 mm. in width (Fig. 4). Post-larval crabs were not taken in the previous month's sampling, April 10–14. On June 18, 1962, crabs-of-the-year were found in the 1st, 2nd and 3rd post-larval stages with the greatest number in the 2nd instar. On June 3, 1961, crabs were also taken in the 1st, 2nd and 3rd instars with the 2nd most numerous. The earliest 2nd instar occurred in 1962 when most of the post-larval crabs taken on May 11 in the San Francisco area were in that stage. It appears that metamorphosis to the 1st instar occurs about the first of May. This is the date I used when calculating the age of crabs from the time of metamorphosis.

All sampling cruises in Bodega Bay yielded good catches of 1961 year-class crabs. Poor recruitment in several successive years made this group of crabs stand out in the width-frequency graph (*Figs.* 4 and 5).

Growth in Bodega Bay

A total of 11,803 crabs was measured during monthly cruises in this area: 5,946 males, 5,507 females, and 350 unsexed post-larval crabs. Early instars were so abundant that a sample of 50 was measured from each tow. After March 1962, all crabs taken were measured.

Data from monthly cruises were summarized and presented in Figs. 4 and 5. Carapace width measurements do not include spines due to the inconsistency of spine length and spine breakage.

The first cruise in Bodega Bay on June 3, 1961 produced an abundance of post-larval crabs, but we did not determine sex data from them. These were in three groups with modes at 7, 12 and 16 mm. (Fig. 4, A), obviously representing the 1st, 2nd and 3rd instars, with the 2nd the most prevalent. The mean sizes of these groups were calculated to be 7, 11·5 and 15·9 mm. respectively. The mean size of the observed instars by month for all the cruises was calculated (Table III). Average sizes of the larger instars were not determined for 1961 and therefore are not included in Table III. During the cruise at the end of June 1961, male crabs were taken in the 2nd, 3rd, and 4th instars with an average size of 11·0, 16·0 and 21·9 mm. respectively (Fig. 4 *b*). There was no cruise in July but a good collection in August showed well-defined modes at 16, 21 and 27 mm. for the 3rd, 4th, and 5th stage males respectively. On September 13, 1961, male crabs were in the 4th, 5th and 6th stages with modes at 21, 28 and 40 mm. (Fig. 4, D). The mean size of these instars was 20·6, 27·8 and 39·0 mm. respectivdly. In November, the group had progressed to the 5th,

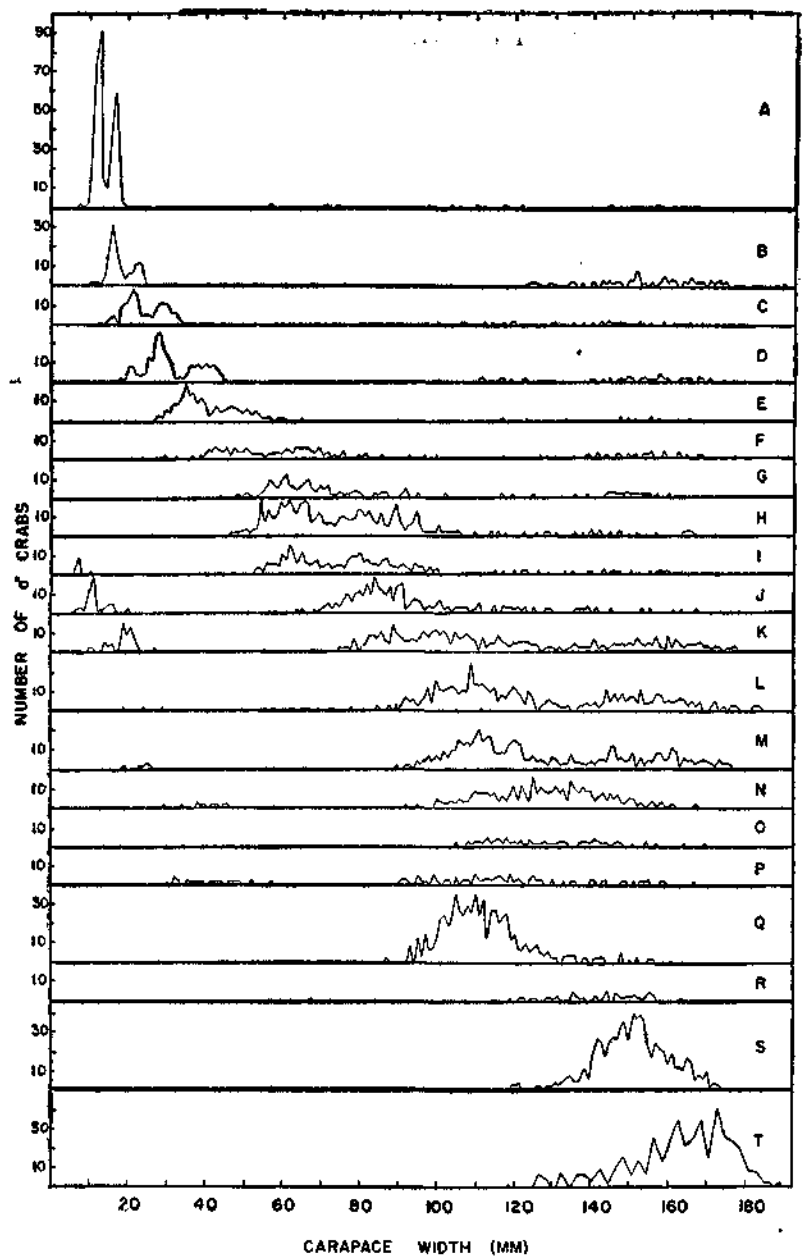

FIG. 4. Carapace width-frequency distributions of male crabs collected from Bodega Bay, California between June 3, 1961 and October 4, 1964: (A) June 3, 1961; (B) June 30, 1961; (C) August 16, 1961; (D) September 13, 1961; (E) November 15, 1961; (F) January 17, 1962; (G) March 14, 1962; (H) April 11, 1962; (I) May 7, 1962; (J) June 18, 1962; (K) July 18, 1962; (L) August 14, 1962; (M) September 12, 1962; (N) January 8, 1963; (O) February 5, 1963; (P) March 7, 1963; (Q) April 4, 1963; (R) May 8, 1963; (S) June 30, 1963; (T) October 4, 1964.

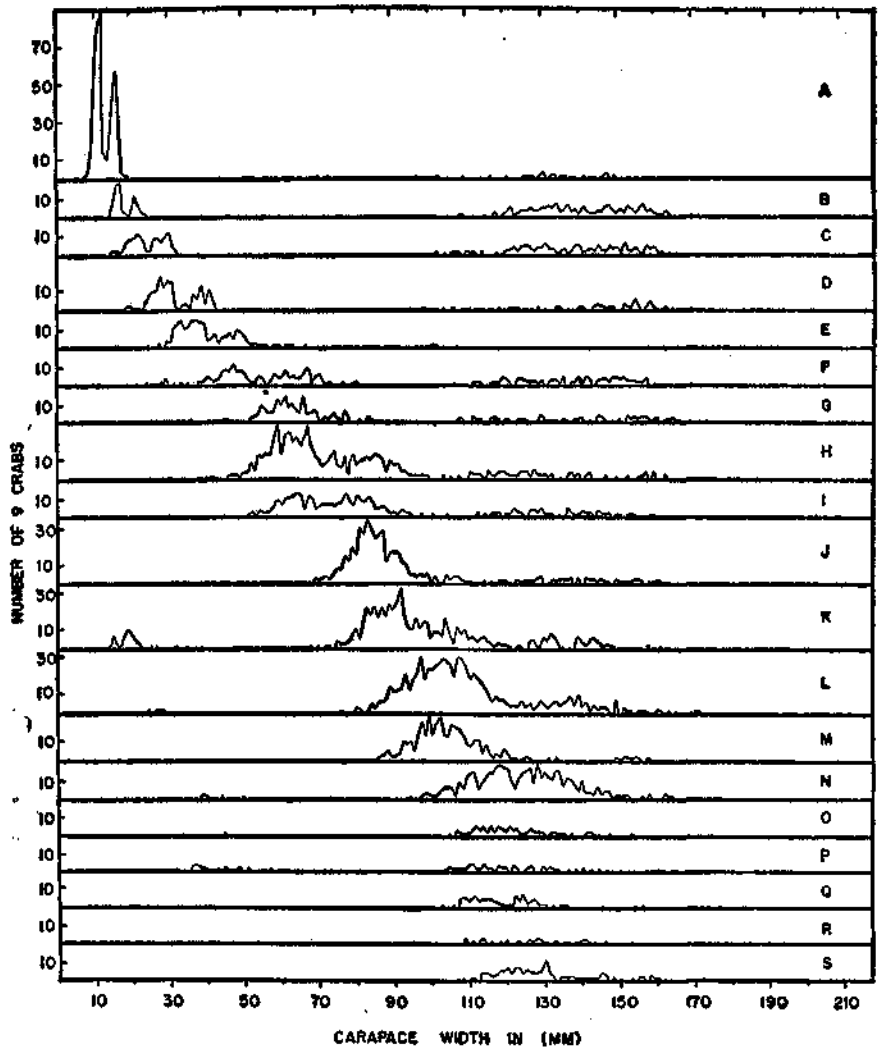

FIG. 5. Carapace width-frequency distributions of female crabs collected from Bodega Bay between June 3, 1961 and October 4, 1964: (A) June 3, 1961; (B) June 30, 1961; (C) August 16, 1961; (D) September 13, 1961; (E) November 15, 1961; (F) January 17, 1962; (G) March 14, 1962; (H) April 11, 1962; (I) May 7, 1962; (J) June 18, 1962; (K) July 18, 1962; (L) August 14, 1962; (M) September 12, 1962; (N) January 8, 1963; (O) February 5, 1963; (P) March 7, 1963; (Q) April 4, 1963; (R) May 8, 1963; (S) June 30, 1963.

6th and 7th instars with modes at 28, 35 and 47 mm. respectively (Fig. 4, E). The 8th instars was poorly represented at this time by a small number of individuals from 57 to 65 mm. The mean size of the 5th, 6th and 7th instars were 28·0, 35·6 and 47·5 mm. respectively. In January 1962, male crabs were taken in the 6th, 7th, 8th and 9th stages with an average size of 33·3, 46·9, 64·5 and 76·4 mm. respectively (Fig. 4, F). Modes of the larger instars were poorly defined and covered a much wider range than the early instars, instar definition becomes a problem at about the 10th stage. Male crabs taken in March were in the 7th, 8th, 9th and 10th stages with most in the 8th (Fig. 4, G). Mean size of the observed instars were 49·2, 63·3, 80·8 and 94·1 mm. respectively. The April cruise showed the 7th, 8th, 9th and 10th instars still were present with the majority of

the crabs in the 8th and 9th instars (Fig. 4, H). The average size of the instars were 49·1, 63·0, 83·0 and 96·8 mm. respectively. In May, the first signs of the 1962 year-class were noted when the 1st and 2nd instars were taken. The 1961 year-class was then in the 8th, 9th and 10th instars one year from metamorphosis (Fig. 4, I). Fifty per cent. of the 1961 crabs were in the 8th instar with an average width of 63·1 mm., 40·3 per cent. were in the 9th instar with an average width of 81·6 mm. and 9·7 per cent. were in the 10th instar with an average width of 94·2 mm. In June 1962, year-class crabs were in the 1st, 2nd, 3rd and 4th; the 1961 year-class was represented by the 8th, 9th, 10th and 11th instars with the 9th dominant (Fig. 4, J). In July, August and September, the 1961 year-class remained in the 9th, 10th and 11th instars with the 10th being prominent throughout the period. The 1962 year-class was represented by the 2nd, 3rd and 4th instars in July; by the 4th and 5th instars in August; and by the 4th, 5th and 6th instars in September (Fig. 4, K–M). By January 1963, the 1962 year-class had progressed to the 5th, 6th and 7th instars (Fig. 4, N) which averaged 29·0, 39·1 and 45·5 mm. in width. At the same time one year earlier, the 1961 year-class in instars 6–10 was predominantly in the 7th and 8th instars with a few individuals in the 10th; these averaged 33·3, 46·9, 64·5, 76·4 and 96·7 mm. respectively. Small samples in February and March of 1963 showed no change in the growth of either year-class (Fig. 4, O–P). The 1962 year-class continued to lag behind the 1961 year-class by at least two instars. In April 1963 bad weather again curtailed sampling except for one tow which yielded over 600 crabs (Fig. 4, Q). Most of these were 10th instars averaging 108·9 mm. in width. During January, the majority of the crabs had progressed to the 11th instar. This decrease in abundance of the 11th stage indicates that the larger crabs may have migrated from the sampling area. Although the May sample was too small for detailed analysis, a satisfactory sample was obtained in June in commercial crab traps (Fig. 4, S). Most crabs in this sample were soft, indicating a recent molt. They were 11th and 12th instars averaging 133·1 and 151·9 mm. in width respectively. Nineteen per cent. of the crabs in the 12th instar exceeded the California minimum legal size of 160 mm. at 2½ years of age. Examination of this group for mating marks during mating season of the preceding year revealed that a very small percentage of male crabs 1½ years old mate. Some of this group is therefore subject to commercial harvest prior to mating. Evidence indicates that no further molting occurred during the summer, thus preventing additional males from entering the commercial catch prior to mating. More than 700 of this group were tagged with the plastic suture tag in an effort to keep track of them.

No samples were taken until October 1964 when crabs of the 1961 year-class were in the 11th, 12th and 13th instars at an average width of 134·7, 152·4 and 169·9 mm. respectively (Fig. 4, T). Growth increments obtained from tagging, from crabs that molted in traps and from other sources reveal that aize increase from the 12th to the 13th instar is smaller than expected. Overlap and commercial harvest of a portion of the 12th instar the preceeding year obviously have an effect on the calculation of the size of the 13th instar. Evidence that this is the same group of crabs was obtained from tag returns from crabs tagged in July 1963 in Bodega Bay that were recovered in November of 1964 at the same location where released.

The majority of the crabs thus reach commercial size in 3½ years with a smaller portion reaching commercial size the following year at 4½ years of age and some possibly requiring 5½ years to reach legal size. A small portion of the crabs at San Francisco are taken prior to mating while a small portion goes through two or three mating seasons prior to harvest.

Larger instars have not been sampled in this study but it is felt from previous data that molting occurs about once a year with some of the crabs molting once in two years. Crabs molting from the 13th to the 14th stage increase 25–30 mm., from about 175–200 mm. in width. The carapace width of the largest crabs measured by our biologists was 226 mm. (240 mm. including spines). We believe this crab was a 15th instar which is probably the final instar occurring off Central California. Considering molting frequency, I estimate crabs of this size to be 6–7 years of age. Examination of male crabs for mating marks and shell fouling indicates that 10–15 per cent. of the male crabs retain their carapace for more than a year. Males reaching this size however are generally free of fouling and retain no mating marks. The maximum age of the market crab in California is no more than 8 years and is probably 7 years.

TABLE III

Number, size range, and carapace width of instars occurring in samples, Bodega Bay, California, 1961–64
(Widths in millimeters, exclusive of 10th spine)

Sample Date	Instar Number												
	1	2	3	4	5	6	7	8	9	10	11	12	13
3–6–1961													
No. Crabs	1	203	146										
Range	7–7	9–14	14–19										
Mean	7·0	11·5	15·9										
30–6–1961													
No. Crabs	0	3	81	40									
Range		10–12	14–19	19–24									
Mean		11·0	16·0	21·9									
16–8–1961													
No. Crabs	0	0	8	74	51								
Range			14–16	18–26	26–33								
Mean			15·2	21·1	29·3								
13–9–1961													
No. Crabs	0	0	0	21	123	71							
Range				18–22	23–33	33–44							
Mean				20·6	27·8	39·0							
15–11–1961													
No. Crabs	0	0	0	0	4	110	67	5					
Range					27–29	30–41	41–55	57–65					
Mean					28·0	35·6	47·5	59·0					
17–1–1962													
No. Crabs	0	0	0	0	0	3	55	53	16	3			
Range						30–37	39–55	57–71	71–86	93–100			
Mean						33·3	46·9	64·5	76·4	96·7			
12–3–1962													
No. Crabs	0	0	0	0	0	0	6	109	19	8			
Range							44–52	54–73	74–87	91–102			
Mean							49·2	63·3	80·8	94·1			
12–4–1962													
No. Crabs	0	0	0	0	0	0	10	225	155	42			
Range							42–52	53–74	74–92	92–106			
Mean							49·1	63·0	83·0	96·8			

8–5–1962														
No. Crabs	..	8	1	0	0	0	0	0	104	84	22			
Range	..	7–7	10–10						53–73	73–90	90–100			
Mean	..	7·0	10·0						63·1	81·6	94·2			
19–6–1962	..													
No. Crabs	..	5	32	6	1	0	0	0	14	181	31	21		
Range	..	6–8	10–13	14–16	20–20				65–75	75–97	97–111	114–129		
Mean	..	7·2	10·8	15·3	20·0				72·2	85·3	103·5	120·0		
19–7–1962	..													
No. Crabs	..	0	4	12	47	0	0	0	0	98	129	69		
Range	..		10–11	14–16	18–23					75–94	94–111	112–132		
Mean	..		10·5	14·9	20·3					86·5	101·7	119·3		
14–8–1962														
No. Crabs	..	0	0	0	2	1	0	0	0	24	221	89		
Range	..				19–24	29–29				78–95	95–116	116–134		
Mean	..				21·5	29·0				91·0	106·5	122·6		
13–9–1962														
No. Crabs	..	0	0	0	1	6	1	0	0	3	215	118		
Range	..				18–18	23–26	34–34			90–93	95–117	117–138		
Mean	..				18·0	24·7	34·0			91·7	108·3	124·5		
9–1–1963														
No. Crabs	..	0	0	0	0	1	7	2	0	2	80	190		
Range	..					29–29	34–43	45–46		92–95	100–117	117–141		
Mean	..					29·0	39·1	45·5		93·5	109·7	129·3		
7–3–1963	..													
No. Crabs	..	0	0	0	0	7	10	6	0	4	56			
Range	..					30–33	35–44	46–57		91–92	95–121			
Mean	..					32·0	39·0	49·8		91·5	109·3			
4–4–1963	..													
No. Crabs	..	0	0	0	0	0	0	0	0	46	507	69		
Range	..									87–98	99–122	122–144		
Mean	..									95·3	108·9	128·9		
30–6–1963														
No. Crabs	..				Commercial traps only used							61	629	
Range	..											119–139	139–172	
Mean	..											133·1	151·9	
2–10–1964														
No. Crabs	..				Commercial traps only used							50	91	270
Range	..											118–140	140–159	160–188
Mean	..											134·7	152·4	169·9
TOTALS														
No. Crabs	..	14	243	253	186	193	202	146	510	632	1314	667	720	270
Range	..	6–8	9–14	14–19	18–24	23–33	30–44	39–57	53–75	71–98	90–122	112–146	139–172	160–188
Mean	..	7·1	11·4	15·8	21·0	28·3	37·0	47·5	63·4	85·1	106·9	126·9	152·0	169·9

The mean sizes of the observed instars were plotted against stage numbers with ages in years of the instars indicated below to produce a growth curve (Fig. 6). Calculated instar sizes were also plotted for comparsion. Assignment of age to the instars is difficult because some larger instars are known to persist for more than 1½ years which would produce considerable overlap. The 15th stage was observed to be the final stage in a crab's life, while the 16th stage was calculated as the final stage. An extra stage is gained in calculations due to smaller molting increments used in calculations. Indications are that growth rate may vary from year to year especially where a strong year-class is preceded by a weak one.

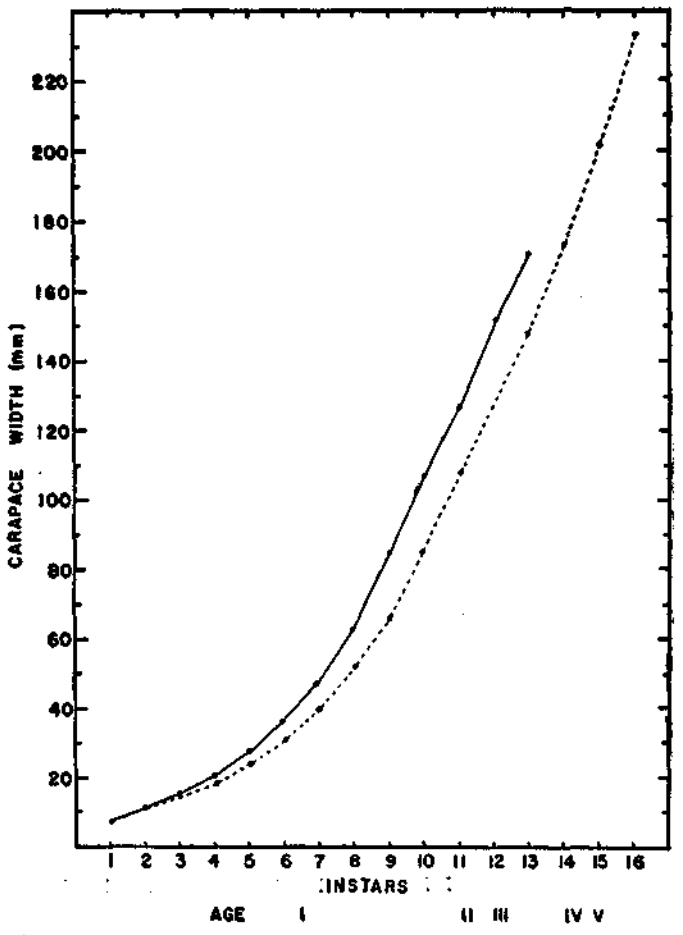

FIG. 6. Growth curve of male market crabs as determined from width-frequency distributions (solid line). Points are means of observed instars. Dotted line represents instar sizes calculated from molting increments. Measurements do not include spines.

Growth of Females

The ratio of males to females during the early instars was 1 : 1. Growth of the females from instars 1–11 (upto 135 mm.) was identical to that of males except in September when male growth exceeded female growth according to the width-frequencies obtained. In January however the females were again in the same stages as the males (Fig. 5, N). Samples of females after this date were not adequate to determine growth. Growth and activity are reduced after females reach maturity as evidenced by fouling of the shells and growth increments obtained by Butler (1961)

which show that the increment of molt decreased when the females reached maturity at about 100 mm.

Females mature in California at about 108 mm. in the 10th instar. According to this growth pattern most females are capable of producing fertilized eggs in the fall of their second year.

Discussion

Age and growth of the market crab has been determined in British Columbia by MacKay and Weymouth (1935) and Butler (1961) and in Washington by Cleaver (1949). Measurements of carapace widths were converted to include spines for comparison with these growth studies using the formula of Weymouth and MacKay (1936) for crabs smaller than 100 mm.:

$$Y = 0{\cdot}0715X - 0{\cdot}029$$

and for crabs larger than 100 mm. by the formula:

$$Y = 3{\cdot}727 + 0{\cdot}0465X$$

which was determined by measurement of 1,263 crabs in the San Francisco region from 1948–51 ranging in size from 105 to 215 mm. in width (H. G. Orcutt, personal communication).

The size of the 1st instar was observed by Butler to range from 5·8 to 8·0 mm. with a mode at 6·9 mm. and by Cleaver to range from 5 to 7 mm. which compares with values obtained by Waldron (1958) of 6·6–8·3 mm. and the present paper of 6·4–8·6 mm. The smallest values given for the 1st instar are 5·2 and 5·0 mm. which were obtained by MacKay and Weymouth (1935) for British Columbia crabs and by Cleaver (1949) for Washington crabs.

The 2nd instar was observed by Butler (1961) to be 10 mm. with a range from 8·2 to 12·5 mm. This is comparable to Cleaver's 2nd stage at 9·4 mm. and Waldron's observation of 10·4. In California, the 2nd instar averaged 12·2 mm. with a range from 9·6 to 15·0 mm. which is comparable to Waldron's observation of the 1954 year-class of 11·7 mm. The size of the 1st and 2nd instar was greatest in Bodega Bay and decreased to the north.

Comparison of the growth increments shows that those obtained in California are slightly smaller than those obtained in British Columbia under the same conditions. Growth calculations using these increments show that instar sizes in California, Washington and the Queen Charlotte Islands are very close from instars 1–8. Instars 9 and 10 are larger in California but the growth rate decreases after that due to the smaller increments obtained.

The growth rate in California is constant through all stages according to the increments obtained. Butler (1961) showed that growth rate changed at or near maturity in British Columbia and Washington. The constants calculated from the growth increments differ in the b value from those obtained by Butler, but the a values (Fig. 3) are quite similar.

Observations showed that at Bodega Bay crabs grow faster than in Washington or Oregon. After 1 year, 50% of the crabs were in the 8th, 40% in the 9th, and 10% in the 10th instars at widths of 63·1, 81·6 and 94·2 mm. respectively; after 2 years, the 11th and 12th instars averaged 133·1 and 151·9 mm. respectively; after 3 years, the 11th, 12th and 13th instars with the majority of the crabs in the 13th instar at an average width of 169·9 mm. Legal size (160 mm.) in California is attained by a small segment of the population in the 12th instar after 2½ years, and the majority are legal in the 13th instar after 3½ years. All in the 14th instar are legal. Thus, a year-class may contribute to the fishery for three years, starting with crabs 2½ years of age in the 12th instar. Observed growth was faster than calculated growth especially in the early instars. The 1st instar increased 60% in width in changing to the 2nd instar, as compared to 43% calculated from the molting increments.

Age and growth studies in Washington and British Columbia showed that legal size there is reached after 4 years by crabs in the 15th and 14th stages respectively. MacKay and Weymouth (1935) estimated that 8 years was required for a male crab to reach legal size. Butler (1961) points out that these estimates are much too high and are not in agreement with data presented.

Summary

1. Data are presented on the growth of the market crab in Bodega Bay, California, from June 1961 to December 1964.

2. Age and growth estimates are based on more than 11,000 market crabs collected over a 3-year period. Instar sizes were determined by width frequencies, calculated from growth increments obtained from recently molted crabs taken in traps and trawl, and from suture tag returns.

3. One year from metamorphosis the 1961 year-class was observed to be in the 8th, 9th and 10th instars with average sizes of 63·1, 81·6 and 94·2 mm. respectively; after 2 years instars 11 and 12 were observed with average widths of 133·1 and 151·9 mm. respectively; and after 3 years instars 11, 12 and 13 were observed with average widths of 134·7, 152·4 and 169·9 mm. respectively.

4. Legal size (160 mm.) was attained in Bodega Bay by some crabs 2½ year old in the 12th instar; most of the crabs reached legal size in the 13th instar after 3½ years. Crabs taken at 2½ years of age may be harvested prior to mating, but most crabs go through one mating season, and some through two, before being harvested.

5. Females were taken in equal numbers with the male during instars 1–11, and growth was the same as male growth during these instars. Subsequent female growth was not determined.

6. Observed growth was faster than calculated growth. Width frequencies showed the crabs reached legal size in the 13th instar and calculations showed the crabs reached legal size in the 14th instar.

7. The 1962 year-class lagged behind the 1961 year-class by 2 instars, indicating that growth may differ considerably from year to year.

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ANNUAL CHANGES IN POPULATIONS OF ANOSTRACA CRUSTACEA

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ABSTRACT

Fairy shrimp populations have been studied in certain temporary ponds in east-central Illinois and north-eastern Ohio since 1936. Annual fluctuations of occurrence were noted as follows: In Illinois 23 ponds were sampled over 6–18 consecutive years between 1936–1962. *Eubranchipus serratus* was common species. In Ohio 59 ponds were sampled 6–23 consecutive years between 1940–62. *E. vernalis* and *Chirocephalopsis bundyi* were the common species. No population remained at a constant level. Only 8 ponds had fairy shrimps every year during observations of 9–20 years. Four ponds had populations only 2–6 years over periods of 8–18 years. Generally, 1947 was the poorest and 1961 the best year for *E. serratus*; 1960 the poorest and 1962 the best year for *E. vernalis*; 1959 the poorest and 1955 and 1958 the best for *C. bundyi*. Indices of annual occurrence for each species, including relative abundance, show fortuitious fluctuations with no relationship among the 3 common species regarding either direction of change or time of peak years. The rainfall pattern with consequent water level in each pond seems to be one of the critical factors, but unknown factors governing the hatching of eggs appear to be most important in producting marked changes in annual occurrence.

For 21 years (1944–64) the life-history of *E. vernalis* was studied in a single temporary pond. First date of hatching, depending on presence of water, ranged from November 8 to April 18. Number of hatchings, depending on rising water level or refilling after water disappeared from complete evaporation or freezing, ranged from 1 to 7. Number of days present for a population which reached maturity ranged from 19 to 155 days. Growth rate per day ranged from 0·12 to 0·76 mm. Maximum size of individuals ranged from 13·0 to 28·0 mm. Date of last collection ranged from March 20 to May 25. Populations were terminated because pond was frozen to the bottom, pond was dried out, or because of high temperature and/or seasonal appearance of predators. Most of the variations were produced by weather factors: rainfall and/or thaw to fill the pond, amount and distribution of rainfall, complete evaporation or freezing solid of the water, and the seasonal march of temperature, with the seasonal development of predators.

FAIRY shrimp populations have been studied in certain temporary ponds in east-central Illinois and north eastern Ohio since 1936.[1] In Illinois, between the years 1936–62, 23 ponds were sampled from 6 to 18 consecutive years. *Eubranchipus serratus* was the common species with a few records of *E. vernalis* and *Chirocephalopsis bundyi*. In north-eastern Ohio 59 temporary ponds were sampled between 1940–62 for 6–23 consecutive years. *E. vernalis* and *C. bundyi* were common species and a single collection was made of *E. holmani*.

Samplings were made during the spring months of each year, particularly in the month of March. In addition, two ponds in Illinois and seven ponds in Ohio were sampled every week from the time of hatching until the population disappeared for certain years. Some of the annual records and life-history studies have already been published (Dexter and Ferguson, 1943; Dexter and Sheary, 1943; Dexter, 1943, 1946; Dexter and Kuehnle, 1948, 1951; Dexter, 1953, 1956).

In determining relative abundance the following method was used. With a common dip net samples were taken throughout each pond. If shrimps were captured with each sweep of the net and with occasional large numbers of specimens, the population size was designated "abundant". If specimens were taken with nearly every sweep of the net, but without high counts,

[1] Between 1956–62 this study was supported by the U.S. Atomic Energy Commission, Contract No. AT (11-1)-411.

TABLE I

Fluctuation of Anostraca populations—East-Central Illinois—1936–62

Pond Number	36	37	41	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	Station Index
V 1	..	A	..	A	D	O	R	C	C	N	S	C	A	D	D	A	C	R	A	C	A	N	7·1
V 2		..	..	..	..	..	..	..	..	..	..	..	N	D	D	O	R	O	R	O	C	O	2·3
C 1	..	N*	O	O	O	O	D	O	D	D	..	..	..	..	..	..	..	..	..	..	..	..	(1·0)*
C 2	..	N*	O	D	O	S*	O	R*	C*	R*	S*	S*,R	N*	D	D	C*	D	D	R*	D	O	flooded	(3·3)*
C 3	..	R*	O	D	R*	O	O	O	S*	O	O	O	O	D	D	R*	D	D	R*	D	O	flooded	0.9*
C 4	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	R	A	N	C	R	A	6·3
C 5	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	D	D	S	O	D	O	1·3
C 6	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	D	A	S	C	A	C	8·0
C 7	..	O	..	..	A	S	O	C	A	R	S	C	N	D	N	A	D	C	R	R	C	O	5·8
C 8	..	A	A	S	A	C	O	A	A, R†	R	N	A	..	..	..	..	..	..	..	..	..	..	7·3
C 9	..	C	C	D	C	N	O	C, R†	A	C	S	D	..	..	..	..	..	..	..	..	..	..	6·7
C 10	..	A	C	O	N	D	D	S	C	N	..	..	..	..	..	..	..	..	..	..	..	..	6·0
C 11	..	A	C	O	N	N	O	C	C	A	..	..	..	..	..	..	..	..	..	..	..	..	6·2
C 12	..	C	N	O	C	R	N	S	C	C	..	..	..	..	..	..	..	..	..	..	..	..	5·6
C 13	..	N	S	O	A	R	S	N	C	O	..	..	..	..	..	..	..	..	..	..	..	..	4·0
C 14	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	O	R	C	O	C	C	N	3·4
C 15	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	C	A	O	D	N	O	4·8
C 17	..	A	O	O	C	C	N	A	A	A	..	..	..	..	..	..	..	..	..	..	..	..	6·9
C 18	..	A	S	N	A	N	S	N	A	A	..	..	..	..	..	..	..	..	..	..	..	..	7·3
C 19	..	A	R	A	A	N	O	N	A	A	..	..	..	..	..	..	..	..	..	..	..	..	7·1
C 22	..	N	S	..	C	C	O	N	R	R	..	..	..	..	..	..	..	..	..	..	..	..	4·5
C 23	..	N	S	..	C	O	O	O	O	R	..	..	..	..	..	..	..	..	..	..	..	..	2·5
C 24	..	O	O	—	O	O	O	R	R	O	..	..	..	..	..	..	..	..	..	..	..	..	0·5
Annual Index (*E. serratus*)	7·4	4·8	3·3	7·8	4·3	1·7	5·9	7·4	5·4	4·5	8·7	7·3	..	6·0	5·0	4·5	8·0	3·5	4·3	8·6	3·8	

A = 10
C = 8
N = 6
S = 4
R = 2

$$\frac{A10 + C8 + N6 + S4 + R2}{\text{Total Number}} = \text{Index Number}$$

Average Index = 5·6

* = *Eubranchipus vernalis;* † = *Chirocephalopsis bundyi;* all others *E. serratus.*

A = abundant; C = common; N = numerous; S = scarce; R = rare; D = drained or dry.

TABLE II

Fluctuation of Anostraca populations—Portage County, Ohio—1941–62

Pond Number	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	Station Index
P 7	..	A	A	A	C	C	C	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	9·0
P 8	..	O	O	O	O	C	R	C	O	N	C	A	A	N	A	A	N	O	N	C	C	C	C	5·5
P 17	..	O	A	R	N	A	R	O	A	C	R	R	N	C	A	R	C	A	N	R	O	O	O	4·7
P 18	..	A	A	R	S	A	O	R	C	A	A	R	C	C	N	S	A	A	C	O	O	A	A	6·5
P 23	..	O	O		O	R	O	O	R	N	C	..	..	..	..	..	..	..	..	..	..	..	..	..	2·0
P 30	..	C	O	O	R	N	O	O	O	N	C	..	..	..	..	..	..	..	..	..	..	..	..	..	3·0
P 37	..	R	O	O	O	N	O	O	R	O	R	..	..	..	..	..	..	..	..	..	..	..	..	..	1·2
P 40	..	O	O	O	N	R	O	O	O	O	O	O	R	N	O	..	..	..	..	..	..	..	..	..	1·1
P 42	..	O	O	100 Intro.	O	R	O	O	R	S	A	R	R	..	..	..	..	..	..	..	..	..	..	..	2·4
P 43	..	O	N	A	A	A	A	R	C	A	A	O	O	O	C	S	C	C	A	A	O	A	C		6·5
P 50	..	N	O	O	R	R	O	R	R	N	N	..	..	..	..	..	..	..	..	..	..	..	..	..	2·4
P 54	..	O	O	D	O	C	A	O	R	O	R	..	..	..	..	..	..	..	..	..	..	..	..	..	2·4
P 55	..	O	O	O	N	C	O	O	C	O	N	..	..	..	..	..	..	..	..	..	..	..	..	..	2·8
P 58	..	O	O	O	A	A	O	A	A	N	C	..	..	..	..	..	..	..	..	..	..	..	..	..	5·4
P 79	..	A	C	S	A	C	R	N	N	N	R	..	..	..	..	..	..	..	..	..	..	..	..	..	6·2
P 80	..	R	N	O	A	A	O	N	N	C	S		..	..	..	..	..	..	..	..	..	..	..	..	5·2
P 88	..	..	..	A	A	A	N	N	N	A	A	A	A	R	N	A	A	A	A	A	A	N	A		8·6
P 89	..	..	..	C	A	A	R	O	R	O	R	O	O	D	N	C	D	D	D	R	R	A	C		4·4
P 90	..	..	..	..	O	A	O	O	R	S	C	..	..	..	..	..	..	..	..	..	..	..	..	..	3·4
P 91	..	..	..	..	S	A	R	O	R	O	O	..	..	..	..	..	..	..	..	..	..	..	..	..	2·6
P 92	..	..	..	..	C	C	C	O	S	D	O	O	O	S	O	O	O	O	O	O	N	D	D		2·2
P 93	..	..	..	..	..	O	R	O	O	O	O	R	N	D	N	R	A	C	D	C	O	D	D		3·1
P 95	..	..	..	..	..	A	D	O	N	O	O	R	R	O	C	O	O	O	O	R	O	A	C		2·8
P 96	..	..	..	..	..	A	O	A	A	S	A	N	C	O	O	O	..	..	..	..	..	..	..	..	5·3
P 104												C, R*	D	R, R*	C, A*	N, A*	N, A*	A*	R	O	N, S*	A, R*	(5·0)*, 4·8	
P 105																A*	R*	A*	C*	O	D		(6·0)*	
P 106																A*	O	A*	C*	A*	A*	A*	(8·3)*	

* = *Chirocephalopsis bundyi;* all others, *Eubranchipus vernalis.*

A = abundant; C = common; N = numerous; S = scarce, R = rare; D = drained or dry.

TABLE III

Fluctuation of Anostraca populations—Stark County—1940–50

Pond Number	40	41	42	43	44	45	46	47	48	49	50	Station Index
C2	...	...	..	R	C	A	C	D	R	C	C	C	6·8
C3	...	...	...	S	R	R	O	O	O	R	O	C	2·0
C6	..	..	...	A	C	N	N	O	R	C	C	A	6·4
C7	...	A	A	A, R†	C	A	A, R†	R	C	C, R†	N	C	8·2, (0·5)†
C8	...	C	C	O	C	A	C	N	S	N	N	S	6·2
C9	...	...	...	A	C	N	N	C	O	R	N	N	5·8
C10	..	...	...	N	R	O	R	S	O	O	O	S	2·0
C11	...	...	...	N	N	S	S	R	R	O	A	C	4·7
C12	...	...	...	N	S	N	N	R	O	R	A	A	5·1
C13	..	..	...	...	C	A	A	A	O	S	N	A	7·3
C14	..	...	...	...	...	R	N	S	O	O	O	A	7·1
C15	..	..	...	...	...	O	O	R	O	O	O	S	0·9
C16	..	..	..	...	...	...	C	A	O	R	N	C	5·7
C17	..	..	...	...	O	O	R	R	O	O	O	O	0·5
C18	..	..	..	C	C	O	N, R†	S	S	C, R†	C	C, R†	6·0, (0·7)†
C19	..	..	..	..	..	..	C	C	N	A	A	A	8·7
C21	..	..	..	..	..	..	S, R*	A	O	S	O	D	3·6, (0·4)*

* *Eubranchipus holmani* ; † *Chirocephalopsis bundyi*; all others *E. vernalis.*

A = abundant; C = common; N = numerous; S = scarce; R = rare; D = drained or dry.

they were recorded as "common". When only half of the sweeps of the net captured specimens the population was called "numerous". If only one-fourth of the sweeps captured specimens, the population was considered "scarce", and if only a few specimens were taken in the total sample, it was considered "rare". A simple and arbitrary formula was devised to give an annual index for each county or area studied and a station index for annual and station comparisons. An index is computed separately for each species. Results are given in Tables 1–4. The formula follows:

$$\frac{\text{No. A} \times 10 + \text{No. C} \times 8 + \text{No. N} \times 6 + \text{No. S} \times 4 + \text{No. R} \times 2}{\text{Total No.}}$$

I. Annual Fluctuations in the Fairy Shrimp Populations of Certain Ponds in Illinois and Ohio, 1936–62

In east-central Illinois, *E. serratus* showed fortuitous fluctuations over a period of 21 years of field observations. The average annual index was 5·6. The year 1961 proved to be the best year with an index of 8·6, while 1947 was the poorest year with an index of 1·7. High peaks were reached in 1936, 1945, 1949, 1958 and 1961. Low levels were recorded in 1941, 1947, 1959 and 1962. A pasture pond (C8) was the best habitat with a station index of 7·3, while a railroad-fill pond (C24) was the poorest habitat with a station index of 0·5.

TABLE IV

Fluctuation of Anostraca populations—Summit County—1940–62

Eubranchipus vernalis

Pond Number	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	Station Index
S 1 ..	A	A	N	C	A	A	C	N	A	C	C	..	..	..	..	..	..	..	..	..	..	..	..	8·5
S 2 ..	A	O	A	O	N	A	N	O	N	O	C	R	R	S	N	O	A	A	O	C	O	A	C	5·0
S 3 ..	A	A	C	R	O	R	O	R	N	S	R	..	..	..	..	..	..	..	..	..	..	..	..	4·2
S 4 ..	..	C	C	O	O	N	O	C	R	O	A	..	..	..	..	..	..	..	..	..	..	..	..	4·2
S 5 ..	..	C	S	R	R	A	C	N	N	A	A	..	..	..	..	..	..	..	..	..	..	..	..	6·6
S 11 ..	..	A	N	N	A	A	O	C	N	C	C	..	..	..	..	..	..	..	..	..	..	..	..	7·2
S 12 ..	..	O	C	S	S	A	C	C	N	N	C	..	..	..	..	..	..	..	..	..	..	..	..	6·2
S 14 ..	..	A	A	A	R	A	A	R	A	C	A	..	..	..	..	..	..	..	..	..	..	..	..	8·2
S 18 ..	..	..	A	N	A	A	A	A	C	C	A	S	S	D	N	A	..	..	..	..	..	..	..	7·6
S 24 ..	..	..	..	..	..	..	..	..	..	..	C	C	C	O	O	O		..	..	..	..	..	..	4·0
S 25 ..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	R	C	O	C	A	S	O	C	D	4·4
Index—*E. vernalis* Port., Stark, Summit Co.	9·6	4·7	5·1	4·3	4·8	7·0	3·7	4·4	4·6	4·8	6·4	3·3	4·6	3·1	5·1	4·1	6·2	6·4	5·5	4·7	1·7	7·6	7·7	Average 5·2

Chirocephalopsis bundyi : Geauga County—1950–62

Pond Number	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	Station Index
G 1 ..	..	..	..	..	..	..	..	..	..	..	A	N	R	R	A	A	A	A	A	C	A	A	A	8·3
G 2 ..	..	..	..	..	..	..	..	..	..	..	R	O	A	A	O	A	A	S	A	O	S	A	A	6·1
G 3 ..	..	..	..	..	..	..	..	..	..	..	..	..	R	O	S	A	C	R	A	O	S	A	A	5·5
G 6 ..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	A	A	A	O	C	A	A	8·3
Index—*C. bundyi* Portage, Geauga Co. ..	..	..	..	..	..	..	..	..	..	..	6·0	3·0	4·0	4·0	4·0	10·0	9·7	5·4	10·0	2·6	5·1	9·0	8·7	Average 6·3

TABLE V

Life-history of Eubranchipus vernalis *in Pond P* 88, 1944–64

Year	Date of first collection M.–D.	Date of last collection M.–D.	No. of days present	No. of hatchings	Average growth per day mm.	Maximum size	Date of first eggs M.–D.	Cause of termination	Temperature at first collection	Temperature at last collection
1944	4–11	5–13	32	1	0·48	..	4–29	Temp.	..	21·7
1945	2–24	4–22	58	3	0·31	..	3–26	Predators	5·0	10·0
1946	1–12	3–15	63	2	0·19	..	3–15	Predators	4·0	12·2
1946	3– 2	4–20	49	..	0·25	..	4– 5	Predators	5·0	16·0
1947	1–12	5–25	133	2	0·19	22·0	4–27	Temp.	0.0	19·2
1948	2–22	4–25	64	3	0·37	26·0	3–28	Temp.	0·5	19·5
1948–49	12–19	12–19	..	..	..	1·5	None	Frozen	0·5	0·5
1948–49	1– 2	5– 1	120	3	0·25	22·0	3– 6	Predators	0·0	16·0
1949–50	12–19	5– 7	140	Continuous to 2–19	0·18	28·0	3–12	Predators	..	15·5
1950–51	12– 3	2–25	85	4	0·20	17·8	..	Predators	4·0	2·5
1950–51	1– 7	4–22	105	..	0·20	28·0	3–17	Predators	1·0	13·0
1951–52	11– 8	3–11	125	6	0·18	26·0	1– 1	Predators	3·0	6·5
1951–52	11–24	4–26	155	..	0·14	27·0	1–27	Predators	5·0	15·0
1952–53	1–18	1–24	7	7	0·07	1·5	None	Dried	6·0	4·5
1952–53	3– 8	3–20	13	..	0·47	7·0	None	Dried	1·0	14·0
1954	4–18	5–21	34	2	0·76	16·5	5– 6	Temp.	13·0	21·0
1955	1– 8	1– 8	..	2	...	..	None	Dried	1·0	1·0
1955	3– 5	4–29	56	..	0·48	22·5	4– 1	Temp.	6·5	19·0
1955–56	11–16	12–24	39	5	0·10	5·6	None	Dried	0·0	10·0
1955–56	1–29	1–30	2	..	..	1·5	None	Dried	0·0	...
1955–56	2–12	5– 5	84	..	0·21	21·0	4– 1	Temp.	3·0	17·0
1957	1–26	4–27	92	3	0·25	27·5	3–15	Temp.	2·0	26·0
1957–58	11–14	2–11	90	6	..	15·5	..	Frozen	10·0	0·0
1957–58	3– 2	5– 4	64	..	0·19	15·0	4–19	Predators	5·0	15·0
1959	1– 2	1– 5	3	3	..	..	..	Frozen	0·0	0·0
1959	1–24	5– 2	99	..	0·20	23·0	3–15	Temp.	0·0	24·0
1959–60	12– 1	4–24	146	1	0·12	23·0	4–16	Temp.	1·0	25·5
1961	2–18	5–14	88	2	0·25	24·0	4–23	Predators	10·0	20·0
1961–62	11–25	11–25	1	2	..	1·0	None	Dried	0·0	0·0
1961–62	3– 3	4–29	58	..	0·19	14·0	..	Predators	0·0	20·0
1963	3–10	5– 4	56	1	0·21	13·0	4– 6	Predators	3·0	21·0
1964	3–5	3–20	16	2	..	3·0	None	Dried	2·0	0·0
1964	4–22	5–10	19	..	0·73	17·0	5– 5	Predators	..	22·0
	Median	Median	Average	Range	Average	Average Adult	Median		Average	Average
	Jan. 8	May 1	84	1–7	0·28	21·8	April 1		3·5	18·5

In north-eastern Ohio *Eubranchipus vernalis* was the most common and widely distributed species. In Geauga County *Chirocephalopsis bundyi* was the common species and it was found by itself in two ponds in Portage County. In a swamp pond of Portage County both of these species have been collected together. At first *E. vernalis* was the more abundant. Later *C. bundyi* became more abundant. Finally *E. vernalis* returned as the more abundant species over a period of eleven years. In Stark County *E. vernalis* was abundant and widely distributed, but on two occasions *C. bundyi* and on one occasion *E. holmani* were found mixed with a population of *E. vernalis*.

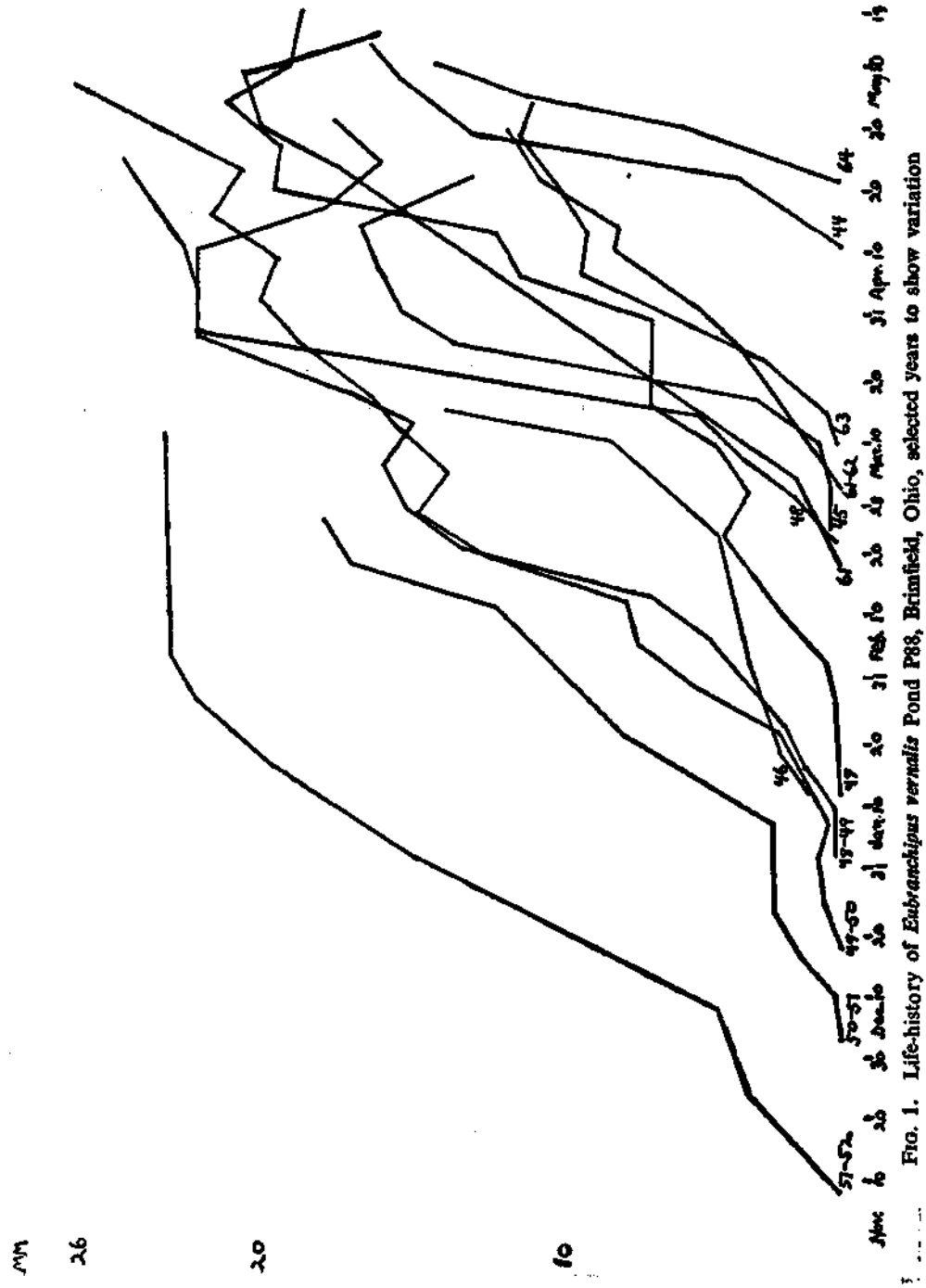

FIG. 1. Life-history of *Eubranchipus vernalis* Pond P88, Brimfield, Ohio, selected years to show variation

E. vernalis in Portage, Stark and Summit Counties had an average annual index of 5·2. The year 1962 proved to be the best for this species with an index of 7·7; 1960 was the poorest year with an index of 1·7. High peaks were registered in 1945, 1950, 1957, 1961 and 1962. Low levels were recorded in 1946, 1951, 1953, 1955 and 1960.

A pasture pool, pond P88 in Portage County, has proved to be the best habitat for this species. The station index was 8·6 (An analysis of annual fluctuations in this pond together with variations in the life-history of this species from year to year are given later in this paper). An impounded rivulent, pond P40 in Portage County, was the poorest habitat with a station index of 1·1.

Ponds examined in Geagua County contained only *Chirocephalopsis bundyi*. The annual index of occurrence averaged 6·3. Peak years were 1955, 1956, 1958 and 1961 with an index between 9·0–10·0. The year 1959 was the poorest with an index of 2·6. Ponds in woods seemed to be the best habitat, with an average index of 8·3.

All three species of Anostraca Crustacea included in this study underwent fortuitous fluctuations with no relationship among the species. This would indicate there is no common environmental factor affecting population size and frequency of occurrence. The year 1951 was rather poor for all species, and 1961 was rather favorable for all of them, but this could be merely coincidence. No population remained at a constant level for more than a few years. Only eight ponds had shrimps every year over a period of 9–20 years. Four ponds had populations for only 2–5 years over periods of observations ranging 8–18 years. Seven ponds contained two species living together, but in only one pond were both species common and the species in that pond had a reversal of ratio twice during the term of this study. Rainfall patterns with consequent water levels apparently are important factors in determining the annual occurrences of fairy shrimps, but unknown factors governing the hatching of eggs may be of greatest importance. It was noted that the range of fluctuations and the pattern of fortuitous fluctuations were the same before and after the advent of radioactive fallout.

II. Annual Variations in the Life-History of the Fairy Shrimp Eubranchipus vernalis *in Pond P88, Brimfield, Ohio,* 1944–64

The annual life-history of *E. vernalis* has been observed in pond P88, a temporary pasture pond, since 1944. Details are given in Table V. Figure 1 shows selected curves to illustrate the annual variation in this one pond.

Analysis of the data shows that the earliest date of the first collection was 8 November and the latest date of the first collection was 18 April. Naturally the first collection followed immediately a period of rain or thaw after cold weather had set in. The median date was 8 January. The date of the last collection each year ranged from 20 March to 25 May. The median was 1 May. The total number of days present, except for those destroyed by drying or freezing before reaching maturity, ranged from 19 to 155 with an average of 84 days. Abundant populations were recorded for the following sixteen years: 1943–45, 1949–52, 1955–60 and 1962–64. Numerous, but much less abundant, populations were recorded for the following five years: 1946–48, 1954, 1961. During the drought year of 1953 fairy shrimps were rare. During seven years there were more than one separate period of hatching. In 1949, 1955, 1958, 1959, 1962 and 1964, there were two separate periods of hatching. In 1956 there were three separate periods of hatching. All of these were separated by periods of complete drying up of the pond water or its freezing solid to the bottom. In all but three years (1944, 1960, 1963) there were two or more distinct periods of hatching as the water level rose from additional precipitation. In the winter of 1949–50 hatching occurred frequently between 19 December and 19 February as the water level gradually increased with frequent, light precipitation. The number of distinct hatchings during one complete season ranged from one to seven with a median and a mode of two.

The average growth per day for the first group hatched to reach maturity ranged from 0·12 to 0·76 mm. The average growth per day was 0·28 mm. The maximum size attained by adults ranged from 13·0 to 28·0 mm. with an average of 21·8 mm. The date of appearance of first eggs ranged from 1 January to 6 May with the median falling on 1 April.

Water temperature at the time of first collection ranged 0·0–13·0° C. with an average of 3·5° C. The water temperature at the last collection of adults ranged 10·0–26·0° C. with an average of 18·5° C. Fairy shrimp life-histories were terminated by one of three means. High water temperature or the development of predators or the combination of both accounted for 31 terminations. In 17 cases the pond dried out, and in seven cases the pond froze solid to the bottom.

Most of the variations of life-history are the result of weather factors: initial rainfall and/or thaw to fill the pond following cold weather; the amount and distribution of rainfall; the complete evaporation or freezing solid of the pond water; and the seasonal development of predators.

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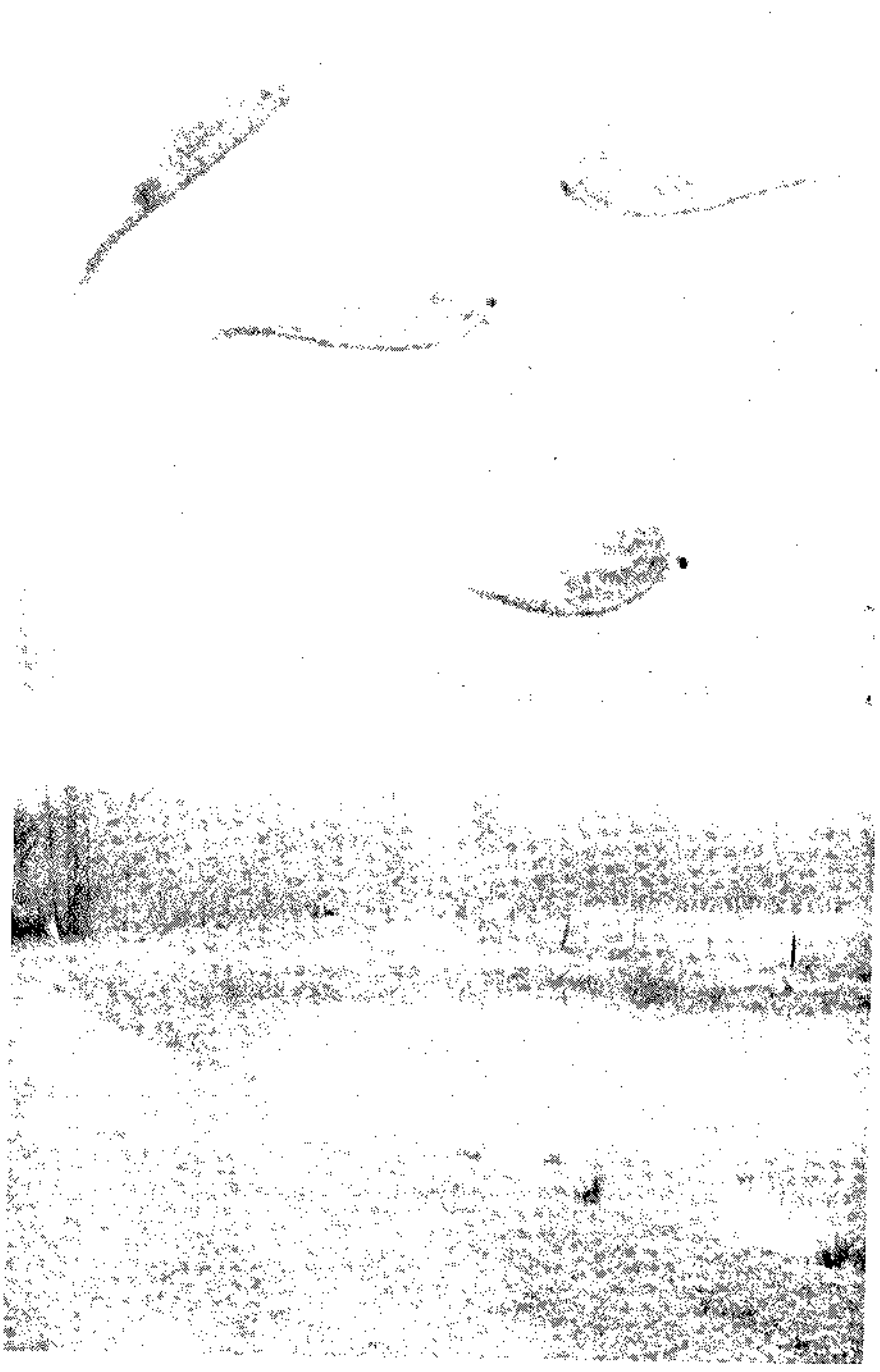

FIG. 1. Life-history of *Eubranchipus vernalis* Pond P88, Brimfield, Ohio; selected years to show variation. Top: *Eubranchipus serratus* (one female and three males). (Photo by R. W. Stark). Bottom: Pond P88, Brimfield, Ohio, in spring of 1956 (Photo by R. W. Dexter)

STUDIES ON *MOINA DUBIA* GURNEY AND RICHARDS (DAPHNID-MICRO CRUSTACEAN) FROM SEWAGE OXIDATION PONDS AT NAGPUR, INDIA

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INTRODUCTION

THE daphnid, *Moina dubia* Gurney and Richards, appears periodically in a bloom in oxidation ponds and forms a visible "red tide" over the surface or slightly below it. It was also found in a medium polluted water tank, Gandhisagar, in certain seasons of the year (Krishnamoorthi and Visweswara, 1963–64). The daphnids feed voraciously on the algae present in the water and thus reduce substantially the population of *Chlorella* and other algae in oxidation ponds and thus reduce the photosynthetic activity and hence their efficiency (Sampson, 1955). The algal population has to be replenished more often. For the successful functioning of the oxidation pond, it is necessary to prevent the appearance of daphnids or to eradicate them as soon as they appear. The maximum number of daphnids present in Gandhisagar is about 16,000 per litre and in the oxidation pond it is about 40,000 per litre. The larger number in the oxidation ponds is due to the richness of the organic and nutrient matter.

This work was undertaken with a view to studying the taxonomy, growth stages, life-history and ecology of this daphnid from the oxidation ponds. The bloom appears at a definite period of the year and evidently new populations arise from eggs which remain inactive in the soil for a long period. This was confirmed in connection with the analysis of water and collection of plankton at Gandhisagar. This tank is partially dry at the periphery in the hot season when dry soil was collected from the periphery and put in a small-sized aquarium containing water, the daphnids appeared. This supported the possibility of the presence of eggs, in the bottom mud in the oxidation pond and the emergence, at some favourable opportunity, of daphnids. The bloom is temporary and disappears after laying eggs which remain dormant in the soil. These eggs are probably parthenogenetic.

The foregoing account presents the background against which work was undertaken. Only some aspects of the problem have been studied and the results are incorporated in this paper.

MATERIAL AND METHODS

Specimens of *Moina dubia* were collected from one of the medium polluted tanks (Gandhisagar) as well as from experimental sewage oxidation pond at Bezonbagh, Nagpur, using a Bolting silk cloth plankton net (200 mesh). For quantitative sampling a known volume of water was passed through the net and the total volume of plankton and number of daphnids were recorded using the Sedgwick rafter occular whipple micrometer method (Welch, 1948) and the daphnids expressed per litre of the sample of water.

Laboratory studies have been currently undertaken to find methods for eradicating this daphnid from the oxidation pond on the following lines:

(*a*) Effect of changes in pH on daphnids and *Chlorella*.

(*b*) The effect of an insecticide ortho-dibrom-8 on *Monia dubia* and *Chlorella*.

(*c*) The effect of increased Oxygen level (super-saturation) on *Moina dubia*.

For studying the effect of hydrogen-ion concentration on these micro-crustaceans the pH values in the first series of experiments were made by mixing appropriate volumes of molar solutions of 0·2 M acid potassium phosphate and 0·2 N sodium hydroxide diluted to 200 c.c. with distilled water (ranges of pH 5·8 to 7·4) and 0·2 N boric acid in 0·2 M potassium chloride *plus* 0·2 N sodium hydroxide diluted to 200 c.c. with distilled water (range of pH 7·6 to 8·2). (Hawk, Oser and Summerson, 1954). The pH solutions so prepared were checked by Beckman Zeromatic pH meter (model 'O').

In addition to the solutions for different ranges as mentioned above the oxidation pond sewage samples were treated with 1% solution of KH_2PO_4 to obtain media for pH measurement on the acidic side and with 1% solution of K_2HPO_4 on the alkaline side.

Different concentrations of the insecticide orthodibrom-8 (10,000 ppm., 5000, 2500, 1000, 500, 250, 125, 100, 50, 25, 12, 5, 2 and 1 ppm.) were used.

Experiments were divided into three parts:

(*a*) Toxicity of ortho-dibrom-8 (of different concentrations) to daphnids using demineralised water as the medium in which daphnids were placed.

(*b*) Toxicity of ortho-dibrom-8 (of different concentrations) to daphnids in sewage water of oxidation pond in aquaria.

(*c*) The toxicity of the ortho-dibrom-8 of the same concentrations to *Chlorella*.

For obtaining higher saturation of dissolved oxygen *Hydrilla* plants were collected from the ponds around Nagpur, a measured quantity by weight was introduced in laboratory aquaria in a known volume of water (16 litres). Experiments were done at room temperature (27°–28° C.). There were adequate controls. 125 gm., 250 gm. and 500 gm. of *Hydrilla* was used in the experiments. Samples of water were drawn at regular intervals (one hour interval), both from the experimental aquarium and from the control and the dissolved oxygen was calculated. The temperature of the water was recorded at each sampling.

In all the above tests (including the effect of pH) 50 to 500 adult animals of *Moina dubia* have been used and the contact period varied from 2 to 24 hours. The total number of living specimens were counted at the end of the contact period and the percentage survival was calculated. *Chlorella* counts were made before and after the contact time in different concentrations using haemocytometer. Experiments were always conducted in duplicate and repeated thrice for every range of concentration at room temperature. In all the experiments proper controls were used and no mortality was observed although in one or two cases a small mortality of 1% due to natural causes was observed.

Oxidation pond

For a correct appreciation of the problem it is necessary to know the details regarding the design of the oxidation ponds, at Bezonbagh, Nagpur, in which daphnids appeared and *Chlorella* declined.

Number of ponds	2
Size	1,273 sq.ft. each
Capacity	27,276 gal./each
Detention time	2 and 4 days
Average value of sewage pumped	5,370 gls.
Depth	5 ft.
Average biochemical oxygen demand of the influent	250 ppm.
Average biochemical oxygen demand of the effluent (unfiltered sample)	50 ppm.

OBSERVATIONS

(1) *Effect of Hydrogen-ion-concentration*

The different ranges of pH studied, the percentage mortality and survival and the contact time are indicated in Table I.

The medium with pH ranging from 5·8 to 7·2 and 8 to 8·2 were lethal and there was 100% mortality when the contact period was two hours. There was 100% survival with pH 7·8 to 8.

The effect of variations in pH on *Chlorella* in these ranges was negligible (death rate was only 2·8% on an average).

The observations indicated above refer to both molar solutions and the pH adjusted with oxidation pond sewage water.

TABLE I

Adjusted with molar solutions and with oxidation pond sewage water

(Initial pH	Temperature 26° C. Final Temperature 26° C.) Percentage survival	Percentage mortality	Contact time
1·6, 2·4, 5·3, 5·8, 6·0, 6·2, 6·4, 6·6, 6·8, 7·0, 7·2	0	100	100% mortality in 5–10 minutes contact time
7·6	0	100	after 65 minutes contact time
7·8, 7·9, 8·0	100	0	100% survival even after 2 hours contact time
8·2, 8·4	40	60	2 hours
8·6	40	60	2 hours
8·8, 9·8	40	60	2 hours
10·8, 11·0, 11·4, 11·6	0	100	5–10 minutes contact time

2. *Effect with insecticide orthodibrom-8*

Table II gives the dosage of insecticide, contact time and percentage mortality of *Moina dubia*. Even in dosage as low as one ppm., there was 100% mortality. The insecticide is quite effective in killing the daphnids. But it cannot be used in an oxidation pond for the eradication of the daphnids because it acts adversely on *Chlorella*.

TABLE II

Effect of Orthodibromo-8 on Moina dubia

Dosage of insecticide p.p.m.	Contact time hrs.	Percentage mortality
10,000, 5,000, 2,500, 1,000, 500, 250	4– 8	100
125, 100, 50, 25	8	100
12·5, 10, 5	12	200
2, 1	Varies from 24–36	100

Table III shows that *Chlorella* is equally affected by the insecticide. *Chlorella* is a dominant algae in the oxidation pond. The main purpose of using an insecticide is to kill the daphnids but not the algae. This particular insecticide cannot be used for this purpose.

The drug affects *Chlorella* and causes morphological distortions and acts as an inhibition agent for their multiplication. *Phacus* is similarly affected. The wall of the algal cells were very much shrunken and a shift in the position of chromotophore was also observed.

TABLE III

Effect of Orthodibrom-8 on Chlorella *cells*

Dosage of insecticide p.p.m.	Contact time hours	Percentage mortality
10,000–250	2	100
100	2	100
50	2	88
12·5–5	2	40
1–2	4–8	30–35

3. *Survival of daphnids in different dissolved oxygen content levels*

From the data collected over a long period of dissolved oxygen values mg. per litre and corresponding population of *Moina dubia* from the sewage oxidation pond and the medium polluted tank (Gandhisagar), it is seen that the micro-crustaceans are not normally affected to any appreciable extent by low dissolved oxygen (range 0 mg. per litre to 2 mg./l.) (Figs. 1 and 2) but they do not withstand higher concentrations of dissolved oxygen. This is confirmed by the total absence of daphnids in one of the sewage oxidation ponds in Benzonbagh, Nagpur, which is aerated. The pond which is not aerated showed the bloom.

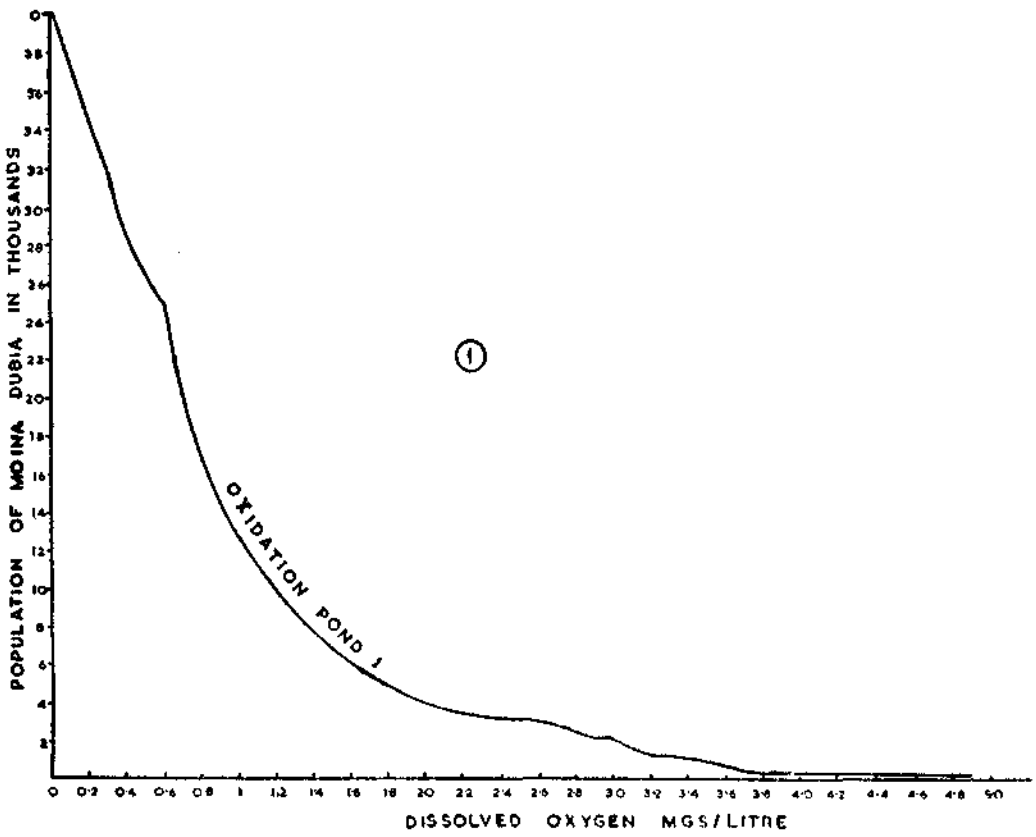

FIG. 1. Graph showing the relation between dissolved oxygen in mg./litre and the population of *Moina dubia* in sewage oxidation ponds

Experimentally, it was found that at higher concentrations of dissolved oxygen levels, the mortality was brought about by oxygen asphyxiation. The increase in dissolved oxygen and the mortality rate are directly proportional (Figs. 3, 4 and 5).

DISCUSSION

Observations show that the daphnids feed on algae and are present in an oxidation pond wherein the dissolved oxygen is low (0 mg./l. to 2 mg./l.). This confirms Sampson's (1955) statements. When daphnids are introduced, (about 100 in number) in 2,000 ml. beaker containing

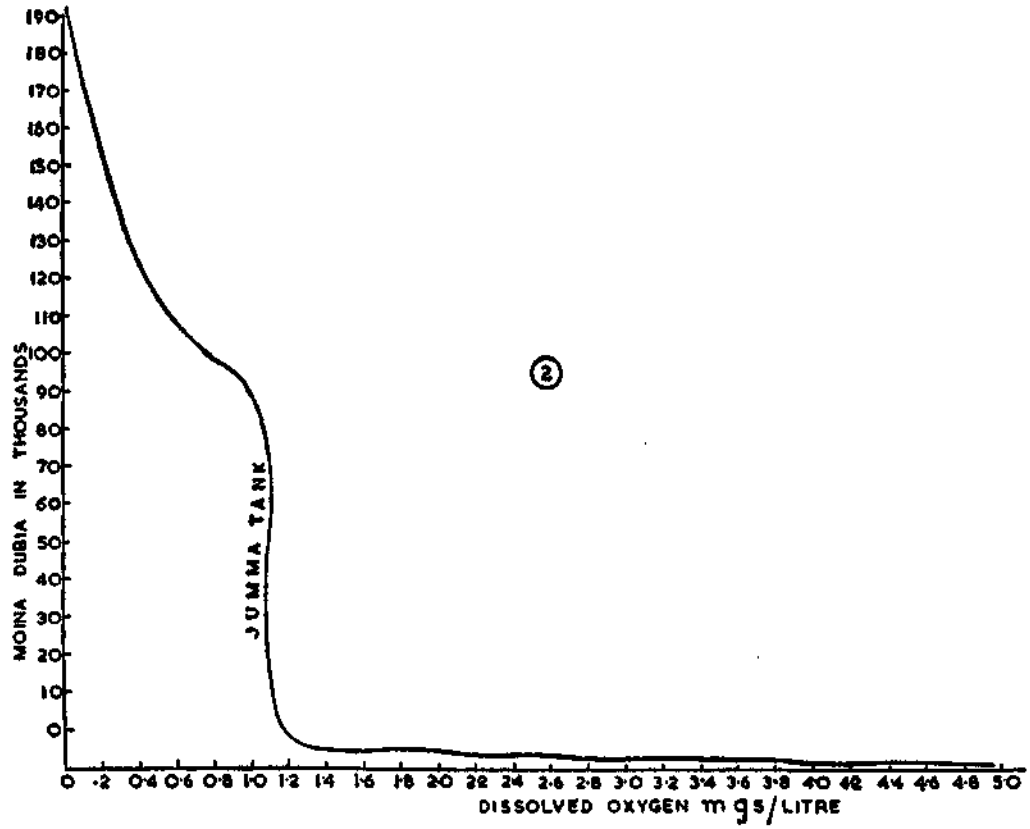

FIG. 2. Graph showing the relation between dissolved oxygen in mg./litre and the population of *Moina dubia* in Jumma Tank

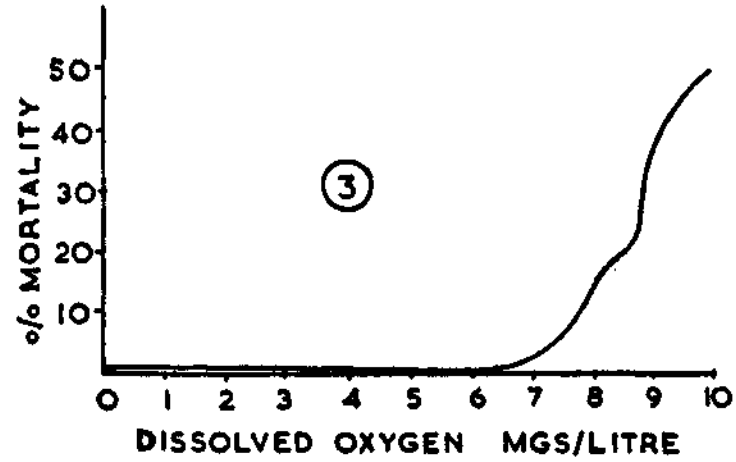

FIG. 3. Graph showing the percentage mortality of *Moina dubia* and dissolved oxygen mg./litre when 125 gm. of *Hydrilla* is used

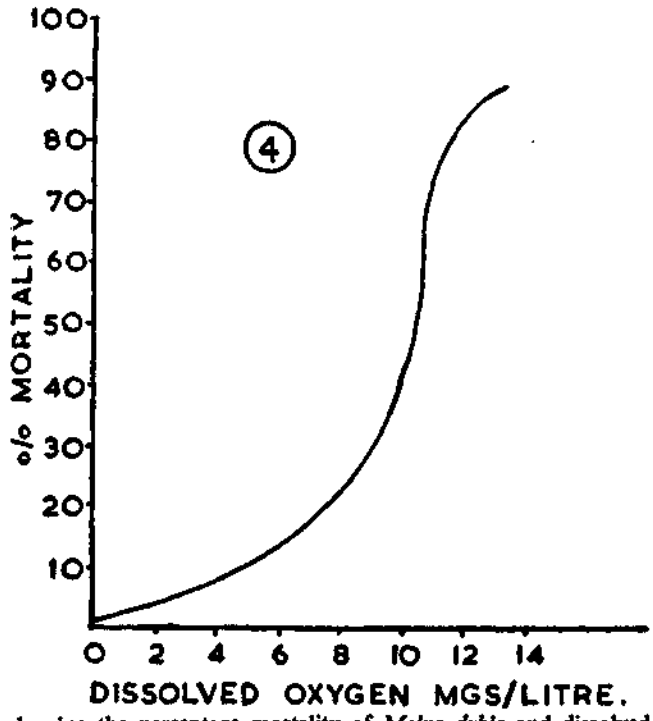

FIG. 4. Graph showing the percentage mortality of *Moina dubia* and dissolved oxygen mg./litre when 250 gm. of *Hydrilla* was used

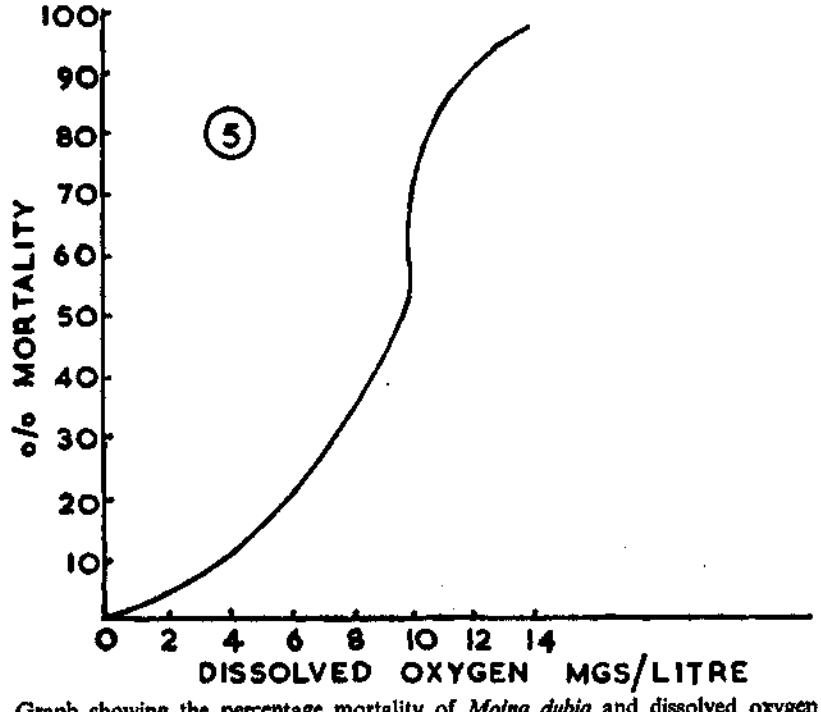

FIG. 5. Graph showing the percentage mortality of *Moina dubia* and dissolved oxygen mg./litre when 500 gm. of *Hydrilla* was used

water from oxidation pond which is green in colour owing to the presence of algae, the green colour completely disappears in about 24 hrs. The alimentary tract of the daphnids is found to be full of *Chlorella* cells and other algae.

In a private communication (1962), Prof. W. J. Oswald informs that he noticed the periodic appearance of daphnids in stabilization ponds and also frequently observed them in ponds particularly with a detention time of 10 days or more. In another private communication (1962) Dr. C. D. Parker of Melbourne informed that the daphnids were unlikely to develop when sewage purification was incomplete and when algal eradication would be detrimental to performance. It is important to note that the ponds referred to by Dr. Oswald and Dr. Parker are in series whereas the experimental oxidation pond at Bezonbagh, Nagpur, is only one pond. The other similar one is aerated.

In a private communication Dr. J. K. Neel of Kansas City, Missouri, stated that the daphnids were encountered in a number of lagoons over a wide-range of seasons. *Moina macrocopa* was one of the commonset cladoceran recorded by him in these lagoons. The occurrence of this cladoceran was correlated with stratification and decline in the phytoplankton population.

The valuable opinion received from these three workers have no direct bearing on the problem, *viz.*, the eradication of daphnids in a single oxidation pond in which sewage is pumped and the detention period is only two and four days.

From the laboratory studies on the effect of hydrogen-ion concentration, it is seen that if the pH of the oxidation pond is maintained between 8 and 9 probably the menace will be reduced to a great extent. The daphnid *Moina dubia* cannot survive if the pH of the water is above 9 under Indian conditions. If it is possible to maintain the pond with this pH value, the problem of eradication of daphnids could be solved. But in an oxidation pond where there is continuous influent and effluent, it is not possible to maintain a constant pH. But it was noted that with the addition of lime which raised the pH of the pond *Moina* disappeared temporarily. It is not known with certainty if they receded in the bottom mud or in the crevices in the brick work on the sides. But certainly after a few days, they reappeared.

Experiments proved that the insecticide orthodibrom-8 is very toxic even in low dosages such as 1 to 2 ppm. to daphnids (also as reported by Haitt in Oswald's paper, 1960). Oswald (1960) does not mention the effect of this insecticide in *Chlorella*. It is clear that this insecticide has a deleterious effect on the algal population even in low concentrations and hence cannot be used. Other insecticides have not been tried.

The dissolved oxygen was measured not only from the surface layers of the water, but also from all depths of the oxidation pond by making use of a Kemmerer's sampler in relation to the population of *Moina dubia* at respective depths. The low dissolved oxygen content in no way affects the density of population of *Moina dubia*. As a matter of fact, at a low dissolved oxygen tension, the density of population per litre is the maximum both in sewage oxidation pond and in the medium polluted tank.

The population density of daphnids in oxidation pond is very much higher than it is in Gandhisagar. This is because of the richness of food material present (*a*) in the form of organic matter and (*b*) thick dense algal growth in the sewage oxidation pond, which is not so much in the medium polluted tank, serving as a source of good food matter for *Moina dubia*.

Moina dubia specimens which are present in abundance on the surface at low oxygen tension tend to scatter away as the oxygen content increases after few hours of sunshine and to a certain degree owing to the vertical migration phenomenon, they submerge below the surface. At the same time, at saturation levels experimentally it is seen that this cladoceran is asphyxiated and ultimately dies.

SUMMARY

1. Laboratory studies on the effect of the hydrogen-ion concentration on the micro crustacea *Moina dubia* which occurs often as a bloom in sewage oxidation pond Bezon Bagh, Nagpur, have been studied. The optimum hydrogen-ion concentration which favours the existence of the form is found to be between 7·8–8. If the pH of the oxidation pond is maintained between 8 and 9 probably the means may be reduced to a grant extent.

2. The insecticide orthodibrom-8 could not be used for eradicating the daphnid because it affects the algae numerically even in low concentrations, although the daphnids are killed.

3. Dissolved oxygen mg./l. and the population of *Moina dubia* per litre of the sample collected for a long period in the experimental sewage oxidation pond and the medium polluted tank, Gandhisagar, show that the population of *Moina dubia* is not affected by low dissolved oxygen.

It is seen experimentally that at high dissolved oxygen levels the mortality was brought about by oxygen asphyxiation.

ACKNOWLEDGEMENT

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OCCURRENCE, GROWTH AND FEEDING HABITS OF *MOINA DUBIA* GURNEY AND RICHARD AND ITS ROLE IN THE STABILIZATION OF SEWAGE

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ABSTRACT

The sewage stabilization in oxidation ponds is primarily due to the biological changes which are due to the mutually beneficial interaction between bacteria, algae, protozoa, crustacea and various other planktonic and benthic communities. An understanding of the roles played by the specific biological components of the ecosystem is very essential in order to give a sound bio-engineering approach for the design of oxidation ponds.

It is hoped that the present paper would contribute to the knowledge of this problem in experimental sewage ponds, Bezon Bagh, Nagpur, with specific reference to the occurrence, growth and feeding habits of *Moina dubia* Gurney and Richard. The culturing methods of *Moina dubia* and its phytoplankton relationship are discussed in detail. Data presented in the paper indicate that a temperature of 28–30° C. and a pH of 7·5–8·2 are favourable for their growth. Diurnal variations of *Moina* in relation to phytoplankton populations and physical and chemical conditions are presented. The results of this study would indicate culture conditions suitable for the mass cultivation of *Moina dubia* which form a rich food for fishes.

INTRODUCTION

THE fish markets in India are insufficiently supplied with fishes. One-fifth of the total fish available in the Indian markets is normally obtained from the sea. According to Day (1958) the chief Indian freshwater fish fauna is represented by the Cyprinidae and Siluridae. Cladocerans form good food for these fishes. *Moina dubia* Gurney and Richard was found to occur and grow profusely in raw sewage experimental oxidation ponds at Nagpur (Lakshminarayana, 1963 and 1964). In the stabilization of raw sewage the biological changes are chiefly due to the mutually beneficial interaction between bacteria, algae, protozoa and various other planktonic and benthic communities. The role of cladocera in the stabilization of sewage was discussed in detail by Loedolff (1964) and he had shown that *Moina dubia* was responsible for transforming energy from one level to another and so be responsible for a certain amount of stabilization. The present paper describes the *growth, feeding habits and the probable means of culturing and maintaining healthy populations* of *Moina dubia* which could be used as a feed crop for the development of pisciculture.

EXPERIMENTAL SEWAGE OXIDATION PONDS AT NAGPUR

Figure 1 shows the experimental oxidation ponds layout at Nagpur. Detailed account of the operational features of these ponds along with the physical, chemical and biological factors operating on the ponds was given by Lakshminarayana *et al.* (1963). These ponds were on parallel operation at 5 ft. operational depth with detention periods ranging from 1·5 to 4 days. The *Moina* blooms were common mostly during winter and pre-summer seasons. Occasionally the *Moina* were carried into the ponds through raw sewage in great numbers, irrespective of the season. The source for these populations at such times could not be traced. There were no clear indications of the decrease in populations of algae prior to the appearance of *Moina*, but there were clear indications and evidence basing on the algal counts in the ponds, showing the grazing of *Moina* on *Chlorella*, the chief algal component of these ponds. Normally *Moina dubia* started coming up whenever there were drops in pH levels of the ponds along with the accumulation of dead organic matter at the sides of the ponds, specially in between the bricks (Lakshminarayana, 1964).

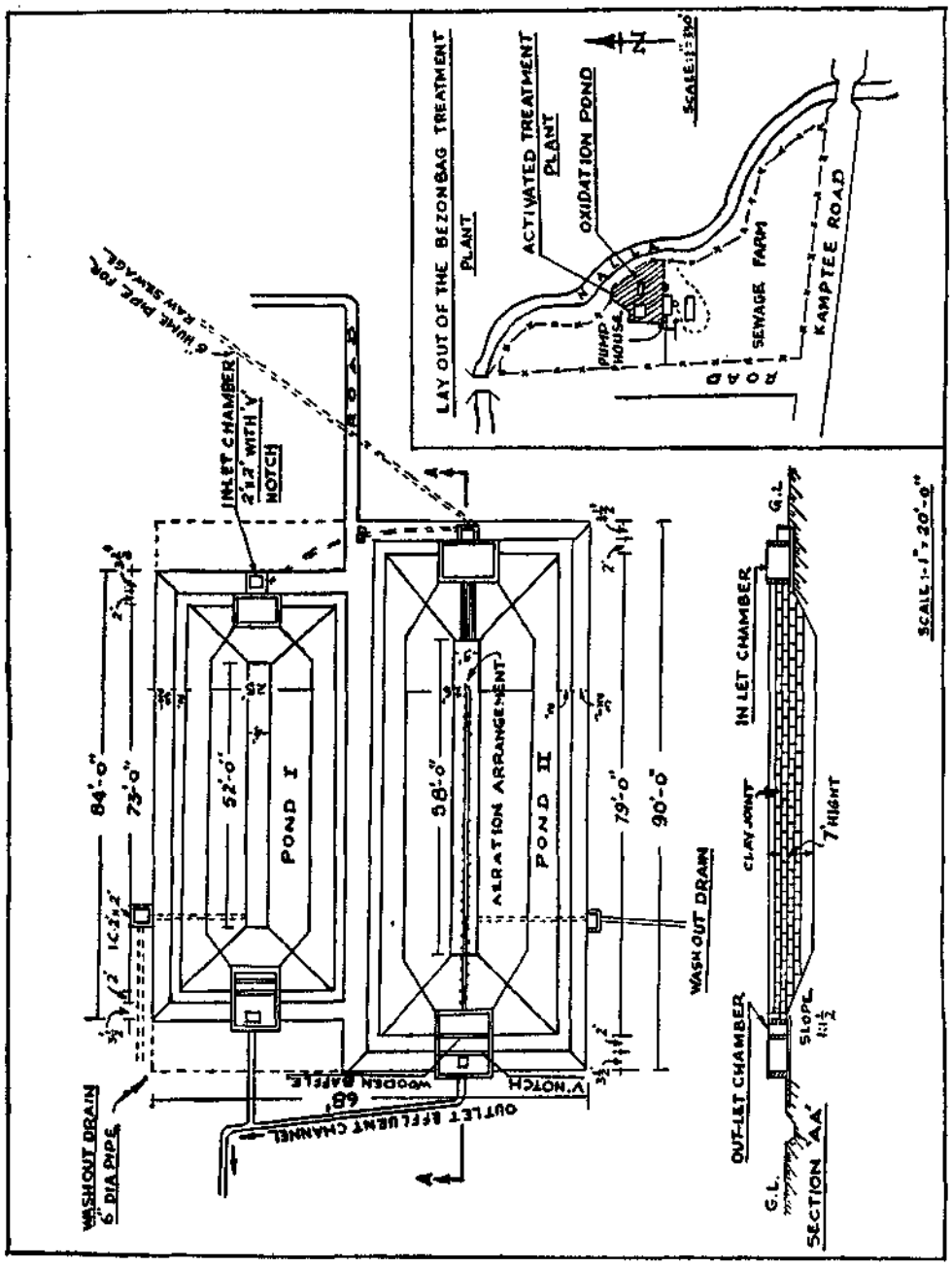

FIG. 1. Experimental oxidation pond at Sewage Research Station, Bezon Bagh, Nagpur

CULTURING METHODS FOR *Moina dubia* GURNEY AND RICHARD

With the help of a plankton net *Moina dubia* were collected in large numbers. These were separated from the other organisms by dip-tube method. Culture media were prepared with extraneous organic nutritive material in the form of sugars—Glucose and Lactose in sterile

distilled water. Concentrations of sugars ranging from 0·5 to 4% were tried. Into each of the experimental flasks 15 *Moina* were added by means of a glass tube. All the tubes were equally illuminated by incandescent fluorescent lamps. The temperature varied from 27·5° to 29°C. The pH of the media in the flasks varied from 7·3 to 7·5. The number of *Moina* in each flask were noted after 24 hr. and 48 hr. There was no change in the *Moina* populations after 24 hr. Most of the *Moina* died within 48 hr.

The addition of cotton-seed extract to the culture flasks gave encouraging results. In these experiments the same method was adopted excepting the addition of cotton-seed extract in place of sugars. 2·5% hot and cold cotton-seed extracts were prepared by taking 2·5 g. of the crushed seeds for 100 c.c. of water. The hot extract was prepared by boiling the crushed seed with water for about 10–15 minutes. The extracts were filtered through Whatman No. 1 filter-paper. 50 c.c. of the solution was made upto 1,000 c.c. with sterile distilled water. The concentration of this final diluted extract will be 0·125% of the original filtered extract. Addition of 5% of this extract to the culture vessels gave prolific increase in the *Moina* populations. It became difficult to count the *Moina* numbers since they were numerous. The increase in numbers of *Moina* were greater in the culture vessels containing hot cotton-seed extract. Various concentrations of the hot extract were tried to find out the suitable concentration but it was observed that 5% of the diluted extract gives the best results.

A. *Effect of pH and temperature on* Moina dubia *Gurney and Richard.*—As described above cotton-seed hot extract media were prepared and distributed 500 c.c. in each conical flask. pH ranges 6·0, 6·8, 7·5, 8·2, 8·8 and 9·5 were maintained in these flasks. They were kept in temperatures 5° C., 20–21° C., 28° C., 31° C. and 37° C. as per the laboratory conditions. All the flasks were inoculated with equal number of *Moina*. The growth was observed after 24–48 hr. It was observed that a pH of 7·5–8·2 and a temperature 28°–31° C. were suitable for their optimal growth.

B. *Food for* Moina *cultures.*—*Moina* raised on cotton-seed extract medium could not grow to their normal sizes and the populations were found to die after 20–30 days in spite of daily changes of the medium. The cotton-seed extract supports only the bacterial growths which serve as feed for *Moina*. The addition of Unialgal cultures of *Chlorella* to *Moina* flasks helped in maintaining the growth of *Moina* for 3–4 months, since *Moina* grazes on *Chlorella* (Lakshminarayana, 1964). If the oxidation pond effluents are added, in addition to cotton-seed extract, daily to the *Moina* flasks in equal quantities replacing the same amounts of liquid from the flasks it was observed that *Moina* flourish well in the laboratory at 28–31° C. The pond effluents contain both bacteria and *Chlorella* which will serve as feed for *Moina*.

Diurnal Rhythms in Algal and *Moina* Populations in Oxidation Ponds

Figure 2 gives the diurnal changes in D.O. levels in the oxidation ponds on a typical day. Tables I–IV will reveal data on the diurnal and vertical changes in oxidation pond temperature, pH, dissolved oxygen, algal and *Moina dubia* populations. This is a typical case where the *Moina* and algal numbers are almost in a balanced population meaning thereby that if sufficient algal and bacterial populations are maintained in proportion to *Moina* growth rate one can always obtain sufficient quantities of *Moina* for piscicultural purposes. The diurnal vertical rhythms of algae and *Moina* depends on changing light penetration during the day and night. When the dissolved oxygen and pH were high in the ponds surface the *Moina* populations were present in larger numbers in the lower depths of the pond. There are some inverse relationships between algal numbers and *Moina* populations in the diurnal variations. In controlled ponds it could be possible for a trained biologist to maintain rich culture stocks of *Moina dubia* populations in nature. This paper does not intend to deal in this place in detail the diurnal variations of dissolved gases and substances, temperature in relation to algal and zooplankton populations in oxidation ponds, Nagpur.

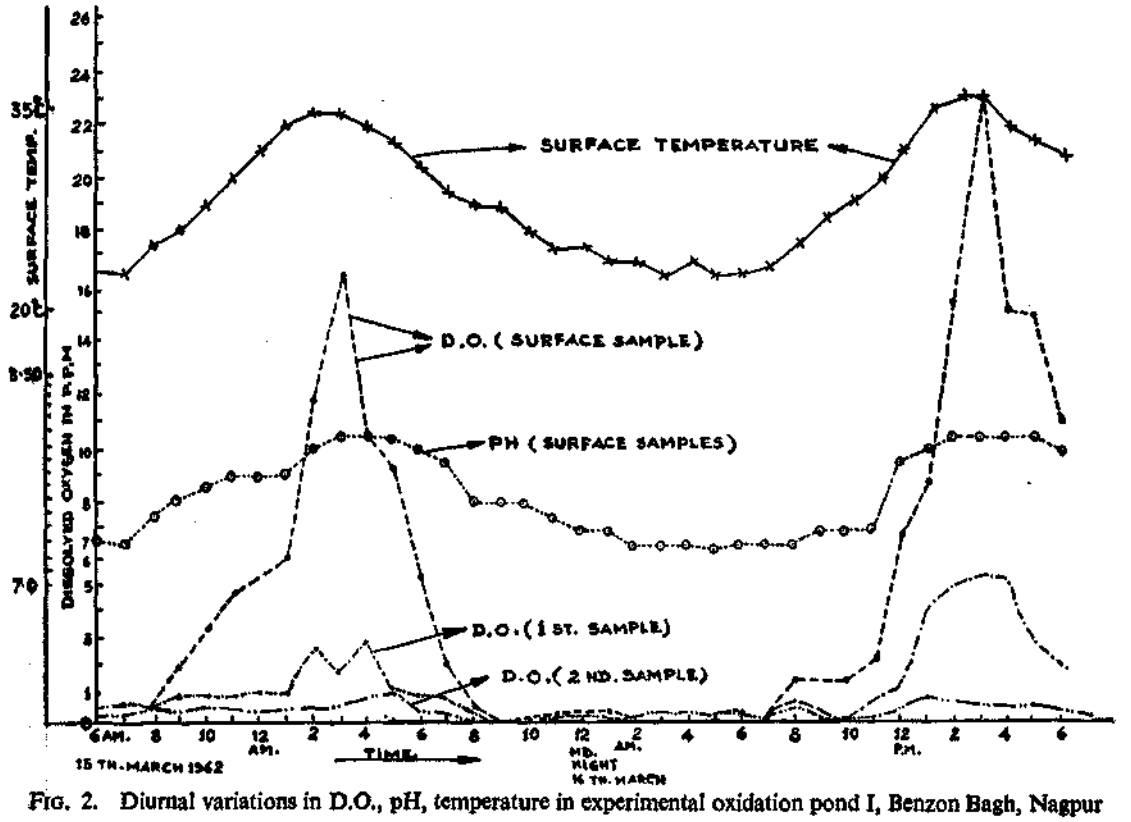

FIG. 2. Diurnal variations in D.O., pH, temperature in experimental oxidation pond I, Benzon Bagh, Nagpur

GRAZING EFFECTS ON ALGAE AND BACTERIA

The grazing of algae by *Moina* and other crustaceans was indicated by many workers (Lakshminarayana, 1964; Loedolff, 1964; Elster, 1964; Hall, 1964; Zhukova, 1963 and Macan, 1961). Zhukova (1963) pointed out that (*a*) in the crustaceans the uptake of bacterial cells can take place in the mid-gut, the fore and hind-gut being chitinized, (*b*) with the help of radioactive tracers, c^{14}, it has been proved that bacteria were not only ingested by the representatives of the plankton, but are also assimilated, and (*c*) the rates of consumption of cells by one small crustacean in an hour were 1·44% (phytoplankton) and 1·04% (bacterial) and that the weight of bacteria consumed was 1/5 that of the weight of phytoplankton. Algae and bacteria serve as feed for most of the crustaceans.

DISCUSSION

Hall (1964) in connection with dynamics of a natural population of *Daphnia galeata mendotae* in Base line lake, Michigan, observed that (*a*) temperature influences the rates of increase in *Daphnia* populations more strongly than food level does under the conditions examined, (*b*) the effects of food and temperature are separable, thereby facilitating the application of experimental data to the field collection, (*c*) the frequency of molting and reproduction, duration of egg development, and physiological life-span are principally influenced by temperature, and (*d*) of the growth per instar, maximum carapace length and brood size are influenced principally by food. Hall (1964) further stated that reproduction in *Daphnia galeata mendotae* occurs every 2·0 days at 25°C.,

TABLE I

Diurnal variations of algal and Moina *numbers in oxidation pond–I on* 11–4–1963 *to* 12–4–1963

Date and time of sampling	Samples from									
	Surface		1 foot deep		2 feet deep		3 feet deep		4 feet deep	
	Algal No./ml.	*Moina*/L	Algal No./ml.	*Moina*/L	Algal No./ml.	*Moina*/L	Algal No./ml.	*Moina*/L	Algal No./ml.	*Moina*/L
11–4–1963 6.00 A.M.	C–2440000 P–10000	200	C–3430000	70	C–1890000 P–10000 M–10000	30	C–2450000 P–30000 Ch–10000	33	C–2300000 Sc–10000	Nil
11–4–1963 10.00 A.M.	C–2540000 Ch–60000	133	C–2470000 P–10000 Ch–10000	30	C–1470000 Ch–20000 M–10000	Nil	C–1290000	Nil	C–1540000 P–30000	Nil
11–4–1963 2.00 P.M.	C–2170000 P–60000 Ch–40000 Chl–10000	20	C–2340000 P–10000 Ch–10000	50	C–1130000 P–10000	37	C–2100000 P–20000 Ch–10000	10	C–1450000 P–20000 Sc–10000	Nil
11–4–1963 4.00 P.M.	C–3990000 S–10000	37	C–2770000 Ch–20000 P–20000	106	C–2070000 P–10000	53	C–1830000	Nil	C–2360000 S–10000	Nil
11–4–1963 8.00 P.M.	C–2560000 P–10000	27	C–3000000 P–20000 Ch–20000	67	C–1890000 P–30000	37	C–1590000 P–20000	37	C–1560000 P–30000	13
12–4–1963 6.00 A.M.	C–2930000 Ch–20000 P–20000	247	C–2160000 P–30000 Ch–1000 S–10000	70	C–1930000 P–20000 Ch–20000	23	C–2850000 Ch–60000 P–20000 S–20000	30	C–1810000 P–50000 S–40000	23
12–4–1963 10.00 A.M.	C–2790000 S–10000 Ch–10000	250	C–5240000 P–70000 Ch–60000	200 *plus* 7 Chiro- nomids	C–4240000 Ch–80000 P–80000 S–20000 Sc–10000 Chl–10000	27	C–1090000 P–30000 S–10000	20	C–1850000 S–30000 Ch–20000 D–10000	33

C—*Chlorella*, P—*Phacus*, Ch—*Chlamydomonas*, Chl—*Chlorogonium*,
S—*Selenastrum*, Sc—*Scenedesmus*, M—*Merismopedia*, Ca—*Carteria*,
D—Diatoms, A—*Ankistrodesmus*, T—*Tetraedron*.

TABLE II

Diurnal variations of algal and Moina *numbers in oxidation pond-II on* 11-4-1963 *to* 12-4-1963

Date and time of sampling	Samples from									
	Surface		1 foot deep		2 feet deep		3 feet deep		4 feet deep	
	Algal No./ml.	*Moina*/L	Algal No./ml.	*Moina*/L	Algal No./ml.	*Moina*/L	Algal No./ml.	*Moina*/L	Algal No./ml.	*Moina*/L
11-4-1963 6·00 A.M.	C-1790000 Ch-20000	20	C-1680000 Ch-40000 S-50000 P-10000	67	C-1300000 Ch-20000 S-20000 P-10000	47	C-1290000 S-20000 P-10000 Ch-10000	73	C-1400000 S-70000 Ch-50000 D-30000 P-10000	33
11-4-1963 10.00 A.M.	C-1360000 Ch-40000 S-40000 P-40000	50	C-1540000 Ch-90000 S-6000	83	C-1450000 Ch-70000 S-10000	90	C-1360000 Ch-50000 S-30000 Sc-10000	20	C-1170000 Ch-20000 S-30000	13
11-4-1963 2.00 P.M.	C-2030000 Ch-70000 S-60000 Ch-20000 P-10000	Nil	C-1400000 S-20000 Ch-10000 P-10000	30	C-2100000 S-40000 Ch-10000	80	C-1880000 Ch-40000 S-10000	13	C-1480000 S-10000 Sc-10000 Ch-10000	23
11-4-1963 4.00 P.M.	C-2220000 S-30000 P-30000 Ch-10000	10	C-3000000 S-50000 Ch-30000	57	C-2030000 S-30000 Ch-20000	27	C-1750000 S-20000	20	C-1510000 S-20000 Ch-20000	10
11-4-1963 8.00 P.M.	C-2640000 S-6000 Ch-10000	123	C-2490000 Ch-60000 S-40000	160	C-2010000 Ch-130000 S-160000 T-30000 P-20000	67	C-2230000 Ch-100000 S-40000 P-10000	33	C-1580000 S-70000 Ch-520000	77
12-4-1963 6.00 A.M.	C-1880000 S-40000 Ch-30000 P-10000	530	C-1690000 Ch-30000 S-20000 P-10000	93	C-1310000 Ch-30000 S-40000 M-10000 T-10000	97	C-1350000 Ch-40000 S-40000 P-20000 M-10000	90	C-1180000 S-60000 Ch-20000 M-20000	53
12-4-1963 10.00 A.M.	C-1840000 S-30000 Ch-30000	869	C-1250000 S-60000 Ch-50000	166	C-1610000 Ch-90000 S-10000	27	C-1090000 Ch-100000 S-70000 A-10000	67	..	..

TABLE III

Variation of temperature, D.O. and pH at different depths and at different times in oxidation pond–I

Time and date	Pond temperature ° C. at different depths (feet)											Dissolved oxygen in p.p.m. at different depths (feet)					pH at different depths (feet)				
	Temp. atm.	SUR.	6″	1′	1½′	2′	2½′	3′	3½′	4′	4½′	SUR.	1′	2′	3′	4′	SUR.	1′	2′	3′	4′
11–4–1963																					
6.00 A.M.	25	27	26½	26	26	26	25½	25	25½	24½	24	0	0	0	0	0	7·5	7·5	7·5	7·4	7·3
7.00 A.M.	28	28	27	26½	26½	26½	27	27	26½	27	27½	..	..	..	..	..	..	..	..	..	..
8.00 A.M.	29	28	27½	28	28	28	28	27½	28	28	27½	..	..	..	..	..	..	..	..	..	..
9.00 A.M.	31	30	29	28	28	30	29	28½	29	29	30	..	..	..	..	..	..	..	..	..	..
10.00 A.M.	34	32	30	29	29	29	29	29	29	29	29	1·0	0·3	0	0	0	7·5	7·5	7·5	7·4	7·4
11.00 A.M.	35½	34	31	30	29	28½	29	28	28	28	29	..	..	..	..	..	..	..	..	..	..
12.00 Noon	36	33	32	31	30	30	30	30	30	30	30	..	..	..	..	..	..	..	..	..	..
1.00 P.M.	37	38	35	33	32	32	31	30	30	30	30	..	..	..	..	..	..	..	..	..	..
2.00 P.M.	38	38	35	33	32	31	31	30	30	30	30	20·0	3·8	1·2	0·1	0	8·1	7·6	7·5	7·5	7·4
3.00 P.M.	35	35	34	33	32	31	31	30	30	30	30	..	..	..	..	..	..	..	..	..	..
4.00 P.M.	36	35	35	34	33	32	31	30	30	30	30	17·5	6·5	2·9	0	0	7·9	7·7	7·5	7·5	7·3
5.00 P.M.	35	35	34	33	32	31	30	30	30	30	30	..	..	..	..	..	..	..	..	..	..
6.00 P.M.	33	33	32½	32	31	30½	30	30	30	29½	29	..	..	..	..	..	..	..	..	..	..
7.00 P.M.	32	31	30	30	30	30	29	28	28	28	28	..	..	..	..	..	..	..	..	..	..
8.00 P.M.	31	31	30	30	30	30	29	29	29	29	28	0·6	0·3	0	0	0	7·7	7·6	7·4	7·4	7·3
12–4–1963																					
6.00 A.M.	25	28	28	28	27½	28	27½	27	27	27	27	0·4	0·6	0·6	0·4	7·5	7·5	7·5	7·5	7·5	7·4
7.00 A.M.	26	27	26	26	25½	26	25½	25½	25½	25½	25½	..	..	..	..	..	..	..	..	..	..
8.00 A.M.	28	28	27	27	27	26½	26½	27	26½	26½	26½	..	..	..	..	..	..	..	..	..	..
9.00 A.M.	30	29	28	28	27	27	27	27	27	27	27	..	..	..	..	..	..	..	..	..	..
10.00 A.M.	34	32	31	30	29½	29	29	29	29	29	29	2·1	0·9	0·3	0·3	0	7·7	7·6	7·5	7·5	7·4

TABLE IV

Variation in temperature, D.O. and pH at various depths and at different times in oxidation pond–II

Time and date	Pond temperature ° C. at different depths (feet)											Dissolved oxygen in p.p.m. at different depths (feet)					pH at different depths (feet)				Light intensity (lux)
	Temp. atm.	SUR.	6″	1′	1½′	2′	2½′	3′	3½′	4′	4½′	SUR.	1′	2′	3′	4′	SUR.	1′	2′	3′	4′	
11–4–1963																						
6.00 A.M.	25	28	27	26½	26½	27	26	25	25½	25	..	0·5	0·3	0·3	0·2	0·4	7·6	7·6	7·6	7·5	7·5	..
7.00 A.M.	28	28	28	27½	27	27	27	26½	27	27	..	..	..	..	..	..	..	..	..	..	..	..
8.00 A.M.	29	28½	28	28	28	28½	28	27½	27½	27	..	..	..	..	..	..	..	..	..	..	..	32,000
9.00 A.M.	31	32	30	30	29½	29	29	28½	28½	28½	..	..	..	..	..	..	..	..	..	..	..	50,000
10.00 A.M.	34	33	31	31	30½	30½	29	29½	29½	28½	..	10·0	3·0	2·5	0·8	2·8	8·2	7·8	7·8	7·7	7·7	65,000
11.00 A.M.	35½	35	32	30	30	29	29	29	29	29	..	..	..	..	..	..	..	..	..	..	..	78,000
12.00 NOON	36	35½	33	32	32	31	31	31	31	31	..	..	..	..	..	..	..	..	..	..	..	82,000
1.00 P.M.	37	37	34	33	32	32	32	31½	31½	31½	..	..	..	..	..	..	..	..	..	..	..	85,000
2.00 P.M.	38	37	35	32	31	30	30	29	30	29	..	26·5	3·0	1·3	1·0	0·5	8·6	7·8	7·7	7·7	7·7	10,000
3.00 P.M.	35	35½	34	32	31	30	31	28	29	29	..	..	..	..	..	..	..	..	..	..	..	5,000
4.00 P.M.	36	35	34	32	31	30	30	30	30	30	..	..	..	..	..	..	..	..	..	..	..	42,000
5.00 P.M.	35	35	34	34	33	32	31	31	30	30	..	..	..	..	..	..	..	..	..	..	..	..
6.00 P.M.	33	34	33	32	32	32	31	31	30	30	..	..	..	..	..	..	..	..	..	..	..	..
7.00 P.M.	32	32	31	30	30	29	29	29	29	29	..	..	..	..	..	..	..	..	..	..	..	..
8.00 P.M.	31	31	30	30	30	30	29	29	30	29	..	0·6	0·4	..	..	..	8·0	7·8	7·5	7·5	7·4	..
12–4–1963																						
6.00 A.M.	25	27	26½	26½	26	25½	25½	25½	26	26	..	0·5	0·5	0·5	0·4	0·5	7·7	7·6	7·6	7·5	7·5	..
7.00 A.M.	26	27	27	27½	26½	26	26	26	26	26	..	..	..	..	..	..	..	..	..	..	..	18,000
8.00 A.M.	28	28	27	27	26	26	26½	26½	26½	26½	..	..	..	..	..	..	..	..	..	..	..	38,000
9.00 A.M.	30	30	29	29	28	27	27	27	27	27	..	..	..	..	..	..	..	..	..	..	..	55,000
10.00 A.M.	34	31½	30	29½	28	28	28	27	27½	27½	..	4·5	1·6	0·5	0·6	0·5	7·9	7·8	7·7	7·6	7·5	70,000

every 2·6 days at 20° C., every 8·0 days at 11° C. and a single adult at 5° C. gave birth to young, 18 days after producing the eggs. Clarke (1957) pointed out that the life-span of *Daphnia magna* is the greatest at 8° C. and in contrast the shortest time for the production of the first batch of young *Daphnia* occurs at 23° C. The optimum from the point of view of the largest number of young daphnids produced is found to be at 18° C. The ecological effect of these divergent optimal values will depend upon whether they are applied to the individual or to the population (Clarke, 1957). Thus the optimum temperature is best thought of as a range of temperatures, and it is the range within which the organism as a whole functions best (Clarke, 1957; Chapman, 1931). In *Moina macrocopa*, when the temperature drops below about 14° C. or rises above 30° C., males appear in the population and sexual eggs are produced (Clarke, 1957). If the *Moina* population becomes crowded males begin to appear. This reaction may be related to the reduction of space attending the drying up of a pond, and necessitating the production of resistant eggs if population has to survive.

The separatability of various factors like food and temperature greatly facilitates the application of these data to the field conditions. Temperature alone can be utilised to predict the frequency of molting, reproduction, duration of egg development and physiological span (Hall, 1964). The tropical inland waters normally have an average temperature variation of 28–31°C., and these bodies of water form ideal grounds for crustacean growth and consequent fishery development. The culture methods suggested above in this paper along with the consideration of important factors like temperature, food and pH are expected to help for developing large hatcheries for crustaceans which serve as an ideal food for fishes. Artificial fertilization of the hatcheries can also be done with dried cow dung or horse dung or limited quantities of sewage. Mixed algal cultures could be maintained in separate tanks to feed the crustaceans. The algae can also be supplied as dried powder. The cotton-seed extract medium can be used conveniently for growing *Moina dubia* in aquaria.

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BIOLOGY OF CIRRIPEDE LARVAE

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ABSTRACT

Liberation of larvae by *Balanus balanoides*, which is thought to be a response by the parents to the spring outburst of diatoms, is seasonally later in the silt-laden water of the Bristol Channel than in clearer water to the west. In rearing experiments, though larvae of this high latitude species need diatoms as food, larvae of oceanic and low latitude barnacles need phyto-flagellates. There are other lines of evidence, too, which indicate that flagellates may be particularly prominent in the phytoplankton of warmer seas.

The relative distributions of young and old *Balanus*, *Chthamalus* and *Elminius* on littoral rocks yield further evidence that the gregarious and space-sharing behaviour patterns of the cyprids are important in reducing wastage and protecting the territory which the species has occupied.

INTRODUCTION

THE larval life of littoral barnacles is bounded by two critical periods, (*a*) hatching, which should occur when food is available for larval growth, and (*b*) settlement, when the future habitat of the individual is determined. Both may involve associated behaviour mechanisms, whereby the parents help to safeguard the future of the larvae and the larvae seek security for their future role as parents.

Hatching as a result of activity by the parents was demonstrated by Crisp (1956) and Crisp and Spencer (1958) in the arctic-boreal species *Balanus balanoides* (L.), which liberates one brood per year, at about the time of the spring phytoplankton outburst. Liberation occurs after the embryos have been incubated (in the mantle cavity) for several months and its onset is not strictly determined by the maturity of the embryos. These are normally mature and ready for liberation many weeks before release actually occurs. Hatching (which is closely followed by liberation of the larvae) could be induced in the laboratory by feeding the incubating parents with animal or plant food or by treating separated masses of embryos with extracts made from adult barnacles. It seemed that the parents react to the presence of food in the water by secreting onto the embryos some substance which stimulates their movement and that this activity of the embryos leads to their hatching. This view was confirmed by Barnes and Barnes (1959 *a*), following earlier and independent studies on the hatching process (Barnes, 1955, and 1957).

Ecological studies have linked liberation in *Balanus balanoides* with the spring outburst of diatoms (Barnes, 1956 *a* and 1957), but it may also take place in the absence of a large diatom crop, or before the major outburst occurs (Barnes, 1962). Rzepishevsky (1959) concluded that naked flagellates rather than diatoms promote release of larvae in this species, but such a response would appear on first consideration to be non-adaptive, in view of the evidence that *Balanus balanoides* larvae need diatoms as food and do not complete their development on flagellates (Moyse, 1963—but *see* p. 5).

Our studies in South Wales have revealed (i) some of the difficulties which should be borne in mind in future work on this problem. We also present here some new observations on (ii) larval feeding and growth in oceanic Lepadidae and (iii), settlement patterns in littoral barnacles.

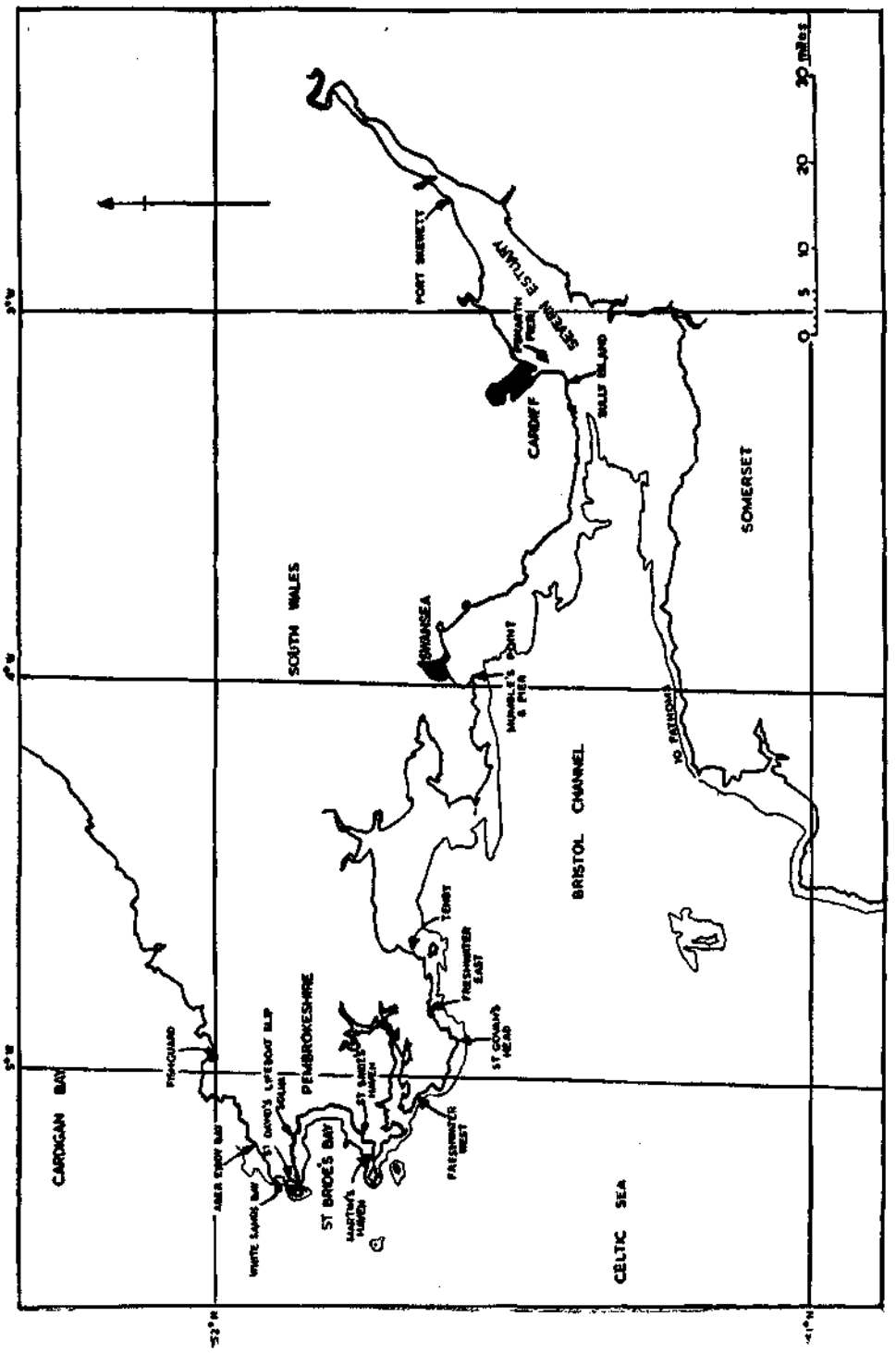

FIG. 1. Map of South Wales, showing the places mentioned.

LIBERATION OF *Balanus balanoides* IN S. WALES

About fifteen sampling sites, distributed along the South Wales Coast (Fig. 1), have been studied during several years. For each sample, at least fifty and usually a hundred adult *Balanus balanoides* were opened and the percentage containing embryos recorded (Fig. 2). Barnacles which were small or isolated were not opened and those found to be parasitised by female *Hemioniscus balani* (Spence Bate) were rejected. Individuals which had liberated the great majority of their embryos were counted as empty. No reliable method was discovered for determining whether completely empty individuals had bred in the current year, but it may be assumed that the great majority had done so, for early in a season the proportion with embryos was usually at least 95%.

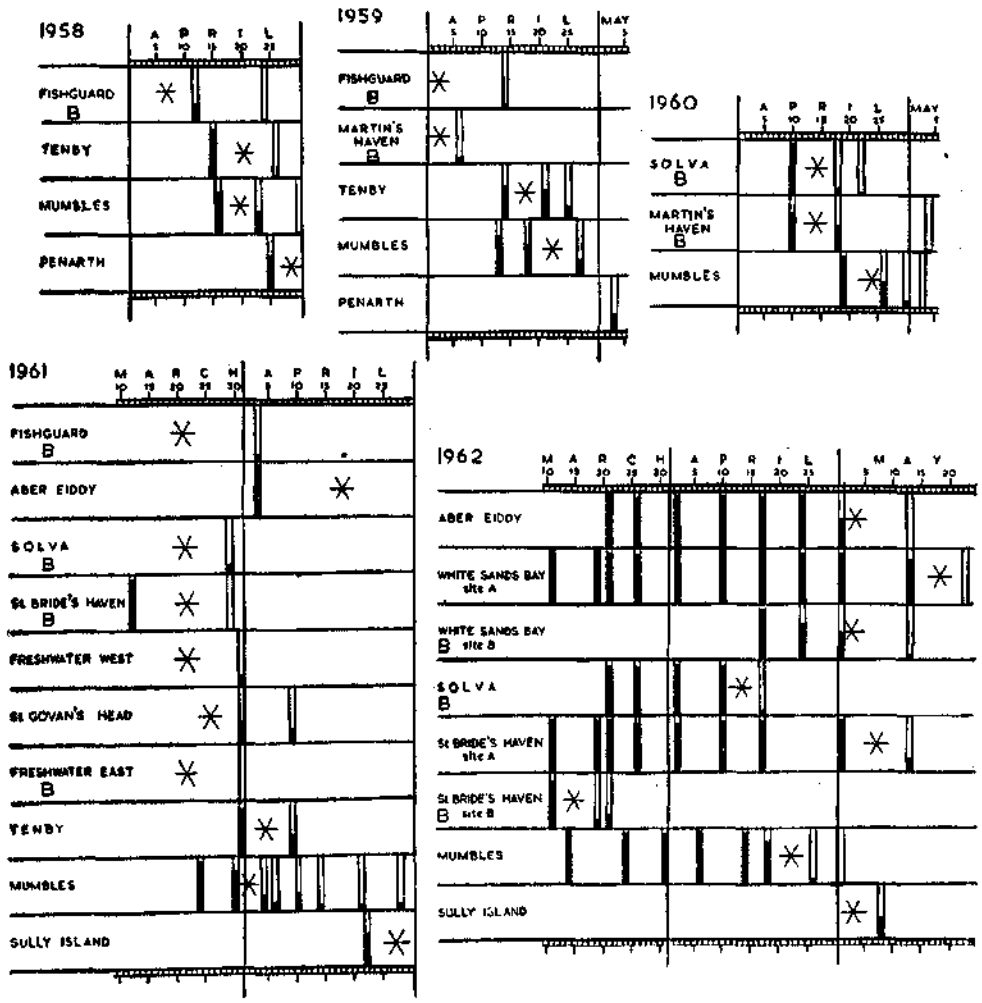

FIG. 2. Analysis of samples of adult *Balanus balanoides*, collected during the liberation periods of five years. The extent of the black section of each vertical column represents the percentage of individuals which contained embryos. An asterisk indicates the estimated middle of the liberation period at each site. Embayed situations, where liberation tended to be early, are indicated by the letter B under the name of the sampling site.

Late in a season a few barnacles (less than 10%) retained their embryos much longer than their neighbours, so it was convenient to regard the main liberation period as having occurred when the proportion of gravid individuals fell from about 95% to less than 10%. As Fig. 2 shows, this period sometimes occupied less than a week (*e.g.* at Solva in 1960 and 1962) and sometimes more than a week (Tenby and Mumbles in 1959; Mumbles in 1961 and White Sands Bay in 1962), but there was no evidence of its occupying more than two weeks at any given site.

The 1962 samples, however, showed that the liberation period in adjacent sites could be very different, with much earlier liberation in embayed situations. White Sands Bay site A was the tip of a rocky promontory (Trwynhwrddyn) and liberation occurred there after 13th May. At the nearby site B, on the side of the promontory adjoining the sandy bay, liberation began about 20 days earlier. Similarly, at St. Bride's Haven, liberation was much later at an exposed site A than at an embayed site B only about 150 metres away. Indeed, there the difference was about 50 days. A survey of the little bay, about a week before liberation occurred in the population just outside it, showed a consistent pattern, with maximum liberation in the most sheltered part (Fig. 3).

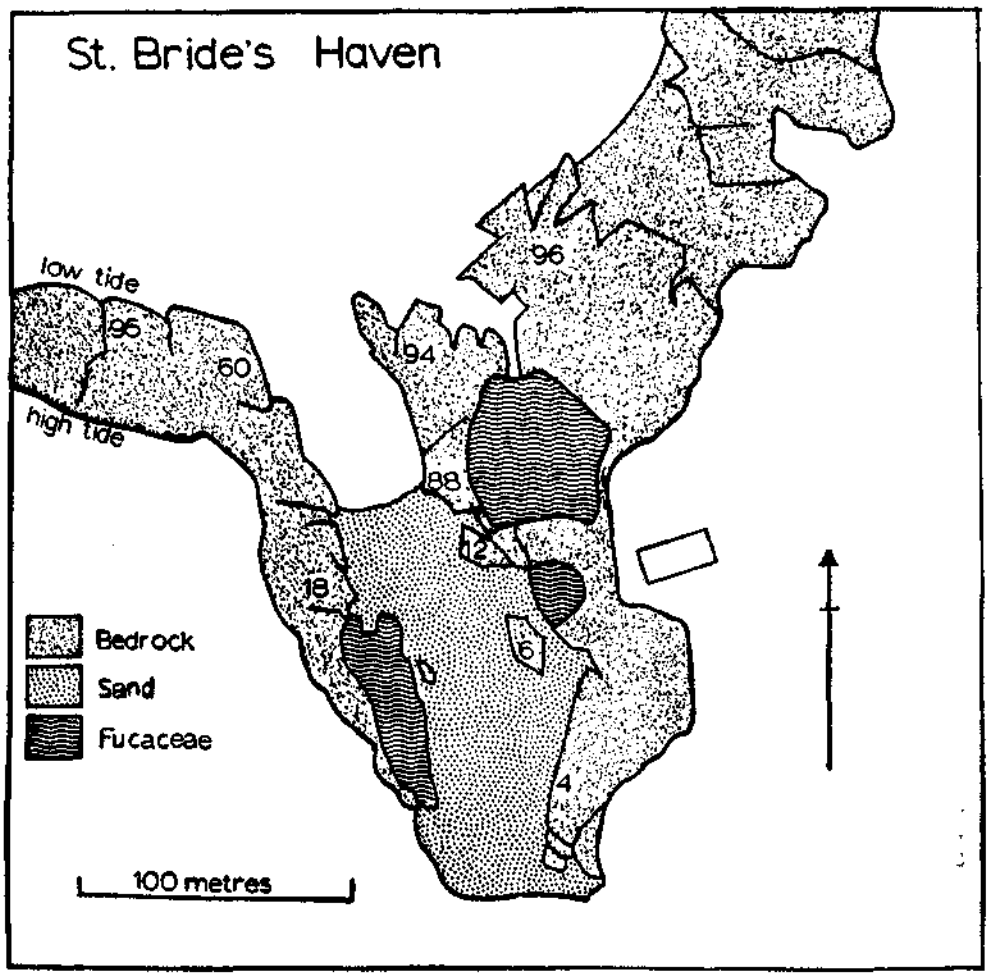

FIG. 3. St. Bride's Haven. Numbers indicate the percentage of *Balanus balanoides* still containing embryos on 1st May 1962, liberations having occurred earlier in the more sheltered parts of the bay.

This striking effect may perhaps have been associated in some way with calm water or liberations of spores by littoral algae. Fertilisation occurs earlier in embayed situations (Crisp, 1959 *a*) and in shelter from currents (Crisp and Clegg, 1960), but it seems unlikely that this would have accounted for the difference in liberation times, since the embryos remain apparently fully developed for so long before liberation. We have also considered and are inclined to reject the possibilities that slight warming of the water or stirring up of littoral diatoms and organic detritus may have been involved. If these had important influences they should have led to liberation being earlier at places further up the British Channel than off Pembrokeshire, but this was not seen. Indeed,

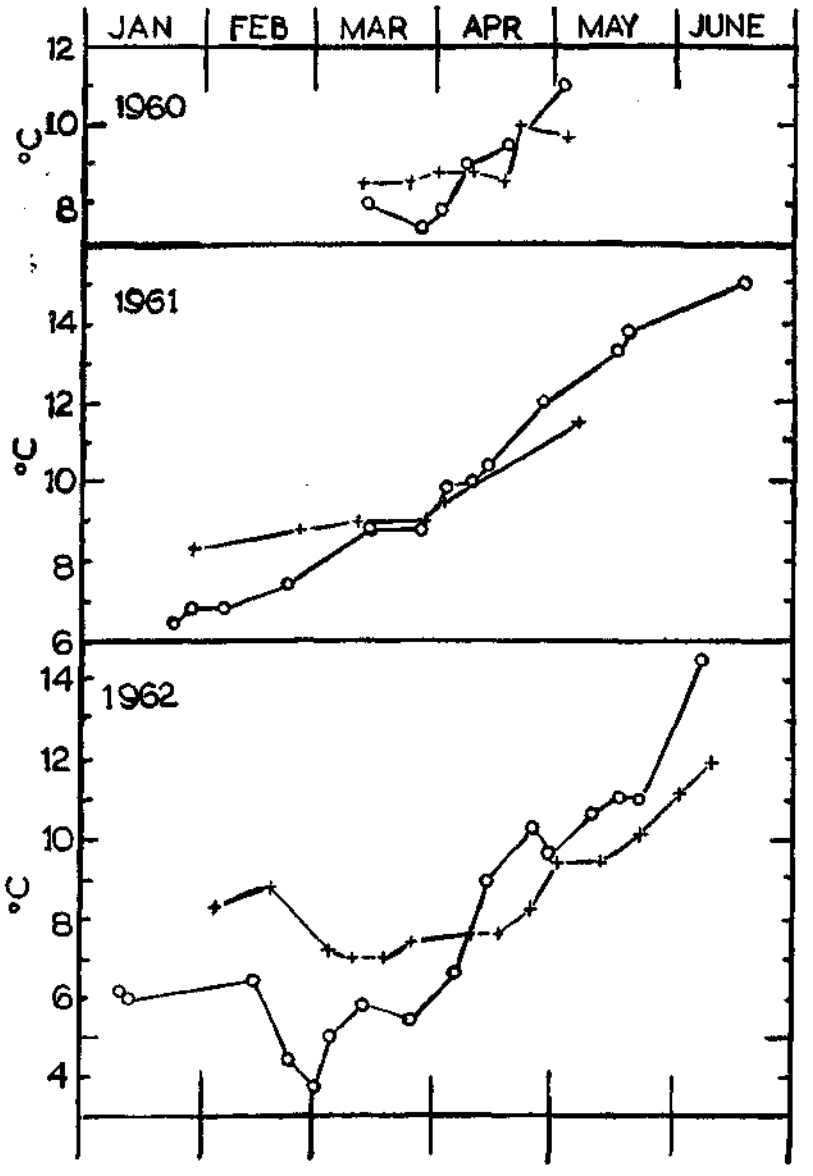

FIG. 4. Water temperatures near the edge of the sea at Mumbles pier (circles), St. Bride's Haven siteA Pembrokeshire (crosses in 1960 and 1961) and St. David's life-boat slip Pembrokeshire (crosses in 1962). The St. Bride's Haven temperatures were taken at half-flood, the others at high tide.

liberations at Penarth and Sully Island, the stations furthest up the Channel, were generally later than elsewhere (Fig. 2). To liberate when the water is more or less still would appear to be of adaptive value, for it would allow the positively phototactic larvae to swim safely away from the surrounding barnacles and actinians, which feed on nauplii and which rely on water movements to bring them food.

Water temperatures were taken during 1960, 1961 and 1962, when collecting samples (*a*) from Mumbles and (*b*) from the tip of Pembrokeshire (Fig. 4). As expected, the range in temperature was greater at Mumbles than off Pembrokeshire, where the sea is deeper. Most liberations of larvae occurred when the sea temperature had warmed to about 9° C. which is warmer than the temperatures recorded by Barnes (1956 *a*) as associated with larval liberation in this species further north (*see also* Barnes, 1959). Such a difference might be expected from the difference in lattiude, but we must remember that transplantation experiments with this species (Crisp, 1962 *a*) have given no evidence of there being geographical races adapted to liberate at different temperatures. North American forms transported to North Wales liberated at the same time as the local population. Moreover liberation at St. Bride's Haven site B in 1962 occurred when the sea temperature off Pembrokeshire was only 7° C. and furthermore, barnacles must be subjected to a wide range of temperatures during low water. In a given locality there seemed to be little or no difference in liberation times between individuals at different tidal levels and on rock of sunny or shaded aspect. It seems unlikely that liberation is linked closely to warming in spring.

For each sample of diatoms, a measured volume of surface water (generally 2 litres) was taken from the edge of the sea and filtered through 200 m.p.i. nylon boulting cloth. The diatoms were washed off and counted in a Sedgwick-Rafter chamber, subsampling with a Stempl pipette if necessary. Table I gives numbers per litre of the various species present. It soon became clear that liberation of larvae is not always associated with particularly high concentrations of net-caught diatoms. Indeed, liberations were generally earlier off Pembrokeshire, where diatoms were sparse, than off Mumbles, where diatoms were abundant.

Total chlorophyll *a* was estimated, using the method and formula of Richards and Thompson (1952). For each sample 3 litres of surface water were filtered through a membrane filter (average pore diameter 300 mμ, maximum 500 mμ). The chlorophyll estimations are shown in Figs. 5 and 6. Liberations of larvae were not associated with well-marked peaks of chlorophyll concentration, but they occurred when these concentrations had increased slightly, from winter values of about 5 mg./m.^{3} Values of more than about 5 mg./m.^{3} were rarely observed. There was no clear evidence of any large spring peak, except from samples taken in the enclosed Queen's Dock in March and from Mumbles Pier in May 1961. The latter may have included much benthic plant material, stirred up in Swansea Bay. Probably turbulence and turbidity delay and reduce the spring outburst in the Bristol Channel (tidal range up to 15 m.), as Gran and Braarud (1935) found in the Bay of Fundy (tidal range up to 17 m.), so that instead of one well-marked spring phytoplankton peak there is a series of peaks, each one slightly higher than the last, corresponding with periods of minimum turbulence.

Apart from the May samples referred to above, the concentrations of chlorophylla off Mumbles were generally no greater than those off Pembrokeshire. We have seen that diatoms were much more abundant off Mumbles than off Pembrokeshire, which suggests that the phytoplankton off Pembrokeshire may have been particularly rich in forms other than diatoms. Since liberation of *Balanus balanoides* larvae was generally earlier off Pembrokeshire than off Mumbles (Fig. 2), our results are not incompatible with the conclusions of Rzepishevsky (1959), that liberation is associated with abundance of flagellates rather than diatoms. Larvae of *Balanus balanoides* grow well initially on a diet of certain flagellates (not on others), but grow better on diatoms and seem to need diatoms to complete their development (Moyse, 1963). It therefore seems unlikely that a response to flagellates could have been selected for, unless these give a particularly prompt reaction to improved conditions, thus heralding outbursts of diatom production.

TABLE I

Numbers per litre of diatoms and other plant cells in samples taken during three years (A) off Pembrokeshire and (B) near Swansea. Asterisks are placed below dates on which barnacles in the area concerned were liberating larvae. Liberation dates were not closely correlated with high densities of diatoms. These occurred more frequently off Mumbles than elsewhere

	1958					1959				1960							
	A		B			A		B		A			B				
	Fish-guard	Tenby	Mumbles		Penarth	Martin's Haven		Mumbles		St. Davids'			Mumbles				
Dates	12–4 *	15–4	11–4	23–4 *	14–4	21–3	14–4	13–3	16–4 *	1–4	18–4 *	22–4	27–3	2–4	19–4	26–4 *	3–5
Asterionella japonica	44	2	5,680	1,223	..	4	..	1,465	195	..	25	..	455	1,550	840	54,300	27,190
Asterionella sp.	..	..	..	..	..	..	..	48	..	..	..	..	..	45	..	..	..
Bacillaria paradoxa	2	43	216	132	17	58	13	74	200	170	215	195	235	225	65	1,300	1,183
Biddulphia spp.	5	30	4	13	8	18	50	28	50	20	20	60	50	85	5	133	67
Ceratium furca	..	..	..	..	..	..	..	..	5	..	..	..	..	..	..	..	..
Chaetoceros spp.	..	70	340	76	..	182	413	104	1,775	60	20	125	915	40	265	2,600	1,334
Coscinodiscus spp.	22	3	32	12	24	55	491	91	135	10	75	50	115	245	90	500	336
Ditylum brightwellii	4	1	12	2	..	11	177	1	5	5	25	20	..	..	..	..	..
Eucampia zoodiacus	..	..	..	..	..	..	..	..	45	..	..	..	..	..	..	..	..
Guinardia flaccida	..	..	..	..	..	..	..	..	5	..	..	..	..	..	..	..	..
Gyrosigma sp.	..	..	..	..	..	..	..	..	..	..	..	..	..	10	1	..	..
Melosira borreri	..	..	..	..	..	..	4	..	..	..	..	..	..	..	..	100	..
Melosira sp.	..	..	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Navicula sp.	3	..	..	..	1	..	..	..		..	..	..	..	..	..	..	..
Nitzschia seriata	..	..	..	..	..	32	21	..	5	..	10	10	125	..	..	..	82
Peridinium depressum	..	..	8	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Rhizosolenia spp.	2	13	60	16	3	3	20	18	20	10	5	..	35	80	100	366	49
Skeletonema costatum	41	529	1,180	413	..	35	260	552	6,550	..	15	..	695	1,765	495	13,866	13,860
Streptotheca thamensis	..	..	4	..	..	3	17	20	15	5	30	40	30	65	10	..	15
Thalassiosira spp.	38	..	8	..	1	39	81	..	40	..	15	65	..	..	..	266	333
Thalassiothrix longissima	..	..	..	..	..	..	..	..	5	..	..	..	..	..	..	..	..
Thalassiothrix nitzschioides	88	5	..	..	2	..	4	..	..	290	265	425	..	40	140	133	336
Unidentified filaments	618	5	60	125	20	3	..	..	75	165	...	30	1,545	1,165	180	600	..

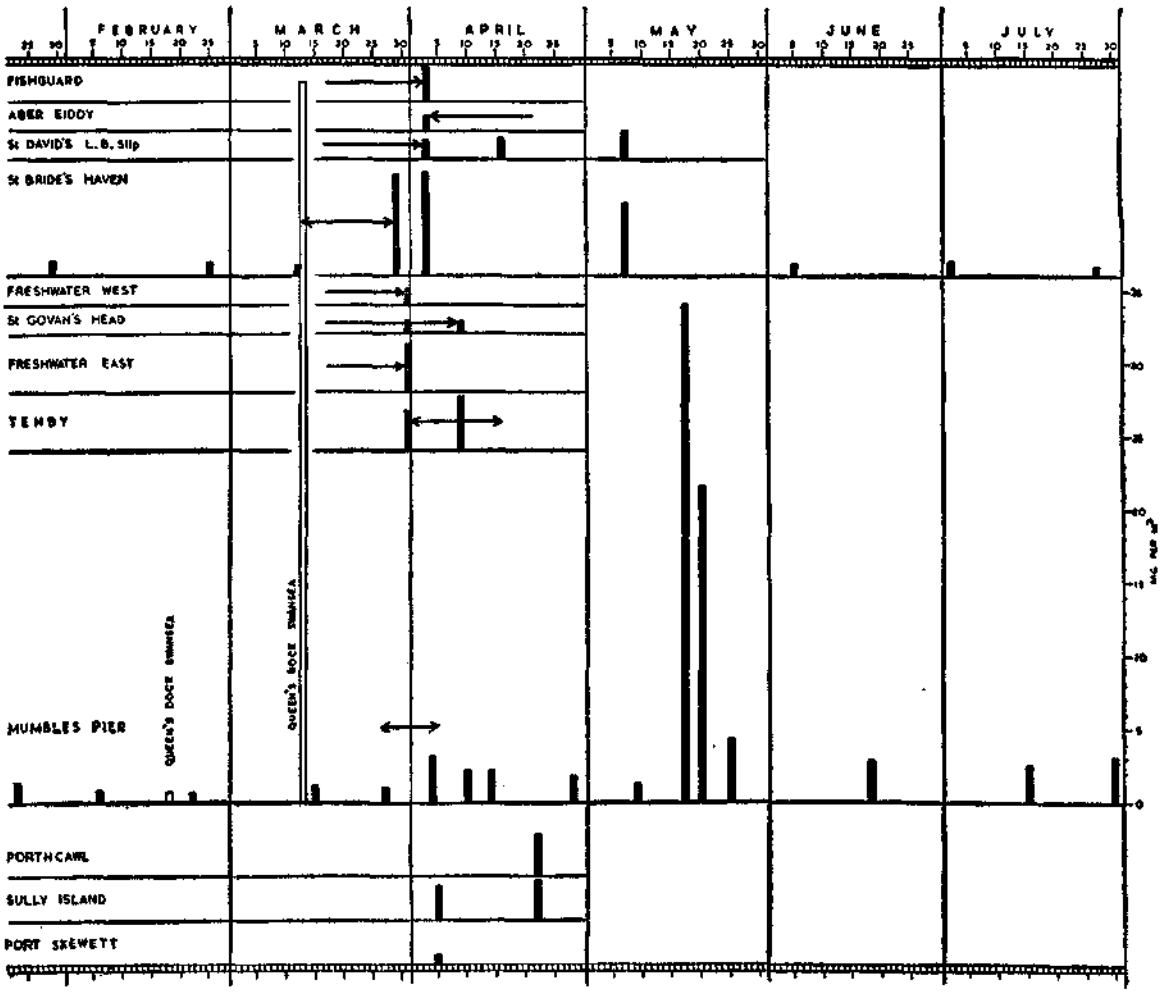

FIG. 5. Concentrations of chlorophyll *a* in surface samples of seawater from various South Wales sites in 1961. The periods within which the local *Balanus balanoides* liberated their embryos are delimited by arrow heads.

The comparative lateness of liberation in the upper reaches of the Bristol Channel was not due to later fertilisation or delayed development. On the contrary, a comparative analysis of development indicated that embryos at Mumbles were slightly ahead of those in Pembrokeshire (Table II). Embryos from both the localities analysed were fully developed by mid-February, to judge from the fact that they would then hatch soon after being placed in seawater in the laboratory. They were, in fact, ready to hatch more than a month before they were actually liberated.

The water in the upper reaches of the Bristol Channel was generally much more turbid than off Pembrokeshire. Figure 7 shows Secchi disc readings taken at the same time as the water temperatures. Values obtained occasionally at Penarth Pier showed that the turbidity there was even greater than at Mumbles. The material involved seemed to be mostly inorganic silt and this is likely to interfere with the feeding of barnacles, at least to some extent. If liberation is a response

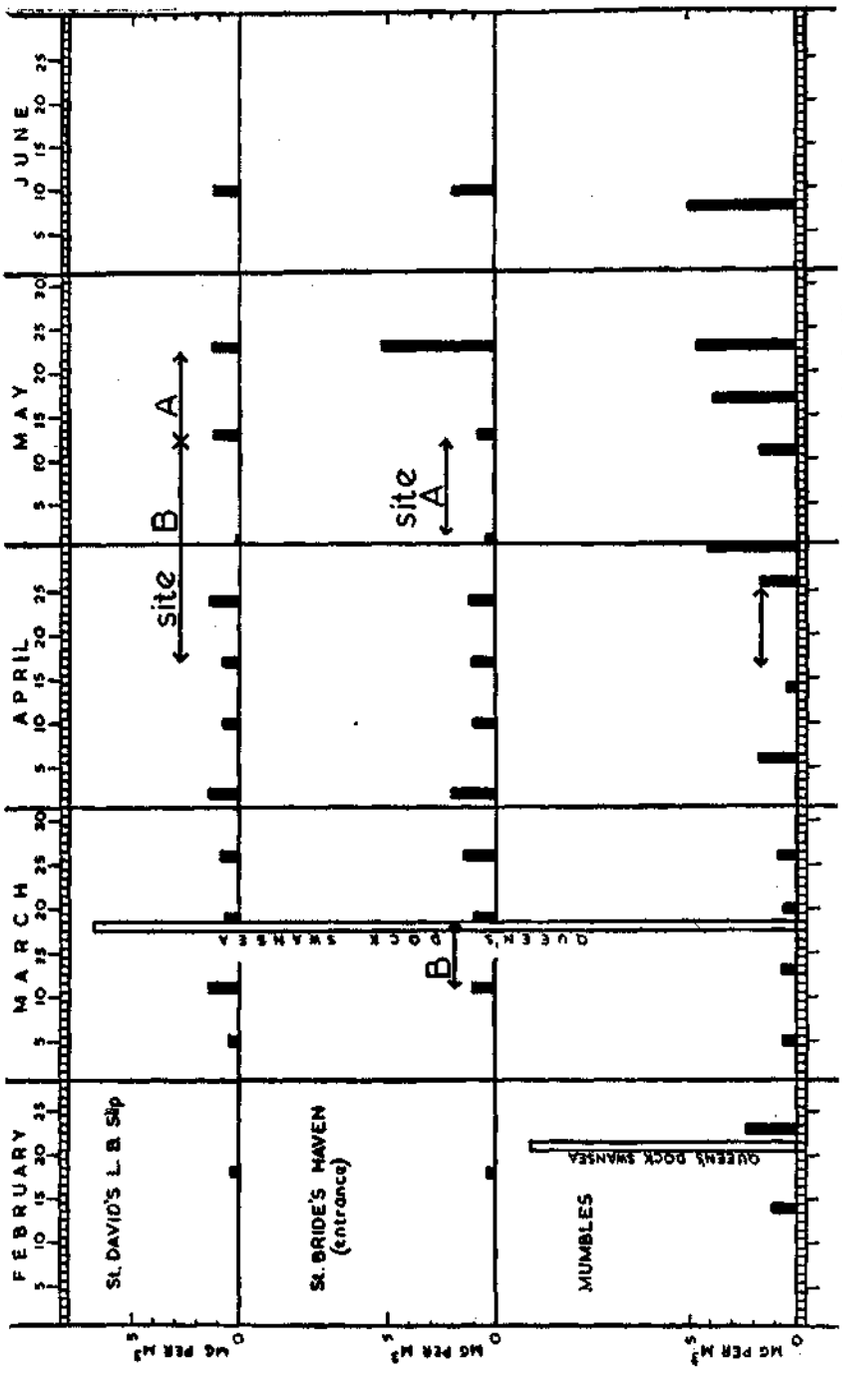

FIG. 6. Chlorophyll *a* in 1962 samples, as in Fig. 5. A and B mark respectively the liberation periods for barnacles on exposed and sheltered sites nearby.

TABLE II

Percentage of Balanus balanoides *embryos at successive stages of embryonic development, classified on a 13-point scale (Crisp, 1954), in samples of adults collected from mid-tide level at Solva (Pembrokeshire) and Mumbles (Swansea) on two dates in the winter of 1959–60. Development at Mumbles was slightly more advanced*

	13th December 1959		31st January 1960	
	Solva	Mumbles	Solva	Mumbles
Embryonic stage				
5	..	..	..	..
6	5	2	..	..
7	93	64	..	..
8	2	34	..	..
9	..	..	4	..
10	..	..	23	8
11	..	..	69	72
12	..	..	4	20
13	..	..	..	..

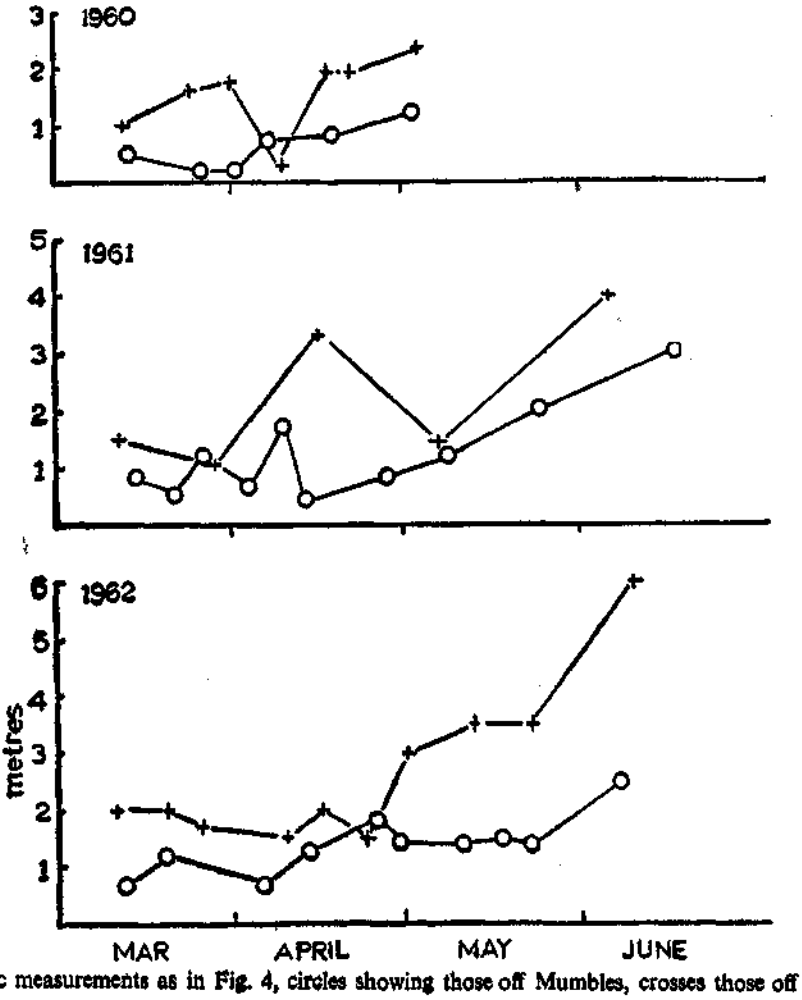

FIG. 7. Secchi disc measurements as in Fig. 4, circles showing those off Mumbles, crosses those off Pembrokeshire.

to feeding, it is therefore not surprising to find evidence of delayed liberation in turbid conditions. However, this delay may arise through lowered oxygen tensions rather than as a direct effect of feeding, for Crisp (1959 *b*) has calculated that the size of an egg-mass is near the limit allowing oxygen to diffuse in sufficiently for the embryos in the centre, and many of the egg-masses collected at Penarth late in the season were dead and decomposing.

Feeding of Nauplii

Rearing experiments with barnacle larvae have shown that the arctic-boreal species *Balanus balanoides* needs diatoms for food, whereas the lusitanian and tropical species *Chthamalus stellatus* (Poli) and *Lepas anatifera* (L.) need flagellates (Moyse, 1963—*see also* Fig. 8). This seems of wide interest, for it may reflect differences in the relative importance of the groups contributing to the phytoplankton of cold and warm seas. So far, not even the taxonomy of phytoplankton is well known and we have only a hazy picture of the distribution of the main groups of larger forms, *viz.*, those which can be caught in fine nets. However, the picture we have (*see e.g.*, Raymont, 1963) is one to which the food requirements of these barnacle nauplii broadly conform. Diatoms are particularly well known for their contributions to the plankton and abyssal oozes of high latitudes and to the phytoplankton peaks of spring, when the water is cold. Dinoflagellates and coccolithophores contribute more to the plankton of warmer seas and summer seasons. We do not know whether the two latter groups are ecologically representative of flagellates in general, but perhaps they are, for we may guess that the motility of flagellates needs more energy than the maintenance of buoyance in diatoms.

The fact that the larvae of *Chthamalus stellatus* have dietary needs similar to those of oceanic barnacles helps to explain the distribution of this species, which contrasts so markedly with that of *Balanus balanoides* (Moore and Kitching, 1939; Crisp, 1950; Southward & Crisp, 1954; Lewis and Powell, 1960). But this western distribution, adjoining deep water, does not necessarily imply that flagellates are not found abundantly elsewhere. For only in such places, where the water is clear, could a fine filtering mechanism operate efficiently, without becoming clogged with silt. At Swansea, in several recent years, there was no settlement of *Chthamalus stellatus*, perhaps because of the generally turbid water. The adults live long however (Barnes, 1956 *b*) and there is a large population here, presumably derived from occasional spatfalls every few years, when the water may clear a little and other conditions become favourable.

More recent laboratory experiments have shown that larvae of *Lepas pectinata* Spengler also need flagellates as food. The larval stages of this species and of *L. anatifera* have been studied and will soon be described. Their feeding mechanism has also been studied, with the aid of cine-photography, and a description is being prepared. There seem to be some differences from previous descriptions of feeding in *Balanus* (Lochhead, 1936; Norris and Crisp, 1953; Gauld, 1959). The antenna is the main food-collecting organ and it bears delicate plumose setae and setules, which form a close-meshed filtering area in the basal region of the endopodite. Fine particles, caught in this area, are scraped from it by the endopodite setae of the mandibles, which are combed in turn by palisades of bristles on the undersides of the labrum. Thence they are gradually pushed into the mouth by the gnathobases and neighbouring processes, during subsequent strokes of the antennae and mandibles.

The limbs would appear to be primarily for feeding. Locomotion is hindered, in the later naupliar stages, by the development of very long processes which trail posteriorly and bear numerous fine spines. These must serve to increase drag and hence the volume of water filtered to obtain food, during each stroke of the limbs. The caudal spine in a Stage VI nauplius of *Lepas anatifera* is about 9 mm. long, but the body is only about 1·5 mm.

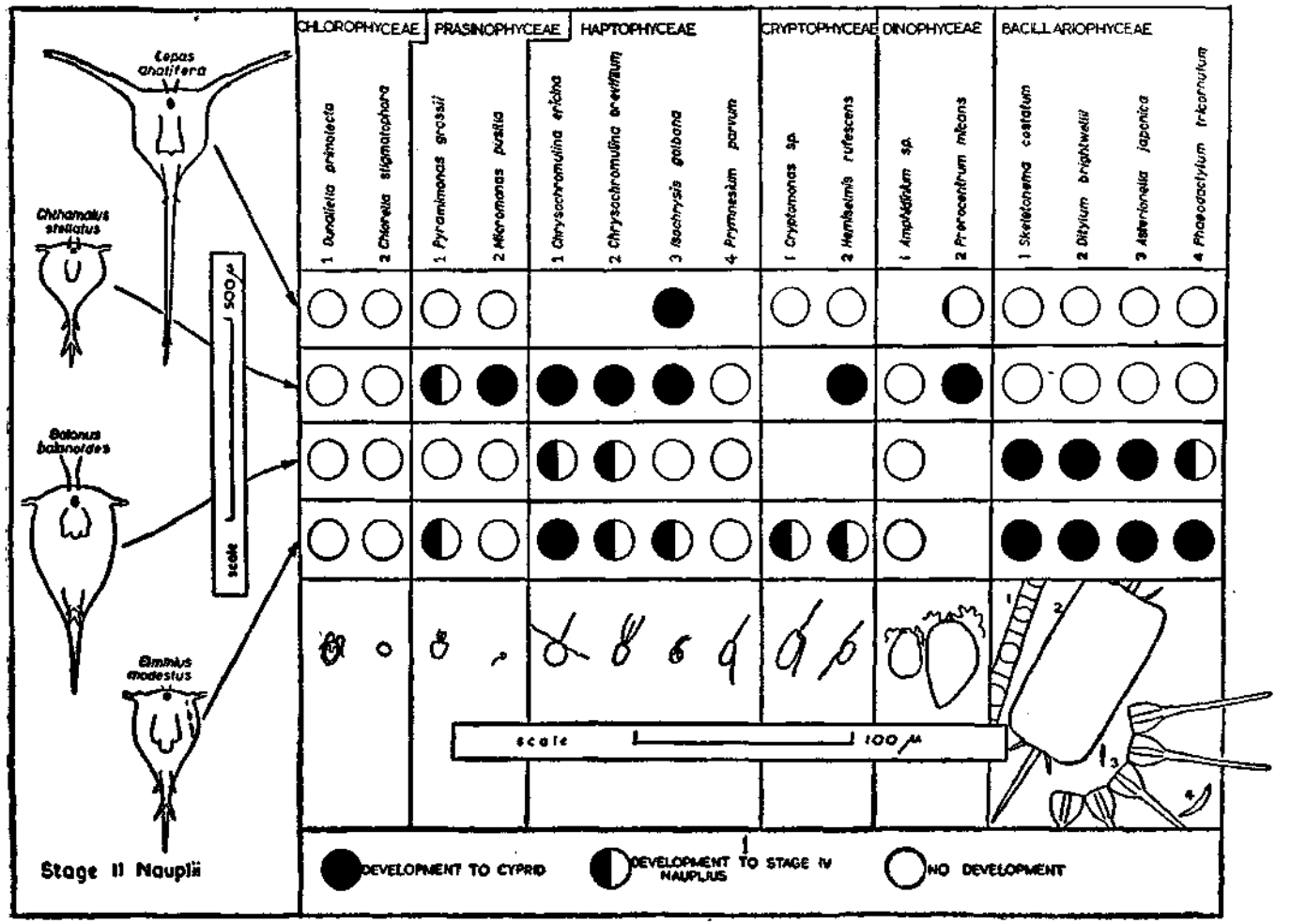

FIG. 8. Diagrammatic summary of the results of rearing barnacle larvae on different unicellular algae. The barnacle larvae are shown at the stage at which they begin to feed. *Lepas* and *Chthamalus* completed development on flagellates, but *Balanus balanoides* needed diatoms. The algae, which were kindly provided by Dr. Parke, are classified according to Parke and Dixon (1964). The algal cells are drawn to a scale about 5 × that of the larvae.

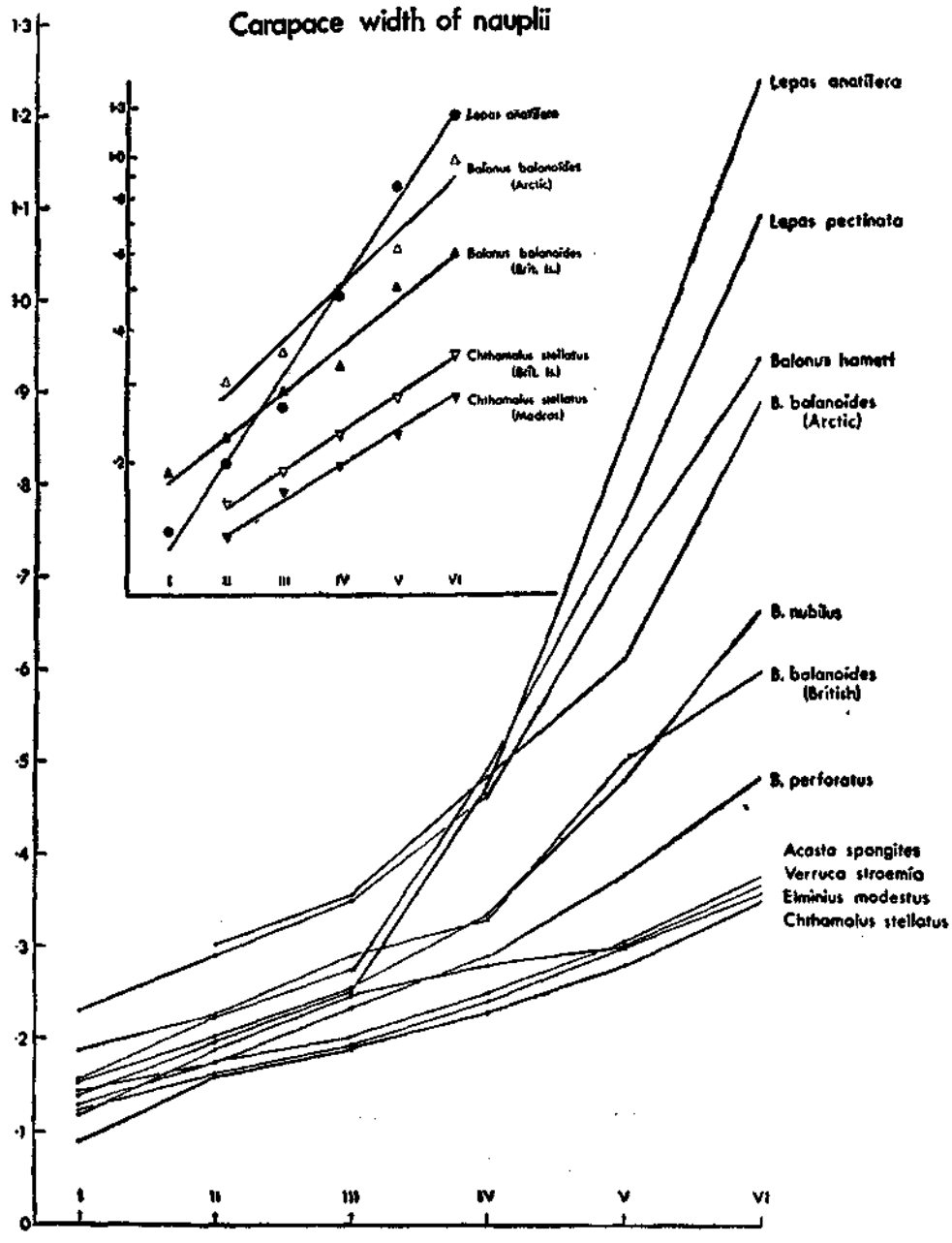

FIG. 9. Relative sizes of nauplii at each of the six naupliar stages, showing the difference between oceanic and littoral barnacles and the trend with latitude. Sizes are plotted as carapace widths in millimetres and a selection is shown on a logarithmic scale in the inset diagram. The following are the authorities for the measurements (the species being listed below in an order which is approximately that of their distribution, from equator to the arctic): *Lepas pectinata* and *Lepas anatifera* (Moyse, unpublished), *Chthamalus stellatus* (Bassindale, 1936 and Daniel, 1958). *Acasta spongites* and *Pyrgoma anglicum* (Moyse, 1961), *Balanus perforatus* (Norris and Crisp, 1953), *Elminius modestus* (Knight-Jones and Waugh, 1949), *Verruca stroemia* (Bassindale, 1936), *Balanus nubilus* (Barnes and Barnes, 1959), *Balanus balanoides* (Crisp, 1962 *b*) and *Balanus hameri* (Crisp, 1962 *c*).

Even without their trailing spines, these late larvae must be amongst the largest nauplii known, but their early stages are quite small, like those of other tropical barnacles (Fig. 9). For these barnacles show the usual correlation between egg size and latitude (*see* Thorson, 1946), which is remarkable, for this correlation is generally associated with the trend towards direct development in high latitudes, whereas all these barnacle larvae are planktotrophic. Presumably the trend amongst barnacle larvae is related to the well-known tendency for large-celled phytoplankton species to occur in high latitudes. It also allows more numerous eggs and shorter planktonic lives in warm latitudes, where life is limited more by predation than by shortage of energy and where the vulnerable planktonic stage is best kept brief. We may particularly invoke the abundance of small fishes in shallow tropical seas to explain why the larval life of *Chthamalus* is so much shorter than that of *Balanus balanoides* (Moyse, 1963). Hence in these littoral species with small eggs, the late larvae are small too.

In Lepadidae larval growth is very different (Fig. 9). These oceanic forms have a remarkably long larval life (Moyse, 1963), with large growth increments, resulting in relatively enormous late larvae. Presumably their size is related to frequent scarcity of the drifting substrata, which the cyprids must find for attachment and metamorphosis. The cyprids probably do not feed, so need large reserves in case their search is prolonged. In littoral barnacles such a long swimming life would add to the hazard of being swept too far from the shore.

Littoral Zonation of Young and Old Barnacles

The searching phase of barnacle cyprids may involve reactions to surface contours and texture (Crisp and Barnes, 1954), algal films (Daniel, 1955), water currents (Crisp, 1953 and 1955; Crisp and Stubbings, 1957), light (Barnes, Crisp and Powell, 1951; Daniel, 1957) and pressure (Knight-Jones and Qasim, 1965). They also respond to the presence of previously settled individuals in a striking fashion, which has been carefully analysed by Crisp and Meadows (1962, 1963). Bearing this gregarious reaction in mind, we recently surveyed the distributions of young and old barnacles on littoral rocks, to see how closely the zonation of recently settled spat copied that of the adult population. We chose Watwick Bay, near the mouth of Milford Haven, for there four easily recognised species occur quite abundantly. The place is also convenient for studying the effects of shading and insolation, for the Old Red Sandstone there runs out eastward (towards the sea) in tall narrow ridges, presenting north and south faces which are very similar, except in the aspect presented to the sun.

Table III

Numbers per square decimetre of adult barnacles at different tidal levels in Watwick Bay, Dale, Pembrokeshire on (S) south- and (N) north-facing rock surfaces. High-water neap tides, mid-tide level and low-water neap tides are at approximately 17, 12·5 *and* 8 *feet above chart datum respectively*

Feet above Chart Datum	*Chthamalus stellatus*				*Elminius modestus*				*Balanus balanoides*		*Balanus perforatus*			
	Adults		Spat		Adults		Spat		Adults		Adults		Spat	
	S	N	S	N	S	N	S	N	S	N	S	N	S	N
19	20	30	0	0	0	0	0	0	0	0	0	0	0	0
17	120	150	2	1	1	6	0	0	5	30	0	0	0	0
15	120	2	3	1	6	20	1	5	40	10	0	0	0	0
13	30	15	6	12	30	20	2	1	100	80	0	0	0	0
11	1	3	4	20	40	10	10	10	160	200	0	5	0	100
9	0	1	4	30	300	50	100	10	406	200	0	6	0	40
7	1	0	110	0	12	2	6	1	247	10	4	27	20	400
5	0	0	0	0	1	0	1	0	0	0	30	6	130	95

We estimated densities of adults and spat at vertical intervals of 1 foot (Table III). The zonation of the adult barnacles conformed to the usual pattern for these species (*see* Moyse and Nelson-Smith, 1963; Lewis, 1964) and all had their upper limits somewhat raised by shading. At lower levels, however, both adults and spat tended to be more abundant on the south sides of the ridges.

The *Balanus balanoides* were all adult, the youngest having settled the previous spring, but there were many recently settled spat of each of the other species, which are summer breeders. The distributions of spat of *Balanus perforatus* Bruguière and *Elminius modestus* Darwin agree closely with those of the adults. Although *B. perforatus* is capable of self-fertilisation (Barnes and Crisp, 1956), it seems highly probable that its cyprids are gregarious during settlement, as those of *Elminius* are known to be (Knight-Jones and Stephenson, 1950; Knight-Jones, 1953). They thus concentrate upon recolonising the zone which the presence of adults marks out as suitable for them.

With *Chthamalus* it was clearly otherwise. Connell (1961 *a*) remarked that many *Chthamalus* spat settle below the zone of abundance of the adults and that the species is excluded from the lower shore only by competition and predation. Table III agrees with his findings and so do our observations on other shores. Perhaps *Chthamalus* settled mostly at low levels on the shore because those are most accessible, or perhaps a large proportion of the cyprids settling higher are desiccated when very young and so escape notice. In any case, the data do not suggest gregariousness in this species, though it remains possible that the cyprids may settle on the lower littoral rocks in response to adsorbed arthropodin (Crisp and Meadows, 1963) derived from the dense population higher on the shore.

We found that very many *Chthamalus* spat on the lower shore had settled in contact with previously settled barnacles of their own and other species, whereas in *Balanus balanoides* and *Elminius* cyprids space themselves out during settlement, seeking bare spaces (Connell, 1961 *b*) and rarely touching their own species (Knight-Jones and Moyse, 1961). The little territories left clear, however, are directly related to the size of the cyprids (Crisp, 1961) and the cyprids of *Chthamalus* are very small, so this matter needs particularly careful investigation. At present, however, it seems that *Chthamalus stellatus* may be less responsive than *Balanus* to the presence of previously settled individuals. Perhaps this species is guided to littoral rocks by no more than its preference for bright light (Daniel, 1957) and rough surfaces (Moore and Kitching, 1939).

Summary

At each sampling site, along the coast of South Wales, the proportion of gravid *Balanus balanoides* fell from 95% to less than 10% within about a week, indicating mass liberation of larvae.

Liberation occurred several weeks earlier in sheltered bays than on neighbouring headlands, suggesting that it was favoured by calm water. It occurred when sea temperatures were between 7 and 10°, and most frequently at about 9°. It was not closely associated with large concentrations of diatoms or total chlorophyll and it tended to be delayed in the turbid upper reaches of the Bristol Channel. If a minimum phytoplankton density is necessary to induce liberation, this threshold is probably greater in water containing much silt, which may interfere with feeding.

Rearing experiments showed that larvae of this high-latitude species need diatoms as food, whereas larvae of certain oceanic and low-latitude barnacles need flagellates. *Lepas* larvae are capable of sieving off 5μ organisms. Their youngest stages are small, as in most warm-water barnacles, but eventually they reach a large size; this presumably helps the fasting cyprids, if their search for floating substrata is prolonged.

The vertical zonations on littoral rocks of *Balanus* and *Elminius* spat agreed with those of the adults, but *Chthamalus* spat mostly occurred far below the main adult zone, which on British shores is comprised mainly of long-lived individuals.

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THE INFLUENCE OF THE CONTOUR OF THE SUBSTRATUM ON THE SHAPES OF BARNACLES

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ABSTRACT

By growing the barnacles *Balanus balanoides* L. and *Elminius modestus* Darwin on convex and concave surfaces we have demonstrated that changes from the normal shape characteristic of barnacles growing on a plane surface can be induced.

Barnacles grown on convex surfaces were taller, with externally convex parietes, relatively wider apertures and were less strongly ribbed than those grown on plane surfaces. Growth on a concave surface led to the opposite characters, namely a more depressed shape, externally concave parietes with an exaggerated development of the longitudinal ribs, and relatively narrower apertures. The distortions induced by a deviation of the contour of the substratum from a plane also caused modifications to the relative weight and size of the compartments.

The change in the shape can be explained on the assumption that the angle between parietes and the surface over which they spread during growth remains constant. A formula derived from this assumption predicted the effect of surface contour on the height/base ratio. The calculated and observed values were in good agreement for *Balanus balanoides* and in fair agreement for *Elminius modestus*.

Since the form of the surface on which the barnacle has grown is so important in determining its ultimate shape, it is a factor that should always be borne in mind in systematic studies.

INTRODUCTION

BARNACLES of a given species show considerable variation in shape. Some individuals assume an unusually low flattened form, spreading out over the substratum. Others may grow exceptionally tall. Tall specimens are to be observed most often in populations where the individuals have become crowded together. The parietes become elongated, often tapering towards the base, so that only a fragile connection with the substratum remains. It is easy to explain distortion from the natural shape in such columnar specimens in terms of lateral compression and plasticity of growth. In this paper, however, we shall consider mainly differences of form found among freely growing barnacles.

We have noticed that individuals of *Balanus balanus* found on the convex surface of shells of *Modiolus modiolus* are frequently taller than those growing on flat surfaces. The parietes are convex externally and less strongly ribbed than they are in the typical form, while the opercular opening is particularly wide. When, as occasionally happens, an individual is found growing on the inner surface of a *Modiolus* shell, we have noticed the opposite characteristics, namely, a low conical shape, the outer surface of the parietes concave in vertical section, the shell strongly ribbed and the aperture rather small. This correlation has now been examined experimentally by growing two species of intertidal barnacles, *Balanus balanoides* (L.) and *Elminius modestus* Drawin, on a series of surfaces of different curvature.

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Experiments on the Growth of Barnacles on Convex and Concave Surfaces

The experimental surfaces were prepared from a cold setting resin which was moulded to the appropriate shape while still plastic. For the concave surfaces a pool of freshly mixed resin was poured out on to a base plate of phenol formaldehyde sheet on which a circular retaining barrier had been placed to prevent the resin from spreading too far before it had set. Metal bolts, screwed through the base plate, thus became embedded in the resin and so fixed it firmly to the base plate as it set. Just before it hardened, glass spheres, lightly coated with glycerine, were pushed into the resin to form spherical concavities. The spheres were removed when the resin had hardened sufficiently. The concave surfaces so formed were rubbed down and polished after the resin had become completely firm.

For the convex surfaces, concave moulds roughly hemispherical in shape were first prepared from Keen's cement, using the same glass spheres. These moulds were then smeared with glycerine to prevent adhesion and filled with the same cold setting resin. Before the resin blocks had hardened completely, a glycerine smeared glass rod was inserted vertically into their free surface to form a hole which was afterwards tapped to take a bolt. After the resin had hardened it was removed from the mould and its flat surface ground smooth. The central hole in this surface was then tapped, the block screwed down to a phenol formaldehyde base plate so that its convex surface could be smoothed and polished.

Before immersion in the sea, small pits were drilled, not only on the convex and concave surfaces, but also on the intervening plane surfaces of the base plate. These small pits localised settlement where required (Crisp, 1960 *a*). Two sets of concave and convex surfaces were thus prepared, one set being exposed to settlement by *Balanus balanoides*, and the other, at a later date, to settlement by *Elminius modestus*. Settlement occurred somewhat sparsely on the more convex surfaces. As the barnacles grew, they were thinned out when necessary in order to prevent their bases from coming into contact, and photographs were regularly taken. At the end of the growing season all the barnacles were removed. The height of each specimen was measured vertically from the base to the top of the carina and rostrum and a mean value taken and the diameters of the base and of the opercular aperture were measured with a travelling microscope along, and at right angles to, the rostro-carinal axis. Each barnacle was dried for 24 hours at 110° and weighed. The tissues were then destroyed by boiling for a short time in strong caustic alkali and the shell plates and valves, after being washed and dried, were weighed individually.

The shell compartments of *Balanus balanoides* were then examined and classified in accordance with the prominence of, and the number of, crenations present. The shape of individuals of *Elminius modestus* was fairly uniform, all possessing eight main vertical folds, two to each compartment.

Variation of Form on Surfaces of Different Curvature

(*a*) *Shape of Barnacles*

In both species the individuals which had grown on convex surfaces were relatively taller than those grown on plane surfaces, while those grown on concave surfaces were flatter. This may be seen from the three specimens of *Elminius modestus* illustrated in Plate I A. The aperture of individuals grown on convex surfaces was wider, in comparison with the mean basal diameter, than that of individuals grown on plane surfaces, and the latter had apertures wider than those of specimens grown on concave surfaces. In Plate I B the same three specimens of *Elminius* have been photographed from above to show the increase in the opercular aperture with increase in the convexity of the substratum.

In Table I the values of the appropriate parameters of relative height and aperture width are given for individuals on surfaces of different curvature. They have been averaged over specimens

TABLE I

Relative height and aperture of Balanus balanoides *and* Elminius modestus *grown on surfaces of different radii of curvature*

Radius of curvature R	*Balanus balanoides*			*Elminius modestus*		
	Number of specimens	Relative height $H/\sqrt{LB}$	Relative aperture $\sqrt{a_1 a_2}/\sqrt{LB}$	Number of specimens	Relative height $H/\sqrt{LB}$	Relative aperture $\sqrt{a_1 a_2}/\sqrt{LB}$
Convex						
— 7·5 mm	4	0·424	0·442	1	0·625	0·570
— 12·5 mm	8	0·411	0·432	8	0·455	0·481
— 17·0 mm	6	0·395	0·455	10	0·428	0·465
— 27·0 mm	16	0·375	0·390	15	0·440	0·500
Plane	33	0·342	0·370	18	0·405	0·475
Concave						
+ 27·0 mm	7	0·288	0·380	4	0·370	0·520
+ 17·0 mm	5	0·277	0·300	3	0·372	0·502
+ 12·5 mm	4	0·259	0·390	3	0·454*	0·540*
+ 7·5 mm	1	0·230	0·360	1	0·322	0·444

* Specimens just touching when removed.

of all sizes growing on each curvature, since no significant trend in shape could be detected between the larger and smaller specimens. The relative height was taken as the ratio of the height H to the geometric mean of the length and breadth of the base, $\sqrt{LB}$, while the relative aperture was taken as the ratio of the geometric mean of the length and breadth of the opercular aperture, $\sqrt{a_1\ a_2}$, to the same quantity, $\sqrt{LB}$. The radius of curvature was taken as half the diameter of the original glass spheres from which the moulds were constructed, and the convention has been used throughout that convex surfaces have a negative and concave surfaces a positive radius of curvature. The change in relative height and aperture with surface shape is well demonstrated in *Balanus balanoides*. The results for *Elminius modestus* showed a similar trend in relative height but the relative apertures were variable.

(*b*) *Folding of Parietes*

In *Balanus balanoides* there appeared also to be an increase in the number and prominence of the crenations or folds of the basal region of the parietes with increased concavity of the substratum. This may be seen in the three examples illustrated in Plate I C. A detailed analysis of the number and character of the crenations in the parietes confirmed this fact as shown by Table II, and the analysis of variance based on these results is given in Table III. The mean number of crenations found in animals grown on convex, plane and concave surfaces increased significantly in that order, though there was no significant difference between two groups of individuals growing on plane surfaces of slightly different texture. The parietes of animals grown on concave surfaces appeared also to be thicker. Considerable variation in the number of crenations was evident between otherwise similar individuals growing on a plane surface, especially in *Balanus balanoides*, where the marginal crenation was less regular than in *Elminius modestus*. The degree of folding of the walls varied with the size of the specimen. Individuals less than 5 mm in diameter had smooth walls, while those of more than 10 mm in diameter almost always had some folding of the wall plates

TABLE II

Number of crenations in the compartments of Balanus balanoides *grown on convex, plane and concave surfaces. The score was a qualitatively assessed index of the prominence of the crenations, taking a score of 2 for deep, 1 for normal and 0 for shallow ridges*

Type of surface	Number of specimens	Mean Score	Mean number of crenations on each of the compartments						Total number
			Carina	Rostrum	Rostro laterals		Carino laterals		
					Left	Right	Left	Right	
Convex ..	25	0·84	2·5	5·0	4·1	4·3	1·3	1·4	18·6
Plane ..	22	1·00	3·0	5·6	4·4	4·5	1·5	1·7	20·5
Concave ..	9	1·56	4·4	7·5	5·7	5·9	1·9	1·9	28·2
TOTAL ...	56	1·02	3·0	5·6	4·5	4·6	1·5	1·6	20·9

TABLE III

Analysis of variance of the total number of crenations counted on specimens of Balanus balanoides *grown on convex, plane and concave surfaces*

Source of variation	Sum of squares	Degrees of freedom	Mean square	Ratio of mean squares
Between convex, plane and concave surfaces ..	617·5	2	308·8	7·25*
Between two types of plane surface ..	109·1	1	109·1	2·57
Between individuals ..	2,214·0	52	42·5	(1·00)

* Significant at 1% probability level.

towards the base. Differences in crenation were quite obvious in specimens of equal size, and generally those which showed strong crenations at an early age continued to grow in this form. A comparison of individuals with strongly crenated margins with others, grown under identical conditions and of the same age, but having weakly crenated margins, is made in Table IV; it revealed no related differences in form. The ratio of the size of the opercular aperture and of the

TABLE IV

Comparison of strongly and weakly crenated individuals from a population of equal age grown under identical conditions

Crenations at basal periphery	Mean weight gm	Mean relative height $H/\sqrt{LB}$	Mean relative aperture $\sqrt{a_1 a_2}/\sqrt{LB}$
Weak ..	0·586	0·315	0·335
Moderate ..	0·623	0·327	0·339
Strong ..	0·737	0·316	0·334

height to the basal diameter were identical. The weight of the more strongly crenated individuals was however greater, but this could be expected, since the degree of crenation increased with the size of the individuals.

There was no evidence that strongly crenated specimens were inherently faster growing. Eighty pairs of individuals of a uniform age of two months were chosen from a population, one of each pair being strongly and the other weakly crenated. They were then allowed to grow for a further five months under similar conditions and were then removed and reweighed. The mean net weight of those with initially smoother margins was 646 mg as against a net weight of 626 mg for those with initially more folded walls. The difference was not significant in relation to its standard error of 28 mg. It is unlikely therefore that the factor which causes differences between the crenation of the margins of specimens of equal size and age is the rate of growth of the individuals. The reasons for such differences are not at present understood.

(c) Relative Weight of Shell Compartments

The mean dry weight and mean shell weight of specimens of *Balanus balanoides* showed no large differences in relation to the type of surface on which the barnacle was growing. Table V compares the weight of specimens of known age and shows a slightly smaller average weight for specimens growing on concave surfaces. The difference was probably caused by the unfavourable effect on growth of a decrease in the flow of water, such as would occur if a barnacle grew in a depressed position. The flow past an elevated barnacle would be correspondingly greater (Crisp, 1960 *a*). It is impossible to distinguish between the influence of water flow and any small influence that the shape of the surface might have on total growth. Hence, we shall consider only the relative weights of parts of the barnacle as percentages either of the total dry weight or of the total shell weight.

TABLE V

Date	Age of specimens	Mean weight of specimens growing on: Convex surfaces	Concave surfaces
	days	mg	mg
13 July ..	50	26·4	20·7
9 September ..	105	171·8	183·2
26 September ..	125	257·1	216·2
Mean weight ...	...	151·8	140·0

Table VI shows that in *Balanus balanoides* the dry tissue weight was a very variable fraction of the total weight, lying generally between 7 and 12%. It showed no clear correlation with surface contour. In *Elminius modestus* (Table VII) the dry weight of tissue occupied a much higher proportion of the total dry weight, the shell being lighter than that of *Balanus balanojdes*. The dry weight in *Elminius modestus* did show a clear correlation with the type of surface on which the specimen was growing, the proportion of tissue weight being high on very concave surfaces. It seems probable that in *Elminius* the total weight of the wall plates is reduced when the barnacle is growing on a concave surface, for not only was the tissue weight relatively greater than the shell weight under these conditions, but also the relative weight of the four opercular valves was higher. In *Balanus balanoides* the ratio of the weight of the valves to that of the shell was smaller in comparison with that of *Elminius modestus*, and it showed no significant variation with the contour of the surface.

TABLE VI

Weights of parts of specimens of Balanus balanoides *grown on surfaces of different curvatures expressed as percentages*

Radius of curvature	Number examined	Dry tissue weight	Carina	Rostrum	R. Laterals	L. Laterals	Mean for R. & L. laterals	Valves
		Total dry weight %	Shell weight %	Shell weight %	Shell weight %	Shell weight %	%	Shell %
− 7·5 cm ..	2	7·6	8·8	29·0	25·6	27·6	26·6	8·7
− 12·5 cm ..	5	11·7	12·8	27·6	28·6	23·8	26·2	7·4
− 17·0 cm ..	5	10·1	15·5	25·7	26·8	25·6	26·2	6·7
− 27·0 cm ...	13	9·9	13·8	27·5	27·0	25·0	26·0	7·0
Mean convex ...	25	10·1	13·5	27·3	27·2	25·1	26·1	7·2
Plane ...	21	11·4	15·7	24·4	26·2	26·6	26·4	7·5
+ 27·0 cm ..	4	10·2	14·7	27·6	24·4	26·0	25·2	8·1
+ 17·0 cm ..	2	8·5	13·0	28·1	29·9	21·1	25·5	8·4
+ 12·5 cm ...	2	12·5	9·5	29·5	27·8	25·5	26·7	7·7
+ 7·5 cm ..	1	9·5	6·4	41·0	12·7	31·9	22·3	7·3
Mean concave ..	9	10·3	12·2	29·6	25·1	25·5	25·3	8·0
Grand mean ..	55	10·6	14·2	26·6	26·5	25·7	26·1	7·4

TABLE VII

Weights of parts of specimens of Elminius modestus *grown on surfaces of different curvatures expressed as percentages*

Radius of curvature	Number examined	Dry tissue weight	Carina	Rostrum	R. Laterals	L. Laterals	Mean for R. & L. laterals	Valves
		Total dry weight %	Shell weight %	Shell weight %	Shell weight %	Shell weight %	%	Shell %
− 7·5 cm ..	1	16·2	18·7	27·9	21·7	21·2	21·5	10·6
− 12·5 cm ..	8	14·5	18·5	28·8	20·7	21·9	21·3	10·4
− 17·0 cm ..	10	13·7	19·8	27·9	21·7	19·9	20·8	10·8
− 27·0 cm ..	15	14·3	21·0	24·5	21·8	21·2	21·6	11·5
Mean convex ...	34	14·2	20·0	26·6	21·5	21·0	21·2	11·0
Plane ..	18	16·3	22·1	24·2	21·2	21·4	21·3	11·2
+ 27·0 cm ..	4	16·7	19·3	25·2	20·8	22·5	21·7	12·3
+ 17·0 cm ..	3	20·0	20·8	26·2	20·1	18·4	19·2	14·6
+ 12·5 cm ..	3	21·6	19·2	24·2	21·1	22·0	21·6	13·6
+ 7·5 cm ..	1	33·0	18·8	18·5	25·8	22·3	24·0	14·6
Mean concave	11	20·4	19·6	24·6	21·1	21·2	21·2	13·5
Grand Mean ..	63	15·9	20·5	25·6	21·4	21·1	21·2	11·5

In both species the relative weight of the wall plates was fairly constant, though in specimens of *Balanus balanoides* growing on very convex or on very concave surfaces the carina was small compared with that of individuals which had grown on a plane surface. Specimens with reduced carinae were usually rather distorted, having somewhat enlarged rostral compartments. It appears probable that the forces caused by growth on an abnormally shaped surface were liable to cause a suppression of the carinal rather than of any other compartment in this species. A slight trend in the same direction can be seen in the relative weight of the carina in *Elminius modestus* (Table VII). In both species the rostral compartment was the largest, though in *Elminius modestus* this compartment appeared to show some reduction as a result of growth on a concave surface.

(d) Compensatory Growth

The lateral compartments (including carino-laterals in *Balanus balanoides*) taken together contributed a very constant fraction of the total shell weight in both species, but there was often a considerable variation between the right and left lateral wall plates in any one individual. When the right lateral was enlarged, tending to tip the operculum down to the left, the left lateral often appeared to be suppressed correspondingly.

We may compare the fraction of the total variation that is due to differences between individuals with that due to differences between the right and left sides of the same individual as follows. If x_{1L}, (x_{1R}) represents the relative weight of the left (right) lateral compartments of the first individual and x_{2L}, (x_{2R}), of the second individual, the total variation for all individuals will be

$$\sum_{n} x_{1L}^2 + x_{1R}^2 + x_{2L}^2 + x_{2R}^2 \ldots x_{nL}^2 + x_{nR}^2 - 2n\bar{x}^2$$

where $\bar{x}$ is the mean relative weight. The variation in each lateral caused by differences between individuals, V_I, will be half the variation of the sum of both laterals, namely

$$\tfrac{1}{2}\sum_{n}(x_{1L} + x_{1R} - 2\bar{x})^2 + (x_{2L} + x_{2R} - 2\bar{x})^2 \cdots$$

Hence

$$V_I = \tfrac{1}{2}\sum_{n}(x_{1L} + x_{1R})^2 + (x_{2L} + x_{2R})^2 \ldots (x_{nL} + n_{nR})^2 - 2n\bar{x}^2.$$

The variation due to differences between the right and left lateral compartments of the same individual V_{RL} will be

$$\sum_{n}\left(x_{1L} - \frac{x_{1L} + x_{1R}}{2}\right)^2 + \left(x_{1R} - \frac{x_{1L} + x_{1R}}{2}\right)^2 \cdots$$

Hence

$$V_{RL} = \tfrac{1}{2}\sum_{n}(x_{1L} - x_{1R})^2 + (x_{2L} - x_{2R})^2 \ldots + (x_{nL} - x_{nR})^2$$

Table VIII demonstrates that in both species the variance due to individual differences, is significantly smaller than the variance between compartments of the same individual. This implies a tendency for the growth of the lateral compartments on one side of the animal to compensate for a lack of or excess of growth on the other. The difference in variance, and therefore the degree of compensation relative to random variation, was more pronounced in *Balanus balanoides* than in *Elminius modestus*.

A similar treatment was applied to the variation of the relative weight of the rostrum and carina to ascertain whether the sum of the weights of these two valves varied between individuals to the

TABLE VIII

Variation in weight of lateral compartments

Species	Surface	Variance between individuals of relative weight of lateral compartments	Degrees of freedom	Variance between relative weight of right and left lateral compartments of each individual	Degrees of freedom	Variance Ratio
Balanus balanoides ..	Convex	3·15	22	21·10	25	6·70*
	Plane	2·58	20	12·55	21	4·87*
	Concave	4·85	6	44·65	9	9·21*
	All Surfaces	3·13	48	21·70	55	6·93
Elminius modestus ..	Convex	1·57	31	13·45	34	8·58*
	Plane	2·77	17	4·05	18	1·46
	Concave	12·15	8	9·19	11	0·76
	All Surfaces	3·44	56	10·05	63	2·92*

* Difference significant at $P < 0{\cdot}05$.

same or to a lesser degree than the difference in weights of the two valves in each individual. An analysis of variance indicated that the individual variation was reduced when the relative weight of the rostrum and carina were added, indicating a similar compensation. As with the lateral compartments the results were more strikingly significant for *Balanus balanoides* than for *Elminius modestus*.

Evidently when the upward growth of the animal is retarded on one side, the rate of growth of the shell plates diametrically opposite is speeded up, with the result that the total amount of material laid down remains proportionate to the growth of the rest of the animal. Similarly, when the growth of the base of the animal is halted in one direction, it continues to expand at a greater rate in other directions (Crisp, 1960 *b*).

ANALYSIS OF CHANGES IN SHAPE CAUSED BY THE CURVATURE OF THE SURFACE

The total and relative weights of the compartments showed little alteration in *Balanus balanoides*, hence in this species the surface curvature caused a change only in the shapes of the barnacles growing on them. The main effect observed was a reduction in height on a concave and an increase in height on a convex surface. The parietes of the largest specimens on a very concave surface assumed a remarkable shape, their basal margins having grown so far up the wall of the concavity that the aperture was scarcely elevated above the growing edge of the base. Their outer surfaces were strongly concave.

Barnacles grown on convex surfaces were tall and their parietes convex, the rostrum usually being particularly strongly arched. The simplest assumption to account for the change in shape in relation to the curvature of the surface is that the angle between the surface and the basal margin of the parietes remains constant.

Darwin (1854) pointed out that the shell of a sessile barnacle grew mainly by accretion at the basal end of each compartment. The base, whether calcareous or membranous, must also expand over the substratum as its circumference increases. The opercular aperture widens more or less proportionately with the growth of the base, so that it becomes necessary to assume that the upper parts of the parietes of most species also increase in girth, probably by the addition of shell along the margins where the compartments touch one another. Costlow's (1956) observations of the position of cells laying down cuticle, chitin and matrix agree well with this view.

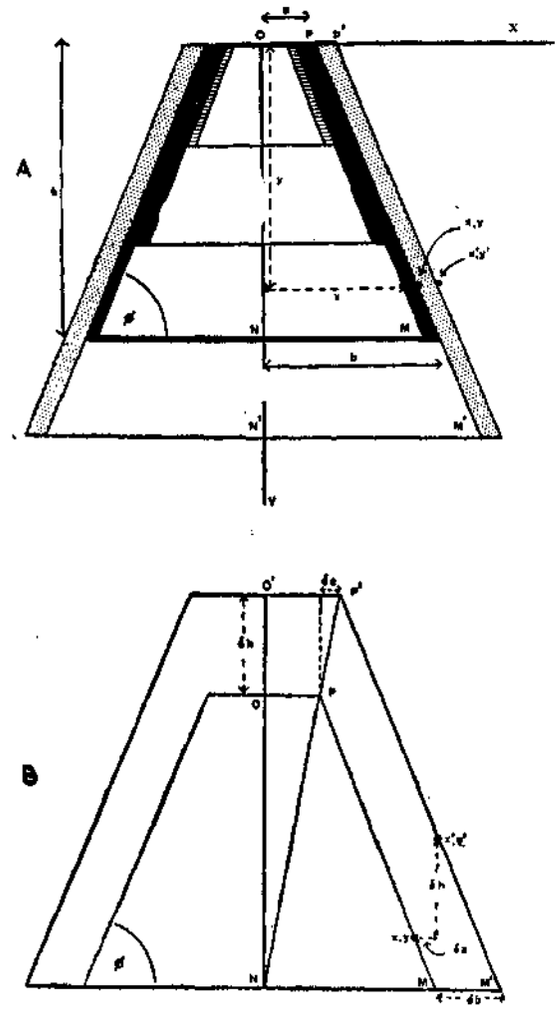

FIG. 1. Diagram of barnacle to illustrate mode of growth assumed in calculations of shape. A. Illustrates by suitable shading successive stages in growth. To make the argument in the text clearer the base has been moved along the Y-axis during growth so that the opercular aperture remains in the same position, with its centre at the intersection of OX OY. B. Shows two stages in growth, NMOP and M'NO'P'. In this figure the more natural condition is illustrated, with the base MN extending to M'N over a level substratum, and the aperture OP growing upwards to O'P'.

In order to account for the changes of shape observed we shall construct a hypothetical model of a growing barnacle based on Darwin's observations of its mode of growth (Fig. 1). We shall make the further assumptions :

(*a*) that the growing basal edge can maintain a constant angle, ϕ, with a hard substratum,

(*b*) that the barnacle is radially symmetrical about a vertical axis through the original point of attachment and

(*c*) that subsequent growth is isometric.

On these assumptions it can be shown (*see* Appendix) that the equation for a profile of a barnacle growing on a curved surface of radius R will be

$$\text{for a convex surface } y = (b - x)\tan\phi + Z \tag{1}$$

$$\text{for a concave surface } y = (b - x)\tan\phi - Z \tag{2}$$

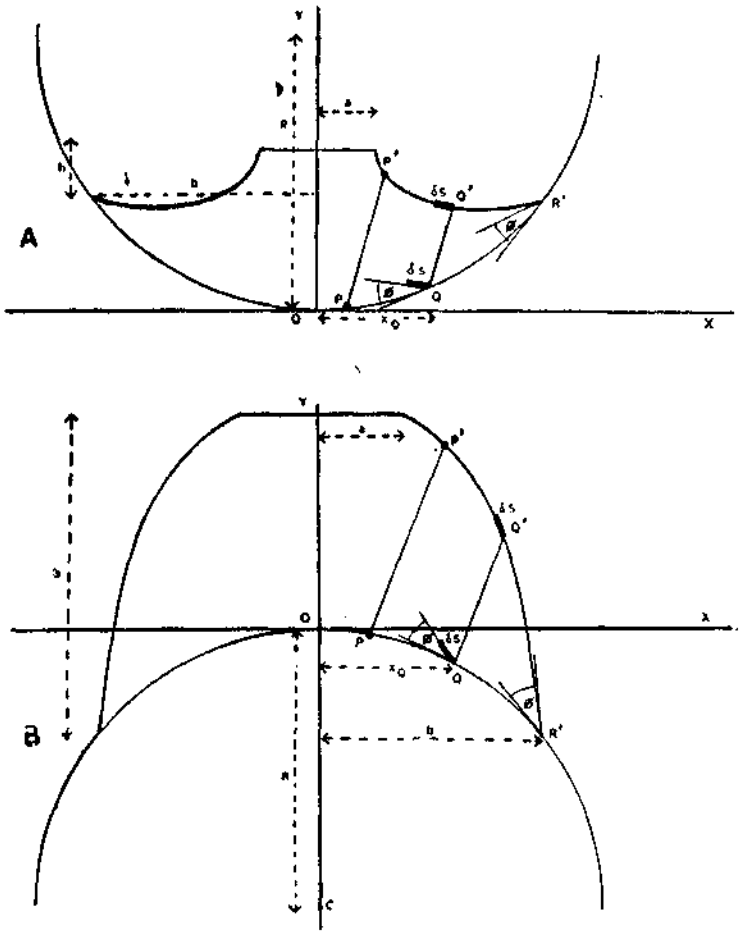

FIG. 2. Diagram of the form assumed by growth of a model barnacle on a (A) concave (upper) and (B) convex (lower) surface. *a*, radius of opercular aperture; *b*, radius of base; *h*, height of barnacle.

where y is the height above the base of the surface of revolution of the exterior of the barnacle at a point at distance x from the centre of the base, of radius b, ϕ is the angle of growth, and Z is a function of the radius of curvature and the shape of the barnacle:

$$Z = R - k\sqrt{R^2 - b^2} - \sqrt{R^2(1-k)^2 - b^2\left(\frac{x}{b} - k\right)^2},$$

k being the ratio of the opercular radius to basal radius ($k = a/b$).

The height of the barnacle measured vertically from the edge of the base to the level of the rim of the operculum will be

$$h = f(b \tan \phi + l) \text{ on a convex} \tag{3}$$

d

$$h = f(b \tan \phi - l) \text{ on a concave surface} \tag{4}$$

where

$$f = (1 - k) \quad \text{and} \quad l = R - \sqrt{R^2 - b^2}.$$

Equations (1) and (2) may be used to predict the profile of a barnacle growing on a concave or convex surface. Equations (3) and (4) similarly allow a simple calculation of the height, h, to be made. In applying both pairs of equations the value of the ratio $k = a/b$, the angle of growth, ϕ, and the diameter of the base, b, must be given. The parameters ϕ and k can be obtained most simply by measuring the mean values of h, a and b for a number of individuals growing on a plane surface. Then $k = \bar{a}/\bar{b}$, $\phi = \tan^{-1} \bar{h}/(\bar{b} - \bar{a})$. The mean values found for *Balanus balanoides* were $k = 0{\cdot}370$, $\tan \phi = 1{\cdot}085$ for individuals of diameter ranging from 5 to 10 mm. These values were inserted into equations (1) and (2), together with the value of R for the curvature of the surface and the value of b for the mean diameter of the barnacle growing on it. The resulting profiles for the smallest radius of curvature are shown in Fig. 3. It can be seen that the profile of barnacles grown on convex surfaces is convex and that of barnacles grown on concave surfaces is concave and of the expected form.

The correspondence between the observed and calculated shape of the barnacle can best be judged from Table IX. The heights, h_o, were calculated from equations (3) and (4) using the con-

TABLE IX

Predicted and observed values of height/base ratio for Balanus balanoides
$\tan \phi = 1{\cdot}085$; $f = 0{\cdot}630$

	Radius of curvature R mm		Mean basal diameter $2b$ mm	$R - \sqrt{R^2 - b^2} = l$ mm	Calculated height/base ratio $h_o/2b = f(b \tan \phi \pm l)/b$	Observed height/base ratio $H/\sqrt{LB}$
Convex	− 7·5	..	7·06	0·88	0·422	0·424
	−12·5	..	9·56	0·95	0·406	0·411
	−17·0	..	9·34	0·65	0·388	0·395
	−27·0	..	11·04	0·47	0·369	0·375
Plane		..	10·75	0	(0·342)	0·342
Concave	+27·0	..	9·46	0·42	0·313	0·288
	+17·0	..	8·20	0·50	0·303	0·277
	+12·5	..	8·30	0·70	0·288	0·259
	+ 7·5	..	10·50	2·15	0·214	0·230

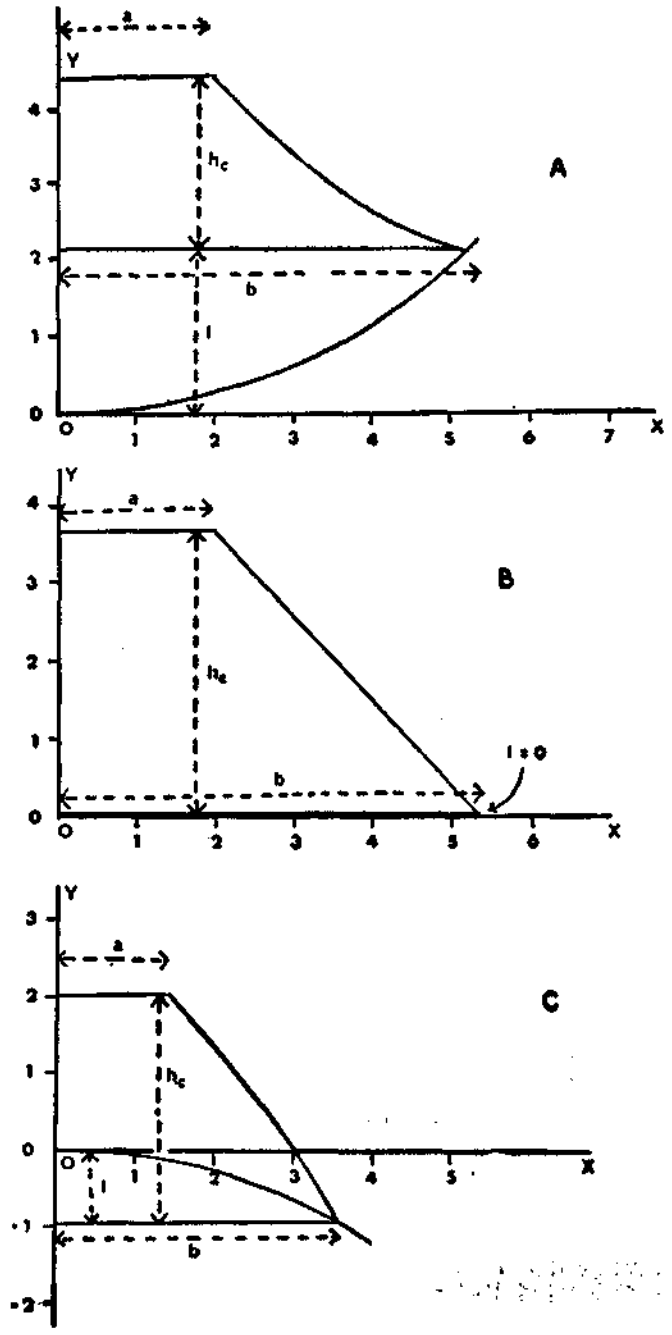

FIG. 3. Calculated profile of *Balanus balanoides* growing on (A) a concave, (B) a plane and (C) a convex surface or radius of curvature R = 7·5, O, and −7·5 cm respectively. The profile is drawn to a diameter *b*, of 10·5 mm for curve (*a*) and of 10·75 mm for curve (*b*) and of 7·06 mm for curve (*c* correspond to the entries in rows 9, 5 and 1 respectively of Table IX.

stants derived from barnacles growing on plane surfaces. The values predicted from the equations agree well both in magnitude and trend with those observed.

Elminius modestus had a steeper profile; the mean value of $\tan\phi$ for individuals growing on plane surfaces was found to be 1·53. The aperture was relatively wider, k being 0·475. The calculated ratio obtained by the application of equations (3) and (4) are compared with observed results in Table X; the agreement is not as good as in *Balanus balanoides*. The discrepancies are probably attributable, in part at least, to the fact that a smaller number of specimens were available for measurement resulting in wider fluctuations of the observed values. There was no clear trend in the divergence between calculated and observed results, but the observed height of the specimen grown on the most convex surface, and illustrated in Plate I, was very much greater than the calculated value. In *Elminius modestus* the wall plates grew to a greater or lesser relative weight according to whether the surface was more convex or more concave (pp. 6–8). This effect, which would tend to accentuate the height of individuals growing on convex surfaces, was not taken into account in the analysis given in the Appendix. The success of the theoretical treatment, for this species at least, may therefore rest to some extent on mutually compensating approximations.

TABLE X

Predicted and observed values of height/base ratio for Elminius modestus
$\tan\phi = 1{\cdot}58$; $f = 0{\cdot}525$

	Radius of curvature R mm		Mean basal diameter $2b$ mm	$R - \sqrt{R^2-b^2} = l$ mm	Calculated height/base ratio $h_o/2b = f(b\tan\phi \pm l)/b$	Observed height/base ratio $H/\sqrt{LB}$
Convex	− 7·5	...	9·60	1·74	0·495	0·625*
	−12·5	...	9·20	0·88	0·454	0·455
	−17·0	...	9·94	0·71	0·438	0·428
	−27·0	...	9·60	0·45	0·427	0·440
Plane		...	10·10	...	0·405	0·405
Concave	+27·0	..	10·42	0·51	0·378	0·370
	+17·0	..	9·62	0·69	0·366	0·372
	+12·5	..	8·40	0·73	0·357	0·454‡
	+ 7·5	..	8·70	1·39	0·318	0·322

* Single individual only. ‡ Specimens touching at end of experiment.

CONCLUSIONS

The experiments leave no doubt that part of the variation in shape of barnacles can be ascribed to the shape of the surface on which they are growing. This is not a new observation: Gregg (1948), for example, observed how surface irregularities left their impression on the walls of barnacles and other organisms that grew in close contact with the substratum, while Gutmann (1960) described in general terms how the shape of isolated individuals of *Balanus balanoides* was modified by the configuration of the substratum. He showed that individuals settled in a hollow had a more flattened shape while those growing over an edge had to develop extended shell plates. Small individuals in grooves became oval in shape with the short axis at right angles to the groove. He explained these changes in terms of the need for the shell to maintain contact with the substratum,

Our observations indicate how this is achieved. The growing edge of the shell not only remains in contact with the surface but also has the ability to maintain an approximately constant angle with reference to it. This imposes changes on the form of the rest of the shell, notably on the relative size of the aperture. Since the angle subtended by the shell to the tangent of a curved surface over which it is growing is kept constant, the angle that the shell assumes in relation to the vertical axis through the centre of the base of the animal must alter. On a concave surface the plane of the shell plates is deflected during growth towards the horizontal, making a larger angle with the vertical axis of the animal. On a convex surface the shell plates incline further towards the vertical, with the result that the shell becomes tubular. Changes in the angle of the shell plates in turn cause modifications of the opercular aperture. Individuals growing on convex surfaces, whose shell plates become arranged in tubular rather than in conical form, are forced to increase the perimeter of the upper parts of the shell relative to the base. Hence the upper parts of the shell plates must become wider in order to maintain close contact; the opercular aperture is thereby enlarged. Animals growing in grooves will have the shell plates inclined to the vertical axis at an angle greater than normal (*i.e.*, more nearly horizontal) in the direction perpendicular to the groove, where the shape of the substratum is concave, whereas in the direction along the groove the angle should approach the natural for a plane surface. The result that must follow is a relative shortening of the shell plates and narrowing of the aperture in the direction at right angles to the grooves. Indeed, shapes assumed by barnacles are, in fact, remarkably analogous to those of water droplets maintaining a constant angle of contact with solid surfaces of various shapes.

It should be stated that to maintain a constant angle with the substratum is not the only way in which the animal might grow. It might maintain a constant shape, and accommodate itself to the substratum by modifying the angle subtended at the base of the shell, or it might alter its shape to maintain a constant volume within the shell. It does not appear to do either of these, presumably because of the overriding importance of not disturbing the normal processes of growth at the basal edge.

Clearly the above principles apply only to freely growing barnacles. They cannot be applied when the growth processes at the basal margin are seriously impeded or deranged as for example, when a barnacle is in contact with an abrupt projection or with another individual over which it does not grow. Similarly, poisons may disrupt the normal processes at the growing edge leading to distortion (Stubbings, 1959).

Increases in the thickness and degree of folding of the shell observed in barnacles growing on a concave surface might be explained in terms of the phenomenon of compensatory growth noted above, in relation to the size of the compartment. A smaller extension of the basal margin of the shell plates would be necessary when growing up a concave surface, and this might allow more shell material to be available per unit length of the outer perimeter, so resulting in folding and puckering at the growing edge. The processes leading to folding are, however, somewhat complex, and require more detailed investigation. Since folding of the parietes can vary so much with habitat, it is of doubtful value as a diagnostic character in systematic work.

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EXPLANATION OF PLATE I

Photographs to illustrate the effect of surface curvature on the form of barnacles

A. Specimens of *Elminius modestus* grown on concave (left), plane (centre) and convex surfaces (right) in side view showing increasing height.

B. The same three specimens viewed from above showing increasing size of opercular aperture.

C. Compartments and valves of *Balanus balanoides* showing increased folding of walls after growing on a concave surface, and decreased folding after growing on a convex surface.

APPENDIX

The radius of the opercular opening, a, will be taken as a constant fraction, k, of the radius of the base, b. From the centre of the operculum at O, the axes OY, OX, are drawn down the central axis to the centre of the base and radially across the aperture as shown in Fig. 1. The equation giving the shape of the edge of the shell, PM, projected on the plane, XOY, will be

$$x = a + (b - a)\frac{y}{h} = a + y \cot \phi,$$

where $h = \text{ON}$, the height of the barnacle, and ϕ is the angle between PM and the base MN namely, the angle made by the edge of the wall plate to the surface over which it is growing.

We shall now allow growth increments, δa, δb and δh, to take place in the opercular aperture, in the base, and in the height respectively. The new form of the barnacle will be that of the figure OP'M'N'. Any point above the base, such as x, y, on PM will then be found at x', y', on P'M'. Since all growth in height is assumed to be restricted to growth at the base, the point x, y is not displaced during growth from the apex of the barnacle, so that $y = y'$. Hence the displacement of the point x on the edge of the shell as it grows from position PM to P'M' will be equal to $\delta x = \delta (a + y \cot \phi) = \delta a$, since y and ϕ are constant. The increase in girth of this model will therefore be $2\pi\delta a$ at all points above the growing zone of the base.

The ratio of the opercular radius to that of the base, b, is $k = a/b$, hence the increase in diameter of the base, δb, must be $1/k\ \delta a$, while the height, $h = b(1 - k) \tan \phi$, from which it follows that

$$\delta h = \frac{(1 - k)}{k} \tan \phi \delta a = \frac{h}{a} \delta a.$$

If now the barnacle is assumed to grow with its base on a reference surface (Fig. 1 B), any point x, y, on its outer surface PM will be displaced from x, y, to x', y', that is upwards along the y-axis by $\delta h = h/a\ \delta a$, and outwards along the x-axis by δa. It will therefore move along a line of slope, dy/dx, of h/a, that is along a line parallel to NPP' joining the centre of the base to the edge of the opercular opening.

Figure 2 A shows a barnacle which has grown in a concavity of radius of curvature + R, while Fig. 2 B is correspondingly annotated for a barnacle growing on a convex surface, where the value of R is assumed to be negative. The co-ordinates, OX, OY, OZ, meet at the point at the centre of the base where growth is assumed to have begun. OY is taken as the axis through the centre of the operculum, and the OX, OZ axes form the plane over which the base would grow on a plane surface. The curved surface on which the barnacle is supposed to be growing has its centre at C and touches the XOZ plane at O. Only that section of the barnacle lying in the plane XOY is shown. OC is therefore the radius of curvature, R. The arc, OPQR', represents not only the surface of the substratum but also the locus that the growing edge of the specimen has occupied at intervals of time. The points, P, Q, originally at the growing edge, come to occupy the positions, P', Q', when the edge reaches position R'. ϕ is the angle made by the intersection of the tangents to the lines Q'R' and QR', and represents the angle made by the base with the substratum. Since growth is assumed to be radially symmetrical about OC, the shape of the barnacle will be fully described by the arc P'Q'R' which is a surface of revolution about OY. An element of this surface, δs, at Q', is a solid ring originally laid down at an angle ϕ to the curved surface at Q and raised during subsequent growth to the position Q'. The angle made between QQ' and the vertical axis OY depends upon the increase in girth caused by growth at the lateral margins of the parieties in

comparison with the increase in height caused by growth at their basal margin. We shall assume that, as shown above for the model of a barnacle growing on a plane surface, growth on a curved surface is similarly adjusted so that QQ′ remains parallel to PP′, the line joining the centre of the base and the edge of the opercular aperture and the slope of the element δs at Q is equal to that of the same element when displaced to Q′. The slope of the spherical substratum at Q will be

$$\left(\frac{dy}{dx}\right)_0 = \frac{\pm x_0}{\sqrt{R^2 - x_0^2}}$$

the sign being positive for concave and negative for convex surfaces.

The slope of the barnacle shell at Q and hence at Q′ will be

$$\left(\frac{dy}{dx}\right)_0 - \tan\phi.$$

Since PP′ is parallel to QQ′, and if x is the co-ordinate of Q′

$$a + x_0(b - a)/b,$$

hence

$$x_0 = \frac{b(x - a)}{b - a}.$$

Hence for the barnacle profile the differential equation will be

$$\frac{dy}{dx} = \frac{\dfrac{\pm b(x - a)}{b - a}}{\sqrt{R^2 - \dfrac{b^2(x - a)^2}{(b - a)^2}}} - \tan\phi$$

or

$$\frac{dy}{dx} = \frac{\pm b(x - a)}{\sqrt{R^2(b - a)^2 - b^2(x - a)^2}} - \tan\phi.$$

Putting boundary conditions $x = b$, $y = R - (R^2 - b^2)^{\frac{1}{2}}$ for a concave surface, the solution is

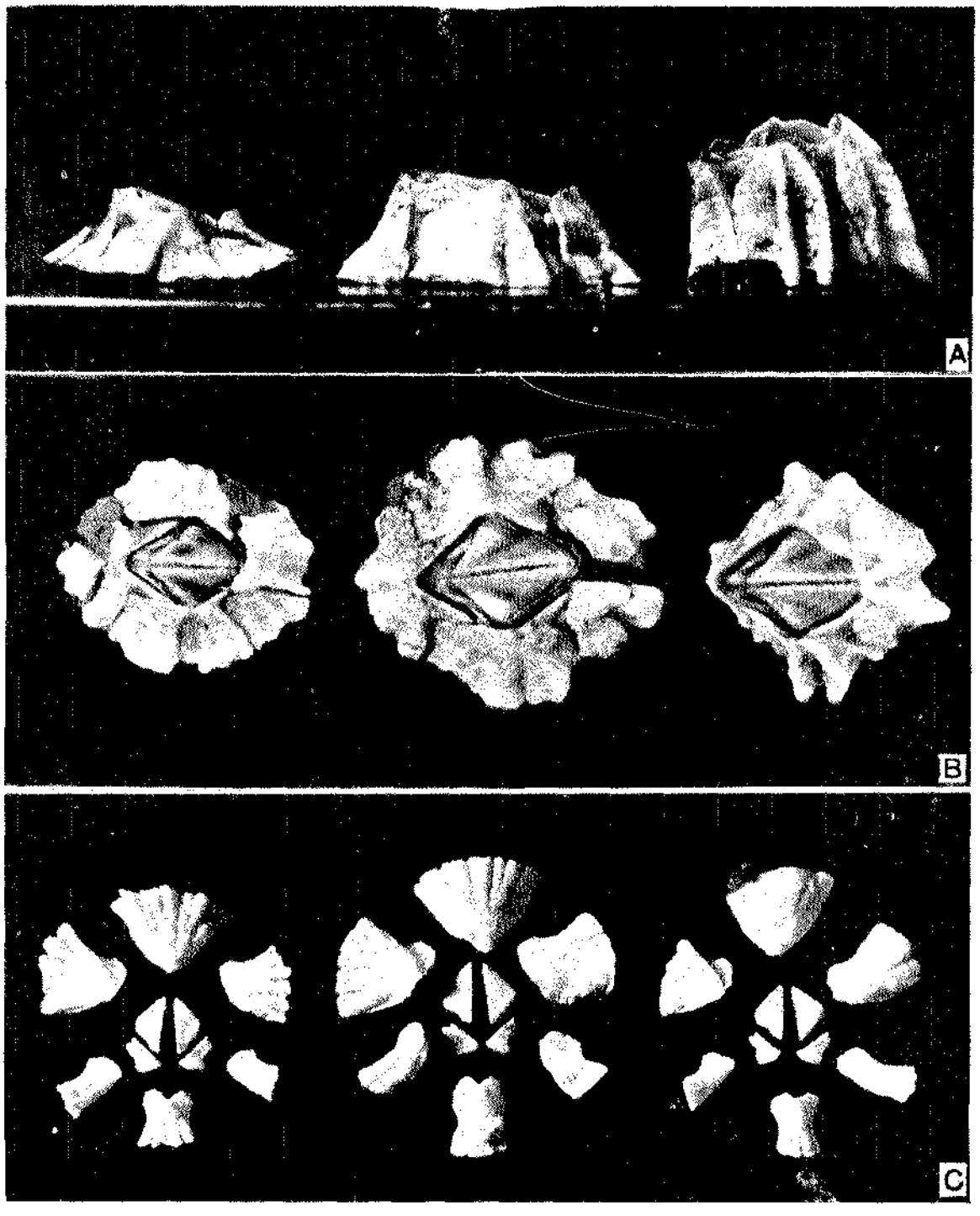
$$y = R - k\sqrt{R^2 - b^2} - \sqrt{R^2(1 - k)^2 - b^2\left(\frac{x}{b} - k\right)^2} + (b - x)\tan\phi \qquad (1)$$

while for a convex surface, with boundaries $x = b$ when $y = -R + \sqrt{R^2 - b^2}$

$$y = -R + k\sqrt{R^2 - b^2} + \sqrt{R^2(1 - k^2) - b^2\left(\frac{x}{b} - k\right)^2} + (b - x)\tan\phi. \qquad (2)$$

From these equations it follows that for a plane surface, $R = \infty$,

$$y = (b - x)\tan\phi.$$



CONCAVE PLANE CONVEX

On a curved surface the height h is generally measured, not from the point O at the centre of the base, but from the periphery of the base at R'. Hence $h_c = y_a - y_b$ where y_a is the value of y_a for $x = a$, and y_b the value for $x = b$; h_c is the predicted height.

For a convex surface

$$h_c = y_a - y_b = f(b \tan \phi + l). \tag{3}$$

For a concave surface

$$h_c = y_a - y_b = f(b \tan \phi - l). \tag{4}$$

Where

$$f = (1 - k) = \frac{(b - a)}{b} \quad \text{and} \quad l = \mathrm{R} - \sqrt{\mathrm{R}^2 - b^2}.$$

THE CUMACEA OF THE INDIAN SEAS

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ABSTRACT

Very little is known about the cumacean fauna of Indian region, the first record being by Calman in 1904 from the Gulf of Mannar, who described 10 species. Subsequently, though the works of Stebbing and Jones in the African coast, Calman in the Gulf of Siam, Fage from the Vietnam coast, Hale from Australia and Kemp and Kurian from the Indian coasts have brought to light a good number of species, much more remains to be done about these small crustaceans, especially from the deep water regions. A comparative study of the Cumacea of the Indian coasts shows that they have a close affinity with those from the coasts of Australia, Africa and Gulf of Siam.

The paper also deals with the food and feeding habits, diurnal migration and seasonal distribution of Cumacea in the Trivandrum region.

THE Cumacea forms a group of small Crustacea that have a worldwide distribution in all the oceans from tidal limits to about 2,500 fathoms. Apart from their biological interest, these small organisms are of considerable importance to the fishery biologists, since they form an important constituent of the food of the bottom feeding fishes especially during their larval and post-larval stages. Cumacea has a very wide distribution in all the seas, but their maximum intensity is observed in the Indo-Pacific.

Though Cumacea has been observed in the plankton, they are essentially bottom forms living in burrows or very near the substratum. Some of the cumaceans are found to be steno-thermal warm water species whereas others are eury-thermal, extending from Mediterranean-Atlantic region to the tropics. While most of the species are stenohaline having their maximum distribution in the inshore waters, a few are found in the estuaries subject to varying changes in salinity.

Very little is known about the cumacean fauna of the Indian region, the first record being by Calman (1904) who has described from Herdman's collections from the Gulf of Mannar sixteen species, the only previous records being by Paulson and Kossman (1880), who have described 4 species from the Red Sea. In 1905 Calman recorded 10 species from the Indonesian region and 1 species from the Sulu Sea (near Philippines).

Again in 1907, Calman recorded 9 species from the Gulf of Siam, 2 from Suez and 1 from Penang and in 1911 he recorded 11 species from the Gulf of Siam, 1 species from Ceylon and 1 from Pamban.

Kemp (1916) recorded 2 species from the Chilka Lake (East Coast of India), Stebbing (1910, 1912, 1913), Zimmer (1908, 1913) and Hale (1952) recorded 28 species from South and East of Cape Town (S. Africa), Kurian (1951 & 1961) recorded 24 species from the West Coast and in 1954, 25 species from the Bay of Bengal. Further, Hale (1928–48) discovered 163 species from the different parts of the Indian Ocean including the Western and Southern Coasts of Australia. Of the 242 species that have been hitherto recorded from the Indian Ocean proper, 152 species are found to be endemic to this region while 16 have been recorded from the seas bordering the Atlantic and 68 species were found distributed in the seas bordering the Western region of the Pacific.

A comparative study of the Cumacea of the Indian seas shows that they have a close affinity with those from the coasts of Australia, Africa, Gulf of Siam and Japan.

Food and Feeding Habits

The Cumacea are essentially burrowing animals and as such their food is constituted mainly of bottom dwelling organisms. Along the Kerala Coast, Cumacea is found abundant at a bottom formed of fine sand with a small percentage of silt and shell fragments. They are rare or completely absent in a rocky as well as muddy substratum. Examination of the stomach contents of *Iphinoe brevipes* and *Gigacuma halei* collected from Trivandrum and Vizhingom coasts show the presence of diatoms, minute foraminifera, crustacean larvae and detritus. The feeding of *Gigacuma* has been watched in a glass trough in the laboratory. The burrowing habit seems to resemble very much that of *Picrocuma*—described by Hale (1943). The current of water that is produced by the setae of the maxillipeds and 1st peraeopod is found to channel small diatoms and crustacean larvae into the oral appendages.

Vertical Distribution and Diurnal Migration

Very little work has been done on the vertical distribution and diurnal migration of the Cumacea, evidently because most of the works in Cumacea have been on preserved specimens brought by expeditions and other individual collections. However, the works of Hale (1943) and Russel (1925) are noteworthy. It is an accepted fact that Cumacea are bottom dwelling animals and that their occurrence in the plankton is rare. Many theories have been brought forth regarding the occurrence of Cumacea in the Plankton. Jones (1955) is of the opinion that in the west coast of Africa, Cumacea were found in large numbers in the Bengula current and that it is owing to the mass migration of these small crustaceans from the bottom as a result of low oxygen content. But, in the Kerala Coast it has been observed that the Cumacea occur even when the dissolved oxygen content is as low as 0·8 ml./l.

A few authors observe that majority of the cumaceans found in the plankton are males. But others do not find any such difference. It is an accepted fact that though Cumacea avoid bright light they are attracted towards dim submarine light of low candle power and this fact has been made use of for collecting Cumacea from different regions. Along the Kerala Coast a number of plankton as well as bottom collections were made during 1943–46 and 1957–63 from the inshore regions extending up to the 200 fathom line. Most of the specimens were collected in the bottom deposits and only rarely represented in the plankton. Detailed observations were made on the vertical distribution and diurnal migration of *Iphinoe brevipes* and *Gigacuma halei*; the two common species found in the Trivandrum-Vizhingom region. *Iphinoe brevipis* is found in plenty at surface during the early hours of the morning and completely absent in the surface collections from dawn to sunset and very rarely represented in the mid-water collections during daytime. *Gigacuma halei* has a slightly different distribution. It is absent in the surface during day and night, found sparsely in the mid-water collections during night and abundant at the bottom during day and night.

Though the previous authors have observed a large percentage of males in the plankton to females, along the Kerala Coast no such difference in sex ratio has been observed.

Salinity.—Most of the Cumacea are marine. But a few have been observed from brackish-water estuaries and freshwater surroundings. Many are stenohaline. But, there has been instances of euryhaline species also. Along the Kerala Coast *Paradiastylis culicoides* has been first observed by Kemp (1916) from the Chilka Lake in water of "specific gravity 1·000 to 1·015". But later, he found that when the salinity of the water increased to that of sea-water outside the lake, all specimens have disappeared. In the Kerala Coast (Kurian, 1951) *P. culicoides* is found in the open sea near the coast. In 1921, this species was collected off Waltair (Kurian, 1954), not

far away from the type locality showing that it is capable of tolerating a wide range of salinity. In the backwaters of Kerala also a few species of Cumacea have been observed (*vide* Kurian, 1961) when the salinity is as low as 12‰.

Seasonal distribution.—In the deep-water regions, no remarkable seasonal distribution is observed. But in the inshore regions, some amount of variation in the intensity is found. *Bodotria choprai, Iphinoe brevipes, Eocuma taprobanicum, Campylaspis platyuropes* and *Campylaspis minor* have a maximum intensity in the Trivandrum region at 12–15 fathoms from January to April, while *Cyclaspis costata* and *Gigacuma halei* are found common in the Vizhingom region from August to October with a maximum abundance in September. All the other species are rather rare in the collections.

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Discussion

Dr. D. G. Frey: What sort of bottom is at 2,500 fathoms?

Dr. C. V. Kurian: The bottom is silty. The depth 2,500 fathoms is actually from other references.

Dr. R. Serene: Collection of Cumacea material is better by light method, especially for taxanomic purpose.

Dr. C. V. Kurian: Yes.

Dr. J. H. Wickstead: Light sometimes doesn't yield any cumaceans.

Dr. C. V. Kurian: Yes. This has been also my experience.

Dr. V. Hansen: In the Baltic Sea where conditions were 15–20% salinity, temperature difference of 5–6°, the cumaceans were collected from 5–6 meters from bottom. Thus you may not be able to collect them often, on the bottom.

Dr. C. V. Kurian: My observation in aquarium tank is that they bury in sand during daytime and they came up to the surface in the night.

Dr. A. L. Rice: Night-life on surface of Cumacea is being studied by several authors. What are your observations?

Dr. C. V. Kurian: Some species don't come to surface at all; never even in dark nights. Some other species came to surface even at dawn. These species generally have a bubble of air and by means of this, they can come up.

Dr. S. Jones: How do you say Trivandrum coast is rich in Cumacea?

Dr. C. V. Kurian: I was making collections in this area from 1943–46. My collections here (Cochin) did not yield any good material.

Mr. K. N. Sankolli: Do these Cumacea occur in places of wave-action?

Dr. C. V. Kurian: Not much. Ideal conditions are provided by places with 2–10% of silt.

Dr. D. G. Frey: You said that they are found at 500 fathoms, what kind of bottom is it, there?

Dr. C. V. Kurian: I have not got the opportunity to examine it.

Dr. A. L. Rice: In some places light is used for collection, as you have said. But if light is placed under water much nearer the habitat, the collection would be more representative.

Dr. C. V. Kurian: Yes.

SIZE DISTRIBUTION AND GROWTH OF *METAPENAEUS DOBSONI* (MIERS) AND THEIR EFFECT ON THE TRAWLER CATCHES OFF KERALA*

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ABSTRACT

Metapenaeus dobsoni (Miers) spawns almost throughout the year. The traditional method of tracing the progression of modes in monthly length frequency distribution to determine growth and age was not very successful. The application of a modified Von Bertalanffy equation furnished expected sizes at different ages. The total instantaneous mortality rate was found out from the approximate formulae of Holt-Beverton.

The size distribution of the catches landed by trawlers were obtained and the role played by the size distribution in influencing the catch and abundance has been discussed.

INTRODUCTION

Metapenaeus dobsoni is caught in enormous numbers both from the sea and also from the backwaters of Kerala and form a major part of the total prawn catch in the State. Traditionally, the fishery of *M. dobsoni* was based on the catches of inshore waters and backwaters. Recently, fishing has been extended to the offshore areas by the use of trawl nets and because of encouraging results, fishing in offshore area is likely to increase substantially within a few years. The trawler catches of *M. dobsoni* from the offshore waters off Cochin show wide fluctuations and it is believed that such fluctuations are due to fluctuating abundance of recruits coming into the fishery of the offshore area. The present paper examines in detail the age structure of the offshore catch of *M. dobsoni*, the age of the recruits to the offshore stock and also the possible causes of fluctuations in the abundance of recruits to the fishable stock. As the fishery of *M. dobsoni* is just being started in the offshore area, a detailed analysis on these lines will permit estimation of some of the essential vital statistics like the natural mortality rate which, at a later stage when fishing in the area will be fairly extensive, cannot be easily estimated.

MATERIALS AND METHODS

The basic data consists of the catch (in weight) and the effort in trawling hours for the 5 fishing seasons from 1958–59 to 1962–63. These are presented in Table I. The details of fishing operations of the trawlers, etc., have been given by George *et al.* (in press). The other data consists of length measurements of samples of *M. dobsoni* collected from the trawler catches every month.

It is well known that this prawn migrates to estuaries and backwaters in its early life and grows for sometime in such environments and then go back to the sea where further growth and attainment of sexual maturity take place. Because of this peculiar migratory habit, the size composition of the catch obtained from the backwaters and from the sea are likely to be different. Menon (1955) has stated that the vast majority of *M. dobsoni* do not grow beyond 60–65 mm. in

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TABLE I

Trawler catches of Metapenaeus dobsoni

Month	Effort (Tr. hr.)	Catch (kg.)	C/E	Month	Effort (Tr. hr.)	Catch (kg.)	C/E
1957–58				1960–61			
August	31·08	..		September	30·16	..	
September	61·47	..		October	167·84	..	
October	67·08	..		November	207·18	99·99	
November	243·17	338·75		December	204·75	4,367·13	
December	301·92	29,620·48		January	243·25	4,537·83	
January	415·83	16,873·63		February	264·09	836·92	
February	287·70	1,986·20		March	432·67	3,219·71	
March	348·75	3,493·18		April	511·25	24,198·80	
April	309·75	12,562·46		May	451·25	2,813·03	
May	519·08	21,817·87		June	98·84	..	
June	147·92	12,608·13					
Total ..	2,733·75	99,300·70	36·32		2,611·28	40,073·41	15·35
1958–59				1961–62			
September	85·83	..		September	93·32	17·07	
October	108·50	..		October	303·42	140·34	
November	339·92	2,750·86		November	442·00	2,852·30	
December	535·63	1,490·93		December	675·00	51,242·92	
January	540·55	17,961·80		January	510·08	14,678·91	
February	511·82	17,053·58		February	506·25	19,736·65	
March	508·55	29,487·55		March	600·08	16,746·34	
April	454·83	39,418·43		April	605·50	30,362·46	
May	440·25	38,605·10		May	827·92	27,086·10	
				June	381·25	11,258·74	
Total ..	3,525·88	1,46,768·25	41·63		4,547·02	1,74,121·83	38·29
1959–60				1962–63			
September	57·00	..		September	91·92	..	
October	107·59	..		October	372·75	..	
November	301·17	385·10		November	679·17	5,793·78	
December	430·00	3,128·42		December	426·00	3,166·15	
January	491·25	5,999·40		January	534·75	8,573·71	
February	692·68	17,780·12		February	392·84	14,503·14	
March	608·75	2,202·56		March	447·50	6,962·54	
April	660·42	9,320·45		April	419·58	2,566·00	
May	387·33	12,737·88		May	399·25	7,673·12	
June	221·50	15,766·14		June	29·58	1,110·42	
Total ..	3,967·69	67,320·07	17·01		3,793·34	50,348·86	13·27

length in the backwaters and from the length data obtained from samples of trawler catches it is found that the majority exceed 60–65 mm. Hence to get an integrated picture of growth, in addition to the length data of *M. dobsoni* from trawler catches, length data of *M. dobsoni* landed at Alleppey and Narakkal by the indigenous boats have also been included. Instead of presenting the original data relating to the different sources, Table II gives the modal size of the catch for each month separately for the two sexes.

TABLE II

The modal values (mm.) of size distribution of M. dobsoni

Month	Modal size in mm. for Males	Females
1957	I. Trawler catches	
March	83	88, 103
April	88	95
May	93	98
June	93	98
..	..	..
December	83, 103	98, 115
1958		
January	83, 103	98, 118
February	73, 83, 103	98, 103
March	78, 88, 103	98
April	83 103	..
May	88	93
June	93	103
November	68, 103	93
December	..	88
1959		
January	78, 98	93
February	83	98
March	83	93
April	83	93
May	73, 88	83, 93, 103
September	88	..
November	103	93
December	68, 103	
1960		
January	73	53, 88
February	78	88, 98
	II. At Alleppey	
1957		
March	60	60
April	73	73
May	73	78
June	88	78, 103
July	93	103
August	98	108
September	98	75 113
October	68, 83, 98	83, 113
November	73	..
December	..	..
1958		
January	68, 83, 103	73, 98, 113
February	68, 88	53, 78, 98
March	53, 73	53, 73
April	73	73
May	73, 88	73, 93
June	78, 88	73, 103
July	93	83, 103
August	98	85, 108
September	98	83, 113
October	63, 98	68, 113
November	63	68, 88
December	68	73, 83

TABLE II (*Contd.*)

Month	Modal size in mm. for Males	Females
1959		
January	68	73, 93
February	58	63
March	73	73
April	73	73
May	73	78
June	88	98
July	83	63, 83, 103
August	93	..
September	93	108
October	103	113
November	63	68
December	68	78
1960		
January	58	58, 73
February	48, 68	48
March	63	58
April	68	63
May	73	73
June	88	78 98
July	68, 88	103
August	63, 93	63, 108
September	98	88, 113
October	..	..
November	..	..
December	53	58
1961		
January	63	63
February	63	63
March	58	58
April	68	58, 68, 78
May	73	68
June	83	68, 83
July	88	103
August	88	103
III. Narakkal		
1957		
March	58	53
April	53, 63	53, 63
May	63, 73	78, 98
July	93	108
August	98	108
September	98	113
1958		
April	58, 73	53, 68, 78
August	..	..
September	98	93. 113
1959		
February	53	53
April	68	73
May	73	73, 83, 93
June	83	68
July	63, 93	63, 88, 108
August	68, 98	78, 113
September	98	113
October	..	113
1960		
February	68	58, 68

Size Composition of the Catch

The fluctuations in the abundance of the different year-classes, particularly the newly recruited class in the fishery, may cause substantial fluctuations in the catches of the fish. Thus if the abundance of the recruited class is high in any year, it will not only influence the catch of that year but may also affect the catch of subsequent years, if the fishery is based on more than one year-class. Thus to explain the fluctuation in catch, it is necessary to know the abundance of the various age groups in the population every year. Since it is almost impossible to estimate the absolute-abundance, generally some indices of abundance are found out. The best index of abundance of an age group in the population in a fishing season is given by the catch (in numbers) per unit of effort.

To obtain data on the abundance of different age groups every year, the following procedure was followed. The raw data available for a month was the total catch (by weight) and the total effort (in trawling hours) and also the length measurements of a sample of *M. dobsoni* for the month together with the weight of the sample.

The length measurements from the monthly sample were arranged in a frequency distribution table. If n_i is the frequency of *M. dobsoni* in the i-th size class in the sample, the estimated number of *M. dobsoni* of the i-th size class in the catch for the month was obtained by multiplying n_i by the raising factor W/w where W is the weight of the catch during the month and w is the weight of the monthly samples. Table III presents the monthwise size distribution of the catch for each fishing season from 1958–59 to 1962–64. Table IV presents the catch (number) per trawling hour for the various size groups for all the fishing seasons from 1957–58 to 1962–63.

If, now, a size-age relation can be obtained, the age distribution of the catch for each fishing season can be easily obtained.

Age and Growth

Mean sizes of a fish at different ages are generally obtained by tracing the monthly progression of modes found in monthly length-frequency distribution of the fish. It is well known that this method will give successful results only if the fish has a restricted short spawning period. When a fish spawns over a prolonged period, different broods continually enter into the stock and samples from such stock will not clearly show the distinct existence of all these broods. In fact it is virtually impossible to follow the modal progression of a distinct brood over any length of time. A new brood can probably be traced over a few months after it enters the fishery. But sometimes when a brood is relatively strong, it can be traced through more months.

Menon (1955) was the first to study the problem of age determination of *M. dobsoni* by the method of length-frequency distribution. Even though he is aware that the species spawns throughout the year with probably a high intensity of spawning from May to December, he tried to follow the method of tracing the monthly progression of modes over the successive months and came to erroneous conclusion regarding the size of the prawn at the end of the 1st and 2nd year of the life of the prawn. In this, he seems to have been largely influenced by the results of the rearing experiments carried out by him. In the rearing experiment, a single post-larval form of *M. dobsoni* lived for eleven months and attained a size of 67 mm. It is difficult to say how he overlooked the biological fact that the growth in artificial condition may be different from that in the natural condition. A logical scrutiny of the length-frequency data indicates the need for the revision of the conclusion arrived at by him. In the length-frequency data of *M. dosoni* collected from West Hill station in 1949–50 and as presented in his paper, he starts with the mode at 43 mm. in July 1949. According to him, it progresses to 53 mm. in August 1949, is absent in September 1949, progresses to 63 mm. in October. The author does not say anything about this group in November but he continues to say that the mode remains at 63 mm. in December 1949 and in the

TABLE III

Size distribution of trawler landing of Metapenaeus dobsoni
(Number in thousands)

Class interval (mm.)	November	December	January	February	March	April	May	June	Total	N/E
1957–58										
51–55			2·6	1·8					4·4	1·6
56–60			10·6	1·8					12·4	4·5
61–65			50·3	3·6	1·6		8·0		63·5	23·2
66–70			100·5	10·3	8·1	9·7	16·0		144·6	52·9
71–75		65·3	140·2	37·4	29·2	124·3	152·3	7·4	556·1	203·4
76–80	52·1	224·9	222·2	33·8	60·0	213·8	304·6	18·5	1,129·9	413·3
81–85	..	466·4	582·0	65·2	60·0	441·2	789·6	111·2	2,515·6	920·2
86–90	52·1	289·2	399·4	70·1	89·2	406·2	990·0	292·8	2,589·0	947·1
91–95	52·1	354·5	220·0	29·6	64·8	301·2	869·8	370·6	2,262·5	827·7
96–100	78·2	1,035·5	410·0	29·0	105·4	281·8	553·1	222·4	2,715·4	993·3
101–105	78·2	802·3	497·3	50·1	95·6	147·7	276·6	341·0	2,288·8	837·2
106–110	..	363·8	190·5	14·5	47·0	77·7	112·2	151·9	957·6	350·3
111–115	52·1	214·6	97·9	8·5	6·5	19·4	32·1	37·1	468·2	171·3
116–120	..	214·6	145·5	6·0	4·9	13·6	12·0	11·1	407·7	149·1
121–125	..	93·3	15·8	3·0	..	..	..	..	112·1	41·0
126–130	..	..	..	..	..	1·9	..	..	1·9	0·7
					E = 2,733·75				16,229·8	5,936·8
1958–59										
51–55			16·4		97·5	8·9			122·8	34·8
56–60	8·8		21·8		113·8	..	21·3		165·7	47·0
61–65	11·0		54·6		108·3	26·7	31·9		232·5	65·0
66–70	17·6		98·3		211·3	17·8	159·6		504·6	143·1
71–75	28·7	59·2	344·1	183·8	417·1	205·0	457·5		1,695·2	480·8
76–80	35·3	30·7	759·2	334·2	704·2	517·0	446·8		2,827·4	801·8
81–85	45·5	24·1	540·7	490·1	1,126·8	2,085·6	1,159·6		5,472·4	1,552·0
86–90	61·7	54·8	469·7	384·3	904·7	1,452·8	1,159·6		4,487·6	1,272·7
91–95	61·7	50·4	584·4	490·1	682·6	1,016·1	1,095·8		3,981·1	1,129·0
96–100	59·5	30·7	486·1	484·6	563·4	820·0	542·6		2,986·9	847·1
101–105	55·1	6·6	207·5	105·8	189·6	543·7	648·9		1,757·2	498·3
106–110	19·8	..	27·3	50·1	48·8	89·1	170·2		405·3	114·9
111–115	..	2·2	..	5·6	4·9	53·5	..		66·2	18·8
116–120	11·0	..	5·5	11·1	..	..	..		27·6	7·8
121–125	15·4	4·4	16·4	11·1	4·9	..	..		52·2	14·8
126–130	..	2·2	..	..	..	..	..		2·2	0·6
					E = 3,525·88				24,786·9	703·0
1959–60										
46–50			26·5						26·5	6·7
51–55			33·1						33·1	8·3
56–60			23·1	8·7					31·8	8·5
61–65		0·7	56·2	92·9	2·8	7·7			160·3	40·5
66–70		9·7	105·8	206·2	10·0	59·1	42·1		432·9	109·1
71–75	1·3	53·1	211·6	320·1	37·2	115·6	98·3		845·2	213·5
76–80	0·4	51·7	167·0	412·3	50·5	170·8	168·5		1,021·2	258·0
81–85	4·7	50·3	145·5	432·6	55·5	183·6	224·7	121·7	1,218·6	300·8
86–90	5·5	65·5	94·2	319·4	48·3	149·0	367·9	347·6	1,397·4	353·1
91–95	9·8	73·1	77·7	142·3	35·0	127·1	272·4	434·5	1,171·9	296·1
96–100	5·9	62·8	74·4	235·2	25·0	118·1	235·9	278·1	1,035·4	261·6
101–105	3·8	42·8	18·2	130·6	12·8	39·8	112·3	260·7	621·0	156·9
106–110	2·5	9·7	8·3	34·8	3·3	3·9	30·9	156·4	249·8	63·1
111–115	3·4	5·5	5·0	14·5	0·6	1·3	..	17·4	47·7	12·1
116–120	3·0	9·7	1·7	2·9	..	..	..	..	17·3	4·5
121–125	0·4	0·7	..	2·9	..	..	..	..	4·0	1·0
126–130	..	..	..	..	..	..	..	..	..	..
					E = 3,967·69				8,314·1	1,993·8

TABLE III (*Contd.*)

Class Interval (mm.)	November	December	January	February	March	April	May	Total	N/E
1960–61									
46–50		4·6	2·1					6·7	2·6
51–55		4·0	2·1					6·1	2·3
56–60	0·1	5·2	7·5	0·7	1·2			14·7	5·6
61–65	0·6	4·6	9·7					14·9	5·7
66–70	1·2	12·6	8·6	1·3			2·3	26·0	9·9
71–75	0·8	51·1	64·6	2·6		67·8		186·9	71·6
76–80	1·0	67·8	186·4	11·2	2·5	209·0	27·5	505·4	193·6
81–85	0·8	31·0	197·2	33·0	11·2	440·7	128·2	842·1	322·5
86–90	1·2	35·0	94·8	23·8	41·2	536·7	155·6	888·3	340·2
91–95	0·6	65·5	128·2	25·1	91·2	570·6	103·0	984·2	376·9
96–100	1·1	72·4	101·3	23·8	128·6	717·5	52·6	1,097·3	420·3
101–105	1·7	71·8	65·7	10·6	149·9	728·8	32·0	1,060·5	406·2
106–110	1·2	37·3	18·3	4·6	32·5	367·2	36·6	497·7	190·6
111–115	0·4	24·7	9·7	4·0	3·7	73·4	4·6	120·5	46·1
116–120	1·8	71·8	14·0	3·3	13·7	67·8	2·3	174·7	66·9
121–125	1·3	44·2	6·5	..	5·0	62·1	..	119·1	45·6
126–130	0·2	1·1	..	..	..	..	..	1·3	0·5
				E = 2,611·28				6,546·4	2,564·1

Class Interval (mm.)	September	October	November	December	January	February	March	April	May	June	Total	N/E
1961–62												1·9
56–60	0·4	..	1·3	..	1·9	..	..	..	..	4·9	8·5	10·7
61–65	0·9	2·6	2·7	..	..	3·4	5·0	..	34·1	..	48·7	22·2
66–70	2·6	1·3	1·3	11·0	1·9	23·6	5·0	..	46·9	7·3	100·9	107·2
71–75	0·9	..	17·4	22·0	48·0	138·1	96·5	17·1	110·9	36·6	487·5	268·4
76–80	0·4	5·2	10·7	73·2	65·2	437·8	220·0	160·0	208·9	39·0	1,220·4	335·6
81–85	0·4	2·6	24·1	124·5	90·2	410·8	342·6	754·1	417·8	268·1	2,435·2	913·4
86–90	..	1·3	18·8	205·0	201·5	572·5	465·7	1,022·6	993·4	672·6	4,153·4	865·2
91–95	..	1·3	38·9	230·7	1,190·0	649·9	592·1	1,022·6	750·4	458·1	3,934·0	1,064·2
96–100	..	..	88·5	783·6	351·1	474·8	514·0	1,233·9	1,112·8	280·2	4,838·9	990·7
101–105	..	2·6	85·9	1,402·4	383·8	505·1	484·0	611·2	805·8	224·2	4,505·0	375·7
106–110	..	2·6	26·8	823·8	176·5	131·3	131·4	182·8	174·8	58·5	1,708·5	496·2
111–115	..	..	26·8	1,362·1	284·0	151·5	161·3	171·4	89·5	9·7	2,256·3	269·9
116–120	..	2·6	36·2	845·8	107·4	53·9	44·9	74·2	60·0	2·4	1,227·4	50·1
121–125	..	1·3	5·4	201·4	3·8	6·7	3·3	5·7	..	..	227·6	2·4
126–130	..	..	11·0	..	..	..	..	..	..	..	11·0	
				E = 4,547·02							27,163·3	5,773·8

TABLE III (*Contd.*)

Class Interval (mm.)	November	December	January	February	March	April	May	June	Total	N/E
1962–63										
41–45	..	..	..	..	10·7	..	..	..	10·7	2·8
46–50	12·2	..	..	..	10·7	0·5	..	..	23·4	6·2
51–55	12·2	2·7	..	..	19·5	0·5	..	..	34·9	9·2
56–60	9·1	1·3	4·7	4·4	23·1	4·9	..	..	47·5	12·5
61–65	24·3	1·3	9·3	13·2	40·8	15·7	..	..	104·6	27·6
66–70	9·1	6·8	84·0	97·1	83·4	39·5	65·3	..	385·2	101·6
71–75	24·3	47·4	136·9	198·6	175·7	73·7	189·1	0·9	846·6	223·2
76–80	9·1	47·4	192·9	278·0	246·8	53·1	294·5	2·3	1,124·1	396·3
81–85	24·3	28·4	180·5	317·7	344·4	62·8	408·3	18·7	1,385·1	365·2
86–90	9·1	23·0	172·7	368·4	285·8	72·0	312·9	56·5	1,300·4	342·8
91–95	30·4	51·4	224·1	434·6	292·9	99·1	244·3	51·0	1,427·8	376·4
96–100	158·1	98·8	306·5	450·1	129·6	73·7	147·3	37·4	1,401·5	369·5
101–105	188·5	125·9	157·1	275·8	60·4	33·6	97·1	24·6	963·0	253·9
106–110	121·6	25·7	66·9	99·3	23·1	10·8	25·1	4·1	376·6	99·3
111–115	121·6	31·1	56·0	112·5	19·5	4·3	3·3	0·5	348·8	91·9
116–120	63·8	35·2	29·6	46·3	3·6	2·7	1·7	0·5	183·4	48·4
121–125	6·1	1·4	6·2	..	..	..	..	0·5	14·2	3·7
126–130	..	..	..	..	..	..	..	..	..	..
			E = 3,793·34						9977·8	2,730·5

TABLE IV

Numbers caught per hour of trawling in sizes (mm.)

Year/Size (m.m.)	46–	51–	56–	61–	66–	71–	76–	81–	86–	91–	96–	101–	106–	111–	116–	121–	126–
1957–58		1·6	4·5	23·2	52·9	203·4	413·3	920·2	947·1	827·7	993·3	837·2	350·3	171·3	149·1	41·0	0·7
1958–59		34·8	47·0	65·9	143·1	480·8	801·8	1,552·0	1,272·7	1,129·0	847·1	498·3	114·9	18·8	7·8	14·8	0
1959–60	6·7	8·3	8·5	40·5	109·1	213·5	258·0	300·8	353·1	296·1	261·6	156·9	63·1	12·1	4·5	1·0	
1960–61	2·6	2·3	5·6	5·7	9·9	71·6	193·6	322·5	340·2	376·9	420·3	406·2	190·6	46·1	66·9	45·6	0·5
1961–62			1·9	10·7	22·2	107·2	268·4	535·6	913·4	863·2	1,064·2	990·7	375·7	496·2	269·9	50·1	2·4
1962–63	6·2	9·2	12·5	27·6	101·6	223·2	296·3	365·2	342·8	376·4	369·5	253·9	99·3	91·9	48·4	3·7	

following two months has moved upto 68 mm. and so on. This interpretation of the progression of modes seems to be fallacious. If the mode 43 mm. in July 1949 can progress to 63 mm. in October 1949, a growth of 20 mm. in three months, it is difficult to believe that it did not grow at all during the next two months, but again had a growth of 15 mm. in the next four months. In fact the author ignored the small mode at 68 mm. in November, to which the growth represented by mode at 63 mm. in October 1949 grew. This group could not be traced in the length-frequency distribution curves of subsequent months. The mode at 63 mm. in December 1949 is obviously the group with the mode at 48 mm. in November 1949 which passes through the modal value of 68 mm., 68 mm., 73 mm., 78 mm., 78 mm. and 83 mm. respectively in subsequent months. The author has ignored the entry of several new broods between November to May.

In the following, the same data has been re-analysed keeping in mind the prolonged spawning habit of the species. The length-frequency data from the trawler catches and also those from the catches at Alleppey and Narakkal have also been taken into consideration. Table V presents the results of the findings. The first column gives the source of the data and the month of the first appearance of a group. The modal value at the first appearance is then given and then the values of the modes in subsequent months as far as the same group could be traced. The relative placement of the first mode is made according to its size and its subsequent growth and the month of its first appearance has nothing to do with its placement. The average value for each column is given at the bottom. From these values, it is seen that the group represented by 28·00 mm. moves to 41·3 mm. next month, showing a growth of 13·3 mm. Thus the group at 28·00 mm. must be the prawn which had completed about 2 months. Following the average values, it is seen that the prawn attains a size of about 97·5 mm. at the end of the 12 months' life.

It may be argued that there is some amount of arbitrariness in making the placement of the first mode and this may influence the average values. It is true that the relative placement of the first modal value is somewhat arbitrary but consideration of the value of the mode and its subsequent growth leaves very little freedom for the placement of the same. To confirm the findings obtained by this method, another method of analysis was adopted which is given below.

It is assumed that *M. dobsoni* obeys the growth law represented by the Bertalanffy's equation:

$$l_t = l_\infty \{1 - e^{-K(t-t_0)}\}$$

where l_t is the length of the fish at any age t ; l_∞ is the asymptotic length; K the growth coefficient and t_0 = an adjustment in the time axis.

Assuming that the size of the prawn was zero at $t = 0$, and $t_0 = 0$, the above equation can be rewritten as:

$$l_{t+1} = a + bl_t$$

a linear form, where $b = -\log_e K$ and $l_\infty = a/(1-b)$. The least squares estimates of a, b could be obtained from the data, if we arrange the data in such a way that if any modal value is represented by l_t during a month, it is represented by l_{t+1} next month. Following this procedure, the values of l_t and l_{t+1} have been written down in Table VI. Only those modes have been taken into consideration which could be distinctly identified and traced for at least a few months.

The least square estimates of a, b are obtained as $a = 15{\cdot}38$ and $b = 0{\cdot}87$. From these the estimated values of K and l_∞ are obtained as:

$$K = 0{\cdot}14 \text{ and } l_\infty = 118{\cdot}31.$$

Taking these estimates, the Bertalanffy's equation can be written as:

$$l_t = 118{\cdot}31\,(1 - e^{-0.14t}).$$

TABLE V

Recognizable modes and their progression through months

Source and the month of first appearance	Values of modes (in mm.) in successive months																	
Menon																		
January 1950	28	38	48															
November 1949	28	43	48															
December 1949	28	..	48	58														
July 1949		43	53	..	63	68												
November 1949			48	63	68	68	73	78	78	83								
Alleppey																		
February 1960 (f)			48	58	63	73	78	..	..	88								
February 1960 (m)			48	63	68	73												
March 1957 (m)					60	73	73	88	93	98	98	98						
March 1957 (f)					60	73	78	78										
June 1957 (m)										88	93	98	98					
January 1958 (m)						68	68	73	73	78								
May 1958 (m)										88	88	93	98	98	98			
May 1958 (f)											93	103	103	108	113	113		
June 1957 (f)												103	103	108	113	113	..	113
July 1959 (m)									83	93	93	103						
July 1957 (f)													103	103	108	113	113	..
Menon																		
July 1949																		113
Narakkal															108	108	108	113
March 1957				58	63	73												113
July 1957				53	68	73	83											
February 1959 (m)							73	83	88	88								
Alleppey																		
May 1961 (m)									83	88	93	93						
Trawler																		
March 1957 (m)										88	95	98	98					
March 1957 (f)							73	78	83	88	93							
February 1958 (m)								78	83	83	83	88						
December 1958 (f)										88	93	..	98					
Average ..	28·0	41·3	48·7	58·8	64·1	71·3	74·8	79·4	83·0	87·6	92·3	97·5	99·9	104·0	108·0	111·7	111·3	113·0	113·0
Estimated age (in months)	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20

TABLE VI

Values of a mode (x) in a month and the corresponding mode (y) next month (in mm.)

x	y	x	y
28	38	93	103
38	48	103	103
28	43	103	108
43	48	108	113
48	58	113	113
43	53	103	103
63	68	108	108
48	63	108	113
63	68	113	113
68	68	83	93
68	73	93	93
73	78	98	103
78	78	103	103
78	83	103	108
48	58	108	113
58	63	113	113
63	73	93	98
73	78	98	98
108	108	58	63
108	108	63	73
108	113	53	68
113	113	68	73
48	63	73	83
63	68	73	83
68	73	83	88
60	73	88	88
73	73	83	88
73	88	88	93
88	93	93	93
93	98	88	95
98	98	95	98
98	98	98	98
60	73	73	78
73	78	78	83
78	78	83	88
88	93	88	93
93	98	78	83
98	98	83	83
68	68	83	83
68	73	83	88
73	73	88	93
73	78	93	98
88	88		
88	93		
93	98		
98	98		
98	98		

$b = 0{\cdot}87$ $\quad K = -\log_e b = {\cdot}14$

$a = 15{\cdot}38$ $\quad I_{\infty} = \frac{a}{1-b} = 118{\cdot}31$

TABLE VII

Estimated size of M. dobsoni *at various ages*

Age (in months)	Estimated size in mm.	Average size in mm. from table V	Age (in months)	Estimated size in mm.	Average size in mm. from table V
1	15·5	..	13	99·1	97·5
2	28·9	28·0	14	101·6	99·9
3	40.6	41·3	15	103·9	104·0
4	50·8	48·7	16	105·8	108·0
5	59·5	58·8	17	107·4	111·7
6	67·2	64·1	18	108·8	111·3
7	73·9	71·3	19	110·0	113·3
8	79·7	74·8	20	111·1	113·0
9	84·7	79·4	21	112·0	..
10	89·1	83·0	22	113·0	..
11	93·0	87·6	23	113·5	..
12	96·3	92·3	24	114·2	..
..	...	..	36	117·6	..

Putting different values of t, in the equation, the estimated sizes of the prawns at different ages are obtained as in Table VII. Alongside the estimated values obtained from the Bertalanffy's equation, the average values at successive months of growth as obtained from Table V are given. Even though there could be some arbitrariness in the first placement of the mode in the first method the agreement between the results of the two approaches were pretty close. On the evidence of these, it can be said that *M. dobsoni* attains a length of about 95 mm. at the completion of age 1 and it attains a length of 114 mm. at the end of age 2 and it becomes nearly 118 mm. at the end of age 3.

AGE DISTRIBUTION OF THE CATCH

Accepting the above age-size relation, the number of *M. dobsoni* of different ages caught per trawling hour in the different years are shown in Table VIII.

From the size composition and therefore the age composition of the catch it is clear that the catch consists primarily of the 0-year class above 65 mm. size and the 1-year class. Hence the fluctuations in catch will be mainly due to the fluctuations in the abundance of the 0-year class. Since the fishery depends both on the 0-year as well as on the 1-year class, good abundance of 0-year class in successive years will yield good catch and poor abundance of 0-year class in successive years will result in poor catch. The age structure of the catch in different years generally conform to this.

TABLE VIII

Abundance of different age groups in catch

Year	Number caught per trawling hour			Mortality rate $\log_e n_1/n_2$
	0-year (n_0) (upto 95 mm.)	1-year (n_1) (96 to 115 mm.)	2-year (n_2) (116 mm. and above)	
1957-58	3393	2351	191	4·62
1958-59	5528	1479	23	5·68
1959-60	1594	494	5	1·47
1960-61	1332	1063	113	1·20
1961-62	2722	2927	322	3·72
1962-63	1763	815	52	..
			Average	3·56

Now the variation in the fluctuation of the 0-year class may be due to either (1) variation in availability or (2) due to variation in the number of spawners in the previous year.

The effects of variations in availability can generally be distinguished from the effects of changes brought about by changes in spawning stock remaining after a fishery. If availability was high, a large catch would be followed by a small spawning but if the catch was high due to appearance of strong year class, a large catch would be followed by a large or average spawning. Similarly a small catch would be followed by a large spawning if availability was low but by a small or average spawning if the catch was small as a result of the presence of week year classes.

In the fishery under consideration, the problem is very much simple. Since the fishery in the offshore area is new and is just starting and the fishery in the inshore and backwaters depend entirely on juveniles below 65 mm. in size, the spawners in the stock are practically unaffected by fishing. Hence any variation in the abundance of recruits, *i.e.*, in the abundance of 0-year class in the offshore stock of *M. dobsoni* must be due to variation in availability.

ESTIMATES OF MORTALITY RATE

If n_t is the number of *M. dobsoni* of age t and n_{t+1} is the number of age $t + 1$, then $\log_e (n_t/n_{t+1})$ gives an estimate of the total instantaneous mortality rate i between age t and $(t + 1)$. In the present case, since the recruitment does not fully take place until the prawn is above 70 mm. the index of abundance of 0-year class is not fully representative. Hence, the instantaneous mortality rate could be calculated by this method only between year classes 1 and 2. This is shown in the last column of Table VIII. The estimated rate varies considerably from year to year and fluctuating availability must account for such variation. The average annual total instantaneous mortality rate based on 6 seasons' data was estimated at 3·56 by this procedure.

Where age cannot be determined accurately, Beverton and Holt has proposed the following approximate formula:

$$t = \frac{K (l_\infty - \bar{l})}{(\bar{l} - l')}$$

where

K = growth coefficient in Bertalanffy's growth equation.

l_∞ = the asymptotic length in Bertalanffy's growth equation.

l' = the size at which full recruitment takes place.

l = the average size of the prawn in the catch above the size of recruitment.

K and l_∞ have already been estimated.

The value of K found in Table VI is in units of month. If the year is taken as unit the value of K becomes 1·68. For each season, the value of l' was taken as the first mode of the length distribution of catch and thereafter l was calculated. The basic data are from Table III. The estimates of i for the various years are as follows:

	Estimates of i from approximate formulae
1957–58	.. 3·33
1958–59	... 5·57
1959–60	... 5·47
1960–61	.. 3·96
1961–62	.. 2·61
1962–63	.. 3·31
Average	.. 4·04

This estimate is not very different from the estimate obtained by the first method.

Since the fishing by trawling in the offshore stock has just commenced and the offshore stock is practically independent of the fishery in inshore and backwaters, the component of mortality due to fishing in the offshore stock must be negligible. In other words, the natural mortality is very high.

The direct consequence of high natural mortality rate of *M. dobsoni* (with short life span) is, as we have seen before, that the annual fishing success would depend heavily on the numerical strength of the incoming year class and would therefore be relatively unstable. This will be exhibited by great fluctuation in the average catch per unit effort among different years. Since the natural mortality rate is very high, the commercial fishing for *M. dobsoni* can be expanded greatly without in any way damaging the offshore stock of the species.

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DISCUSSION

DR. B. RASMUSSEN: Are there different year groups represented in the catches ?

MR. S. K. BANERJI: In the offshore catches the late 0-year class and the first year class are mostly represented. In the backwater catches only prawns upto about 70–75 mm. are represented.

DR. B. R.: When do they mature ?

MR. M. J. GEORGE: In our studies we have found that the post-larvae of these prawns which come into the backwaters at very small sizes grow upto about 70–75 mm. in this environment and then migrate back to the sea. No mature females have been caught in the backwater although sometimes mature males are met with. Maturation takes place in the marine environment.

DR. J. H. WICKSTEAD: In Singapore, some of the prawns come to the brackish waters for breeding. I wonder whether that is the case here.

MR. M. J. G.: In the case of some of the palaemonids in these waters they are found to breed in the brackish water environment and the post-larvae ascend the river.

DR. S. Z. QASIM: Von Bertalanffy's equation has 3 parameters, namely l_{∞}, k and t_0. I would like to know if, while modifying this equation, you included any other parameters.

MR. S. K. B.: No other parameter was included.

DR. S. Z. Q.: The value 3·56 that you have given for the mortality rate refers to F + M or only one of the two ?

MR. S. K. B.: It is an estimate for F + M. But since the fishing has only just started in this area F is negligible and, therefore, the estimate may be taken to represent the natural mortality coefficient M only.

DR. S. Z. Q.: Beverton and Holt's model generally refers to total mortality from which the natural mortality is calculated. But how did you directly estimate M ?

MR. S. K. B.: The former answer explains this.

DR. S. Z. Q.: Unless the year-classes are clearly defined it seems rather difficult to fit in Von Bertalanffy equation, with the length-frequency data.

MR. S. K. B.: Differentiating the Von Bertalanffy equation we can get it in a form from which k and l_{∞} could be obtained. Some work has been done on these lines by the Inter-American Tropical Tuna Commission.

OBSERVATIONS ON THE FISHERY AND BIOLOGY OF THE GIANT FRESHWATER PRAWN *MACROBRACHIUM ROSENBERGII* DE MAN*

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ABSTRACT

Results of a study of the biology and fishery of the giant freshwater prawn *Macrobrachium rosenbergii* de Man in Central Kerala during the years 1959–1963 are reported.

The common methods of fishing, annual trends in production, effort and catch rate and monthly fluctuations in the fishery are discussed.

Using the length frequency data from the various centres, the age and growth of the two sexes contributing to the fishery have been studied. Males are found to grow slightly more than females. Among females, 1-year class are very rare, whereas among males they are common. Females are not usually found surviving far into the second year of life.

By following the maturity condition of the gonads and the abundance of berried and spent forms in the fishery the time and place of breeding have been fixed. Fecundity of the species was studied by estimating the number of extruded eggs. The seasonal migrations of the species are dealt with in the light of observations made along the course of the Pampa River.

The possibility of an over-fishing problem has been posed and certain conservation measures suggested.

INTRODUCTION

THE giant freshwater prawn, *Macrobrachium rosenbergii* de Man, supports a lucrative fishery in the rivers and backwaters of Central Kerala. The relatively large size of the species and its availability in fairly large numbers account for its popularity with the shrimp packing industry. This fishery was not of much significance until 1953 when the freezing and packing industry was established at Cochin essentially for the purpose of exporting prawns as a foreign exchange earning commodity. Encouraged by higher returns more and more people took to fishing for the species and various indigenous methods were adopted for catching them from all possible places. The fear of depletion, though available data do not confirm it, lead the industrialists to devote more attention to this species than to the other equally or more important marine prawns. Consequently the Standing Fisheries Research Committee appointed by the Government of India decided at its meeting early in 1959 that systematic investigations on the biology and fishery of this prawn should be taken up at the Central Inland and Marine Fisheries Research Institutes. The present account is based on the investigations carried out at the Central Marine Fisheries Research Sub-Station, Ernakulam.

Our knowledge of the biology and the fishery of this species is limited to the accounts given by Chopra (1943), Chacko (1955), Mary John (1957), Panikkar and Menon (1955) and Ling and Merican (1961). The early larval stages of this species from the Cochin backwaters have been described by Menon (1936). Rajyalakshmi (1961) studied the breeding and maturation of this species in the Hooghly river. But much of the life-history and bionomics remain unknown.

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M. rosenbergii is generally caught from the Vembanad and Kayamkulam lakes and the important rivers opening into them, *viz.*, Muvattupuzha, Meenachil, Pampa and Achankovil. The Periyar river, a branch of which opens into the Cochin backwaters, is not of any significance to this fishery since this species is seldom caught from this river. The Vembanad lake, which opens into the Arabian Sea at Cochin, is the largest body of backwater on the west coast of India extending for about 56 kilometres from Cochin to Alleppey. The widest part is the southern end where the Pampa, Meenachil and Achankovil rivers open. At this part the lake is about 15 kilometres wide and it gradually narrows towards the north. The rivers are comparatively short, narrow and fast flowing with mostly sandy bottoms. In the lower reaches, however, the river-bed is slushy and muddy. The bottom of the lake is muddy for the most part. The Muvattupuzha river opens near Vaikom at about the middle of the lake. The water in the southern part of the lake is almost fresh during the major part of the year. Salinity during the dry months, February to May, varies from 10 to 18‰. During the rest of the year the water is nearly fresh and especially so during the monsoon months—June to September. The tidal influence of the sea is more pronounced in the northern parts, where the water becomes fresh only during the monsoon months, and is felt up to a distance of 30 kilometres or more upstream. The salinity of the water in the lower reaches of the rivers also shows a slight increase during the dry months. At a point about 15 kilometres up the Pampa river mouth the highest salinity recorded is 3·50‰ during April. This may vary from month to month due to occasional rains. The water level in the river rises slightly during high tide even at places 60 or 70 kilometres above the river mouth. But the water never becomes saline beyond the village of Pulikizh about 30 kilometres up the river.

Methods and Materials

Regular fortnightly samples were obtained from commercial catches at Kumarakom and Ramankari (Fig. 1) during the fishing season and monthly experimental fishing was conducted with cast net and baits at five centres along the course of the Pampa river. From the river mouth upwards these centres are Pallathuruth, Ramankari, Pulikizh, Aranmula and Ranni roughly 15 kilometres apart. Experimental fishing was conducted with cast net and baits on the same lines as in commercial fishing. Surface plankton was taken by using a half-metre plankton net made of organdy and a specially designed bottom sledge trawl was used in the search for juveniles. An effort was also made to compare the catches obtained by the two commonly used gears, *ottal* nd cast net. The assessment of the total landings at both the regular centres was made from the figures of the purchasing agents who supply the prawns to the freezing companies. Annual production figures for the region were computed from the records of the freezing companies as the local consumption of the species was negligible due to the high prices offered by the companies.

Each sample was sorted out in the field itself and the sex ratio, total length (from tip of rostrum to tip of telson), carapace length and maturity were noted. In the case of berried specimens the nature of the eggs was also recorded. Size of the moulted specimens was specially noted. Ovarian eggs were examined in the laboratory and their size frequency recorded. This was carried out in the case of berried and spent specimens also. The number of extruded eggs was estimated by counting a weighed portion of the berry and computing the total.

Fishery

Fishing for *M. rosenbegii* is generally carried out by individual fishermen using *veechu vala* (cast net) or *ottal* (a conical contrivance open at both ends made of thin bamboo strips) with the help of a small dug-out canoe. Occasionally various types of drag nets such as *vadi vala*, *koru vala*, and *peru vala* also catch small numbers of this prawn along with fishes. *Vatta vala* (a pouch net) and *anta vala* (a drag net) are used for catching the species from among submerged vegetation. While fishing with cast nets, baits are dropped in water and their position marked by poles.

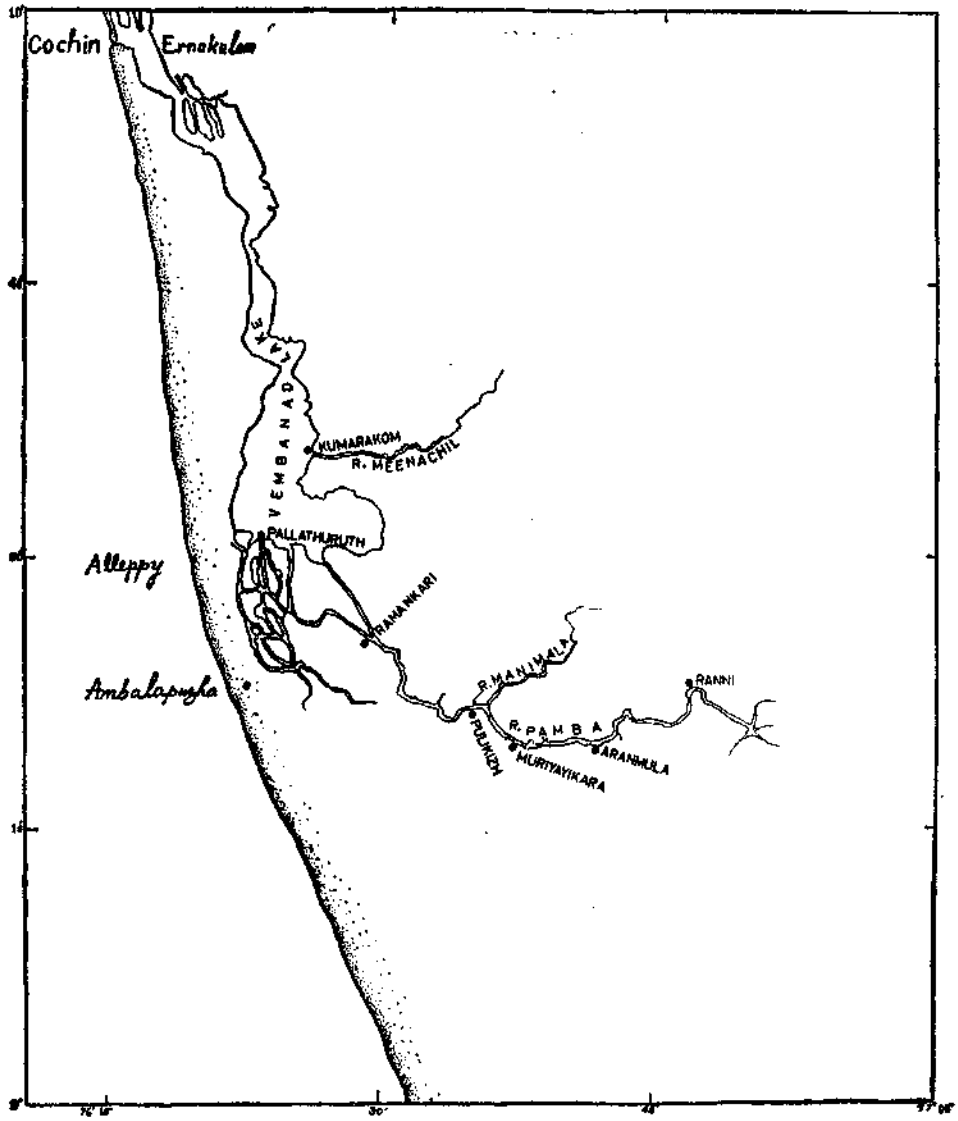

FIG. 1. Showing the Vembanad lake with Pampa river and the observation centres.

After allowing some time for the prawns to approach the bait the cast net is operated over the baits. This type of fishing is usually carried out at night in depths varying from 3 to 6 metres. *Ottal* is used in shallow areas 1-2 metres deep. Same type of baits attached to small floats are dropped in the fields and when the float is found moving the *ottal* is plunged above it and the prawns are collected with bare hands. *Vadi vala* is used for fishing in the shallow parts of the rivers and backwaters and *M. rosenbergii* occasionally occur in their catches also.

In some places the species is also taken with hook and line while fishing for other fishes. This is common in the northern parts of the Vembanad lake between Vaikom and Cochin.

The fishery started in May at Ramankari and in June at Kumarakom during 1960. The landings increased during July and reached a peak in August (Table I). In september there was a slight fall in the catch at both the centres and in October again it improved. In the following months the landings gradually dwindled. In the next season there was only a single peak in September and in the next three months the landings gradually decreased. At Ramankari the fishery in 1961 started very early in March and at Kumarakom as usual in June.

TABLE I

The estimated monthly landings of the two observation centres for the seasons 1960 *and* 1961

Months	1960		1961	
	Kumarakom (kg.)	Ramankari (kg.)	Kumarakom (kg.)	Ramankari (kg.)
March ..	...	..	..	680·25
April ..	...	..	..	1,000·00
May ..	..	1,360·77	..	1,200·00
June ..	4,085·00	3,630·00	2,500·00	1,500·00
July ..	9,075·00	4,540·00	9,200·00	2,200·00
August ..	15,880·00	6,805·00	13,525·00	3,000·00
September ..	8,950·00	2,217·00	14,220·00	2,000·00
October ..	11,283·00	3,642·00	11,750·00	1,100·00
November ..	3,122·00	200·00	4,000·00	200·00
December ..	300·00	..	..	..
Total ..	52,695·00	22,394·77	55,195·00	12,880·00

The estimated annual production figures from 1957 to 1962 (Table II) shows that the catches of the species remained more or less steady around 300 m. tons till 1961. The maximum production of the species—429 m. tons—was recorded in 1960 while 1962 production was the lowest recorded (189 m. tons).

TABLE II

The estimated annual production for the years 1957–1962

Years	Total production in m. tons
1957	356
1958	296
1959	378
1960	429
1961	307
1962	189

Catch effort data collected from the two observation centres are presented in Table III. Unit of fishing effort (unit per day) is computed on the basis of one individual working with a craft and gear.

TABLE III

Total effort, total catch and catch per unit of effort at the two observation centres

	1958	1959	1960	1961	1962	1963
I. Ramankari						
Fishing effort (unit/day) ..	2081	3622	2807	1428	415	1427
Total catch (kg.) ..	2987·3	5584·4	5826·6	2621·1	488·4	2778·4
Catch per unit of effort (kg.) ..	1·436	1·542	2·076	1–835	1·177	1·947
II. Kumarakom						
Fishing effort (unit/day) ..	..	..	..	1869	715	1045
Total catch (kg.) ..	..	..	..	4944·1	1064·2	1596·1
Catch per unit of effort (kg.) ..	..	..	..	2·644	1·488	1·527

Of all the years, for which data are available for Ramankari, 1960 seems to be the most productive as shown by the highest catch per unit of effort (2·076 kg./unit/day) and 1962 the least productive (1·177 kg./unit/day). In 1959 both effort and catch rate showed increase from the previous year. In 1960 and 1961 the effort is less. The minimum of effort expended is recorded in 1962 which was a poor season and the reduction in total effort is an outcome of this poor yield. But the effort in 1963 shows a threefold increase and the catch rate is also high. This catch per unit of effort is better than those of 1958, 1959 and 1961. At Kumarakom also 1962 is a very poor season with the lowest effort and catch rate among the three years for which data are available. Here also the catch rate has shown a slight improvement in 1963.

AGE AND GROWTH

In Table IV size ranges and dominant size groups among males and females from the two centres for the years 1960–63 are indicated. The length data for the years 1960–61 from the two centres are grouped into 20 mm. groups and monthly length frequency histograms drawn for the two sexes separately for following up the growth rate. When the regular fishery starts at Ramankari in June 1960 the mode among males is at 181–200 mm. (Fig. 2). This shifts gradually to 261–280 mm. by October thereby showing a growth of about 80 mm. in four months. At Kumarakom the fishery starts in June with a mode at 221–240 mm. (Fig. 3) which moves over to 261–80 mm. by August. A lesser mode at 201–220 mm. is present in the cast net sample in July at this centre. This corresponds to the regular mode at Ramankari. In August this moves over to 221–240 mm. and by October to 261–280 mm. indicating identical growth rate. In the succeeding season also the same trend is noticed (Figs. 4 and 5). However, the mode at 181–200 mm. appears in June itself at Kumarakom and shifts to 221–240 mm. by August as in the previous year. The usual mode of June (221–240 mm.) shifts to 261–280 mm. by August as usual. The modal size in September and October is at 261–280 mm. After reaching this size the growth seems to be very slow and the modal group of August (221–240 mm.) may also be growing and contributing to this larger mode by October. Some of them seem to be returning to the rivers as is evidenced by the presence of such specimens at the upper reaches of the Pampa river from December onwards. An increase in the number of males towards the end of the season at the river centre (Ramankari) may also be taken as an additional evidence indicating their return. Towards the end of the season

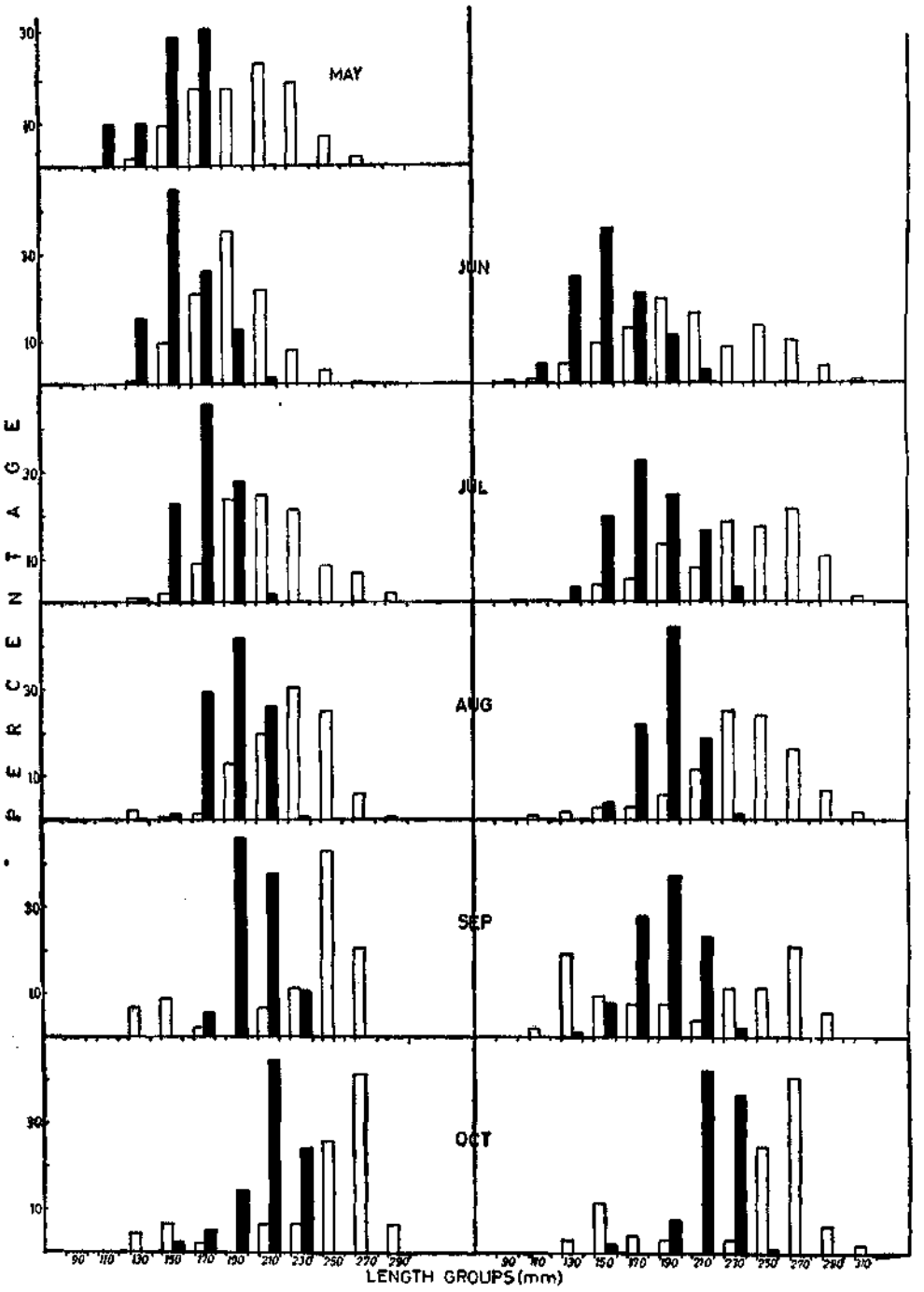

FIG. 2. Monthly percentage of *M. rosenbergii* from the landings of two gears—*Ottal* (left side) and cast net for Ramankari during 1960. Females shaded.

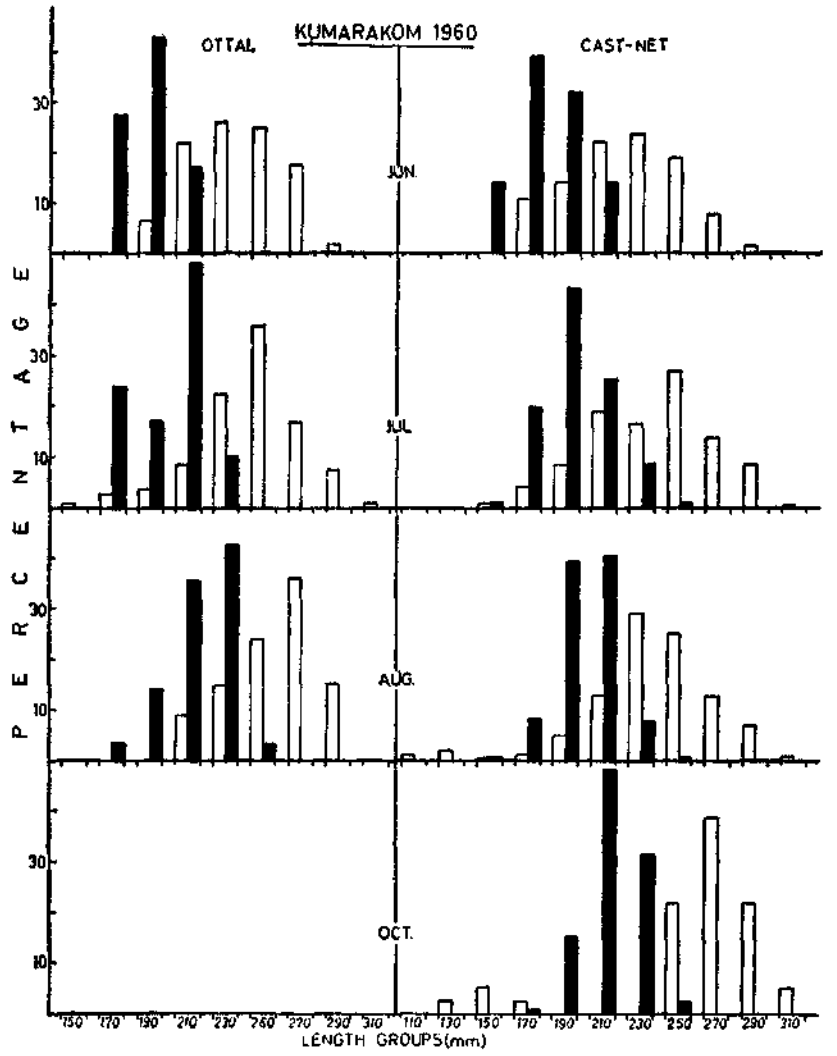

FIG. 3. Monthly size frequency of *M. rosenbergii* taken from *Ottal* and cast net during 1960. Females shaded.

a dominant size group appears at both the centres at 121–140 mm. or 141–160 mm. They also seem to return to the rivers after November.

In January when the regular fishery is over younger specimens of both sexes are caught from Pampa river around Muriyayikara, a fish-landing centre in the river east of Pulikizh (Fig. 1). The males with a larger size range show two dominant size groups—at 61–80 mm. and 141–160 mm. (Fig. 6). These two groups may be considered as the later and earlier broods of the same period just ended. There is also a minor mode 221–240 mm. which is continued through February and March. The smallest mode (61–80 mm.) is present in February and March also probably due to fresh recruitment. The mode at 141–160 mm. is also present in March and moves over to 161–180 mm. by May. The 61–80 mm. group present up to March moves over to 101–120 mm. in April and continues in May also. A mode present at 181–200 mm. in February shifts to 201–

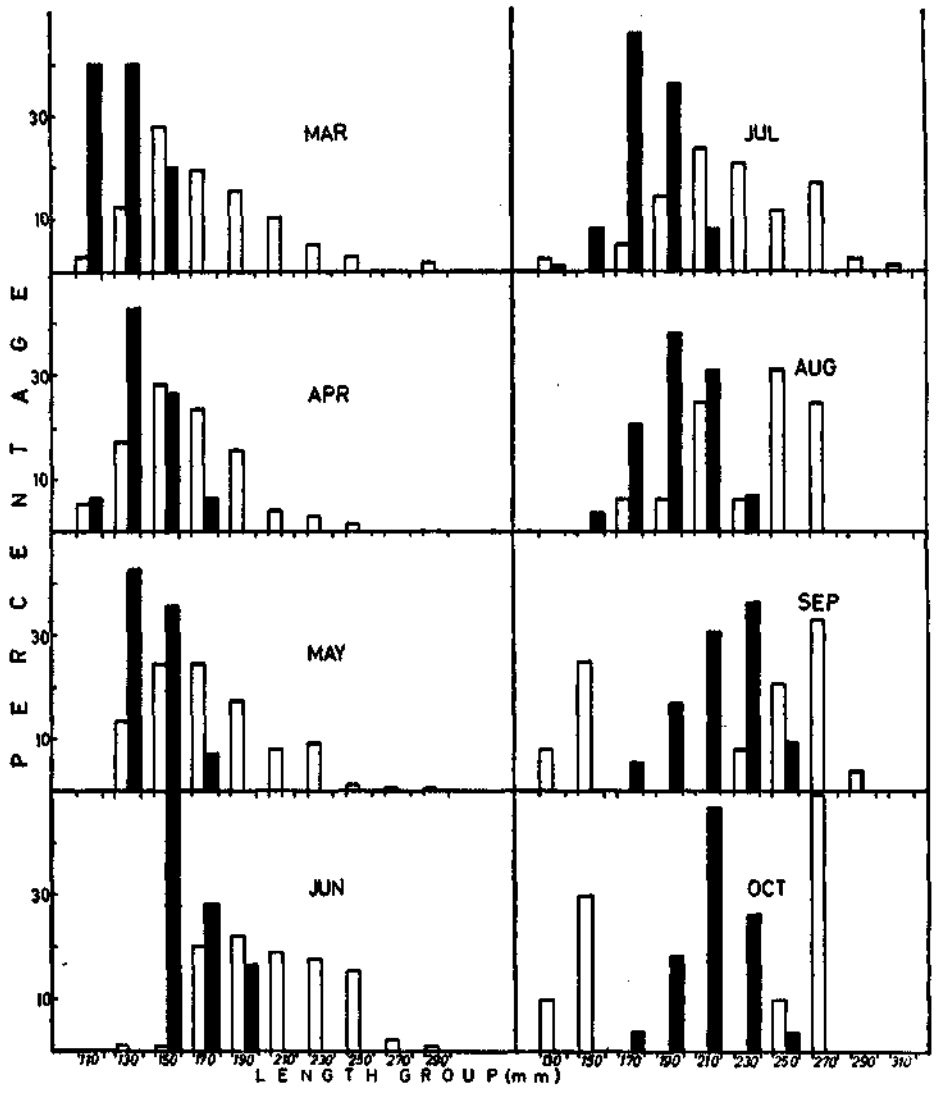

FIG. 4. Monthly frequency histograms of *M. rosenbergii* from Ramankari during 1961. Females shaded.

229 mm by April. This and the minor mode referred to above (221-240 mm) are the previous years' brood, perhaps the products of late and early breeding. They are the bigger modal groups at the lower centres like Ramankari and Kumarakom in May and June. As growth advances, the two groups merge and appear as a single mode in the catches of the next season—221–240 mm. mode of May and 261–280 mm. mode of July 1961 at Ramankari, 221-240 mm. mode in June at Kumarakom. The earlier brood of 1960—the 161–180 mm. group of Muriyayikara and Ramankari in May 1961 and the modal group of 181-200 mm. of June at Kumarakom and Ramankari—seem also to merge with the larger mode referred to above by the end of the season. Some of them also move up the river after August.

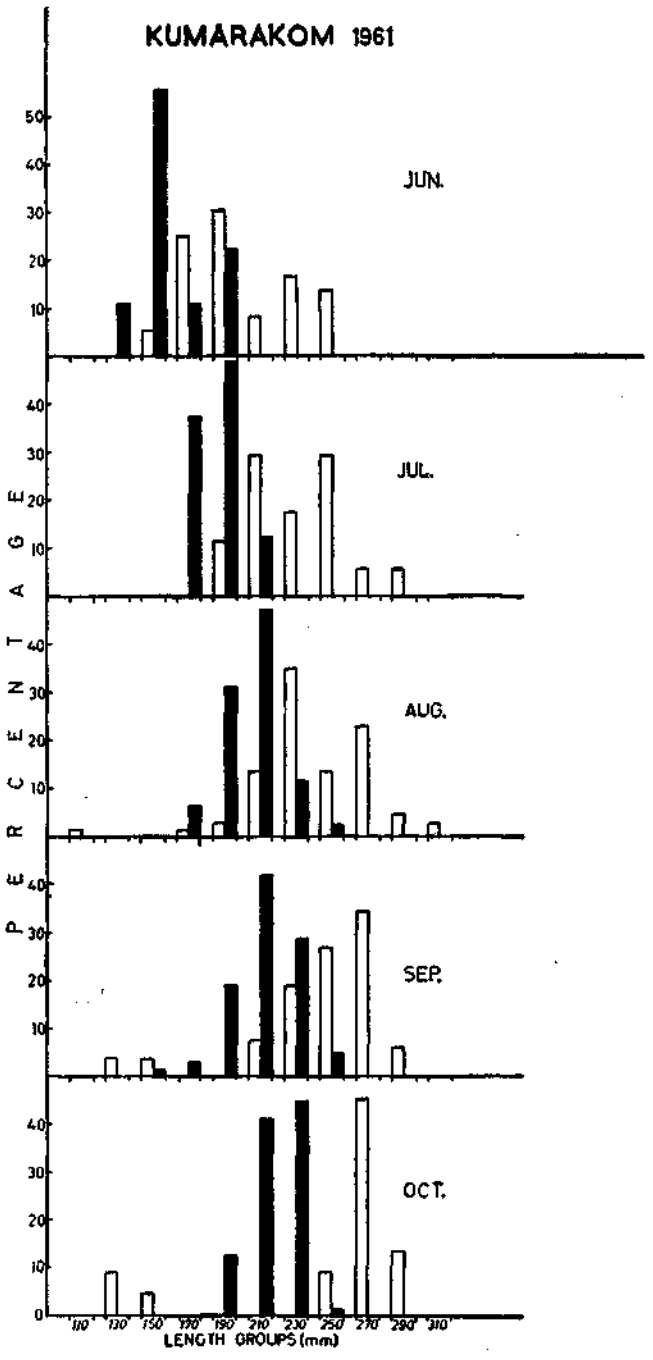

FIG. 5. Monthly frequency histograms of *M. rosenbergii* from Kumarakom during 1961, Females shaded.

TABLE IV

*Size range and dominant size groups * at Kumarakom and Ramankari for the years* 1960–1963

Months	1960		1961		1962		1963	
	Size range and (dominant size) in mm.		Size range and (dominant size) in mm.		Size range and (dominant size) in mm.		Size range and (dominant size) in mm.	
	♂	♀	♂	♀	♂	♀	♂	♀
At Kumarakom								
June ..	161–300 (221–240)	151–220 (161–180)	141–260 (181–200) and (221–240)	131–200 (141–160)	..	..	..	..
July ..	151–320 (201–220) and (241–260)	171–250 (181–200)	181–290 (201–220) and (241–260)	161–210 (181–200)	161–300 (261–280)	161–240 (181–200)	155–310 (201–260)	132–229 (181–200)
August ..	101–320 (221–240)	91–250 (201–220)	111–310 (221–240) and (261–280)	161–260 (201–220)	181–290 (261–280)	181–240 (201–220)	201–309 (241–260)	161–224 (201–220)
September ..	..	..	131–290 (261–280)	151–260 (201–220)	241–310 (281–300)	201–261 ..	195–304 (221–240)	191–250 (221–240)
October ..	121–320 (261–280)	171–260 (201–220)	131–300 (261–280)	191–250 (221–240)	131–310 (261–280)	201–262 (221–240)	..	..
November ..	..	..	..	..	261–310 (281–300)	221–260 (221–240)	..	..
At Ramankari								
March ..	..	..	101–300 (141–160)	111–150 (101–120)	..	..	..	..
April ...	..	..	111–200 (141–160)	111–170 (121–140)	..	...	91–260 (121–140)	91–180 (101–120)
May	121–280 (201–220)	111–180 (161–180)	131–290 (141–160, 161–180 and 221–240)	121–170 (121–140)	...	...	...	..
June ...	121–270 (181–200)	121–220 (141–160)	151–290 (181–200)	141–190 (141–160)	161–270 (161–180 and 201–220)	161–200 (181–200)	131–280 (201–220)	111–160 (141–160)
July ..	131–300 (201–220)	131–220 (161–180)	161–290 (201–220 and 261–280)	141–210 (161–180)	..	..	171–280 (221–240)	131–240 (181–200)
August ..	131–290 (221–240)	151–230 (181–200)	171–280 (201–220 and 241–260)	151–230 (181–200)	..	..	171–280 (221–240)	131–240 (181–200)
September ..	121–280 (241–260)	171–230 (181–200)	121–290 (141–160 and 261–280)	171–260 (221–240)	..	..	131–280 (241–260)	201–260 (201–220)
October ..	131–300 (261–280)	141–240 (201–220)	131–280 (141–160 and 261–280)	171–240 (201–220)	141–290 (261–280)	181–261 (221–240)	..	..
November ..	..	..	..	..	..	..	256–301 (261–280)	170–225

* Figure in parenthesis denote dominant size groups.

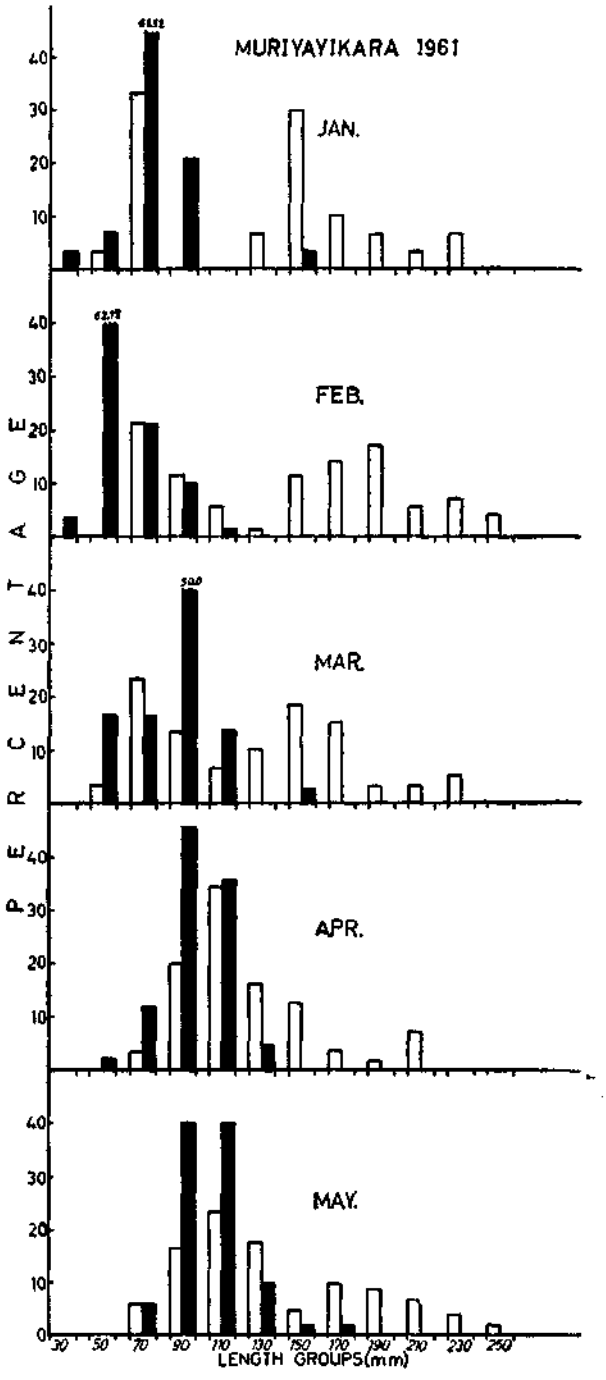

FIG. 6. Monthly frequency histogarms of *M. rosenbergii* from Muriyayikara during January–May 1961. Females shaded.

TABLE V

Percentage of various stages of maturity in males and females during the seasons 1960–1963, *at Ramankari*

Month	Male		Female				
	Immature	Mature	Immature	Maturing	Mature	Berried	Spent
1960							
May ..	3·7	96·3	90·0	10·0	..	Nil	Nil
June ..	5·3	94·7	42·7	54·6	2·7	,,	,,
July ..	2·0	98·0	23·6	55·1	21·3	,,	,,
August ..	3·4	96·6	10·3	67·0	22·7	,,	,,
September ..	14·6	85·4	16·3	35·0	30·9	17·9	,,
October ..	2·9	97·1	Nil	1·6	19·5	78·9	,,
1961							
March ..	21·9	78·1	100·0	Nil	Nil	Nil	,,
April ..	28·6	71·4	92·9	7·1	,,	,,	,,
May ..	17·0	83·0	92·9	7·1	,,	,,	,,
June ..	2·2	97·8	80·0	20·0	,,	,,	,,
July	2·6	97·4	54·2	44·4	1·4	,,	,,
August ..	Nil	100·0	24·1	37·9	37·9	,,	,,
September ..	8·3	91·7	Nil	11·5	46·2	42·3	,,
October ..	24·0	76·0	,,	Nil	40·8	59·2	,,
1962							
June ..	6·8	93·2	92·6	7·4	Nil	Nil	,,
October ..	3·0	97·0	Nil	Nil	22·8	77·1	,,
1963							
April ..	60·6	39·4	100·0	,,	Nil	Nil	,,
June ..	13·7	86·3	97·8	2·2	,,	,,	,,
July ..	Nil	100·0	36·1	59·0	4·8	,,	,,
August ..	,,	100·0	6·2	71·6	22·2	,,	,,
September ..	3·3	86·7	Nil	33·3	66·7	,,	,,
November ..	Nil	100·0	,,	Nil	Nil	100·0	,,

The males entering the fishery consist of a number of groups moving down the river in several batches beginning from March. As seen in the samples from Muriyayikara (Fig. 6) they are (1) the early brood of 1960 season (141–160 mm. mode of January), (2) the later brood of 1960 (61–80 mm. group of January) and (3) those which survived from the previous year's brood (181–200 mm. group of February and 201–220 mm. group of April and 221–240 mm. group of January, February and March). The former may be traced back to the mode at 121–140 mm. or 151–160 mm. seen at the fishing centres during the close of the fishing season and the latter is a continuation of the size groups similar to the 201–220 mm. mode of August 1961 at Ramankari. The minor mode appearing at 121–140 mm. or 141–160 mm. during September–November at the centres are to be traced back to the 101–120 mm. group of May at Muriyayikara (Fig. 6). Some of them are perhaps remaining upstream and probably coming down only late in the season by August–September. The growth during the time June to August seems to be rather slow (30 mm. in 3–4 months). Later in December a modal group appears at 161–180 mm. at Pulikizh (Table VIII). The growth rate to a large extent appears to depend on area inhabited, being slow up the river and fast in the backwaters. During the monsoon the growth appears to be very fast in the backwaters and this may probably be due to the flooding of paddy fields and availability of good

TABLE VI

Percentage of various stages of maturity in males and females during the seasons 1960–1963 *at Kumarakom*

Month	Male		Female				
	Immature	Mature	Immature	Maturing	Mature	Berried	Spent
1960							
June	.. ..	100·0	52·8	41·4	5·8	..	..
July	.. 0·9	99·1	21·8	50·4	27·7	..	..
August	.. 3·9	96·1	3·1	51·6	44·3	1·0	..
October	.. 5·6	94·4	1·1	1·7	14·5	58·7	24·0
November	.. ..	100·0	..	..	..	100·0	..
1961							
June	1·5	98·5	64·3	35·7	..	..	..
July	.. ..	100·0	27·3	67·3	5·5	..	..
August	.. 1·5	98·5	13·2	31·6	52·6	2·6	..
September	.. 7·7	92·3	..	12·9	58·1	17·7	11·3
October	.. 13·6	86·4	..	..	11·3	76·3	12·5
November	.. 5·3	94·7	..	..	..	42·0	58·0
1962							
July	.. ..	100·0	40·7	51·9	7·4	..	..
August	.. ..	100·0	6·3	56·3	37·5	..	..
September	.. ..	100·0	..	20·0	80·0	..	..
October	.. 5·9	94·1	..	..	0·7	70·8	28·5
November	.. ..	100·0	..	..	..	72·7	27·3
1963							
July	.. 5·1	94·9	45·9	41·4	32·7	..	..
August	.. 1·2	98·8	4·3	29·2	66·2	..	..
September	.. ..	100·0	..	..	70·0	25·0	5·0

quantities of food. Mary John (*op. cit*). observed large quantities of paddy in the stomachs of the species during this time.

The 0-year class approaching one year age is present in the catch as a mode at 141–160 mm. in March, 161–180 mm. in April and 181–200 mm. in June at Ramankari. This shifts to 261–280 mm. by October and even to 281–300 mm. in November in some years. On the assumption that they represent the early brood of last season it is apparent that they grow to about 200–220 mm. in one year. The larger ones are the products of the previous years breeding and hence more than one year old, while those forming the mode at 261–280 mm. found in July–August have already entered the second year.

When the fishery starts in March in 1961 at Ramankari the modal size among females is at 101–120 mm. This moves over to 141–160 mm. by June. At Kumarakom the mode is at 141–160 mm. when the fishery starts in June. This shifts to 201–220 mm. by September–October at both the centres. In November when samples could be obtained this mode is found at 221–240 mm. Thus in one year the females grow to a size of about 180–200 mm. The maximum sizes noted are in the 241–260 mm. group, but very rarely above 260 mm. The latter may probably be more than one year old. So it is evident that as far as the females are concerned the fishery is based largely on the first year group only. The small females do not remain upstream as in the case of males and

so there is no minor mode at a smaller size in September–November. Perhaps, no female returns upstream after the breeding season for completing a second year of life.

TABLE VII

Size range and dominant size groups in mm. at the five points along the Pampa river where experimental fishing was conducted during December–May*

Month	Pallathuruth		Ramankari		Pulikizh		Aranmula		Ranni	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
December	141–307	177–227	Nil	Nil	166–295 (161–180)	Nil	Nil	Nil	114–212 (161–180)	Nil
January	Nil	Nil	194–204	Nil	148–281	Nil	141–200 (141–160)	Nil	168–200	Nil
February	Nil	Nil	106–242	Nil	150–259 (161–180)	79– 90	Nil	Nil	Nil	Nil
March	Nil	Nil	126–231	Nil	86–240 (161–180)	97	Nil	Nil	146–196 (161–180)	Nil
April	141–218	Nil	Nil	Nil	100–232 (121–140 and 161–180)	73–132 (101–120)	Nil	Nil	185	Nil
May	74	87–105	Nil	Nil	121–214	96–145 (121–140) (121–140)	156–218 (201–220) (161–180)	143 and	143–216 (161–180) (201–220)	156
	Sex Ratio (numbers)									
December	..	12	3	..	..	7	Nil	..	12	Nil
January	..	..	..	2	Nil	7	Nil	9	Nil	2	Nil
February	..	..	..	10	Nil	33	2	..	..	..	..
March	..	..	..	12	Nil	30	1	..	..	6	Nil
April	..	2	Nil	..	..	28	14	..	..	1	Nil
May	..	1	3	..	..	10	8	5	1	13	1

* Figures in parenthesis denote dominant size groups.

The females occurring at the fishing centre east of Pulikizh in January range between 21 and 90 mm. with a mode at 61–80 mm. In February a new modal group appears at 41–60 mm. evidently due to fresh recruitment. In March however, there is only one mode at 81–100 mm. From February onwards there seems to be a movement among females. Those reaching 100 mm. or above are moving away from these areas. The evidence is more in favour of a movement down to the backwaters where they seem to grow faster. At Muriyayikara for instance the mode at 81–100 mm. in March continues through May, but at Pulincunnu a centre down the river near the Vembanad lake in April the mode among females was at 121–140 mm. showing a downward migration of larger specimens and faster growth in brackish water. During the same month a sample from Pulikizh shows the modal size as 101–120 mm. (Table VIII) showing a downward migration of larger females. The continuation of the mode at 81–100 mm. in April and May at Muriyayikara may probably be due to growth among the smaller groups and migration of larger ones away from the area. It is due to this migration that the earlier broods of the season are not seen among females

TABLE VIII

Size frequency distribution (numbers) of samples obtained during experimental fishing

Size groups	Pulikizh											Ranni						
	Nov.	Dec.	Jan.	Feb.		Mar.		Apr.		May		Dec.	Jan.	Feb.	Mar.	Apr.	May	
	♂	♂	♂	♂	♀	♂	♀	♂	♀	♂	♀	♂	♂	♂	♂	♂	♂	♀
71–80	..	..		..	1			..	1	..								
81–100	..	..		..	1	1	1	1	2	..	1							
101–120	..	..		..	..	4	..	3	7	..	2	2	..	..	..	..	..	..
121–140	..	..		..	..	6	..	8	2	3	3	1	..	..	..	..	..	..
141–160	..	..	2	2	..	6	..	5	..	..	2	2	..	..	3	..	2	1
161–180	1	4	1	10	..	11	..	6	..	3	..	6	1	..	2	..	7	..
181–200	1	1	2	9	..	1	..	3	..	..	..	..	1	..	1	1	2	..
201–220	..	1	..	8	..	1	..	1	..	4	..	1	..	..	..	..	2	..
221–240	..	1	..	2	..	1	..	1	..	..	..							
241–260	1	..	1	2	..	..	..	..	..	..	..							
261–280	..	..	..	..	..	..	..	..	..	..	..							
281–300	..	..	1	..	..	..	..	..	..	..	..							

at Muriyayikara. However, a very small group at 141–160 mm. found in January and March probably belong to this group. Down the river and in the backwater these two groups grow side by side and by the time they enter the fishery they seem to merge so that there is only one mode in the frequency histogram.

MATURITY AND BREEDING

The ovaries of most of the specimens are narrow transparent or whitish strands when the fishery starts in June–July. In August they begin to develop gradually when yellow dots appear on the surface of the ovaries. In mature specimens the ovary is bright orange in colour and more massive occupying a large part of the cephalothorax just behind the rostral base extending backwards even into the first abdominal segment and could be easily made out even without removing the carapace. Just before the extrusion of the eggs the mature individuals are easily recognisable by their bulging abdominal pleura and the development of feathery hairs on the basipodites of the pleopods. The eggs when extruded get attached to them with the help of a sticky substance. The fringes of the pleopods are blue or violet in colour during this period. Spent specimens are seen with mud-coated pleopods and hairs with remnants of egg membranes. In most of the berried and spent specimens ovaries are found to regenerate and in some spent specimens mature and maturing ovaries are observed thereby showing the possibility of breeding more than once in the same season. This is in agreement with the laboratory observations of Ling and Merican (*op. cit.*). Eggs are bright orange in colour when they are first noticed on the pleopods turning grey as the development advances. In grey eggs the developing embryo could be easily made out.

When the fishery starts in May–June practically all the females obtained are either immature or maturing. Mature females generally begin to appear in the catches from July onwards (Tables V and VI). Thereafter their percentage increases and by October most of them are either mature

or berried. The testes are well developed in most of the specimens. Fully grown sperimatozoa are observed in specimens measuring 150 mm. The percentage of mature males is never less than 85 in any month (Tables V and VI).

Although berried specimens are caught in the fishery sporadically from various centres in late July and early August in some years they become common only in September when about 20% of the females are berried. Their percentage increases in October and November. In December also berried ones are caught, but the total number of females with or without eggs becomes much reduced during this month. Spent specimens occur in September, their percentage being about 10. This also increases in the subsequent months. It is thus evident that the breeding period extends from August to December with a peak in October–November. Spent specimens are seen only at the backwater centre—Kumarakom—but they are very rare at Ramankari which is a river centre. At a point near the opening of the Pampa river into the backwater (Pallathuruth) the same phenomenon has been noticed. The species therefore seem to prefer backwaters for hatching of eggs. This conclusion is also supported by the presence of large numbers of larvae in the backwaters during the breeding period. Grey coloured berries are very common at Kumarakom and other backwater centres, whereas the berries of almost all caught from the freshwater centres along the Pampa river are orange-coloured. It is therefore clear that later stages of development leading to hatching are passed through only in brackish-water environment. This is in agreement with the observations of Mary John (*op. cit.*).

Rajyalakshmi (*op. cit.*) has observed the breeding period of the species in the river Hooghly as December to July with a peak in March–May. This period follows the north-east monsoon which exerts pronounced influence on the physical features of the area. It is interesting to note that the breeding period of the same species observed during the present study also follows the predominant monsoon of the area, *viz.*, south-west monsoon. The number of eggs carried by a berried individual varies with length. In the present study it varied from 5,03,000 in a specimen measureing 181 mm. to 1,39,600 in one of 229 mm. However, fully mature ovary of a larger specimen (241 mm.) was found to contain 2,28,850 eggs. According to Chacko (*op. cit.*) the number of eggs extruded at a time varies from 1,00,000 to 1,60,000 depending on the size of the female and Rajyalakshmi (*op. cit.*) has estimated the maximum number of eggs extruded by a female as 1,11,400 at 200 mm. total length and the minimum 7,000 eggs at 136 mm. total length.

Larvae and Juveniles

From September onwards good numbers of the larvae of the species are seen in surface plankton hauls taken from Pallathuruth and Kumarakom, the backwater centres, but are very rare in collections from Ramankari. In late October and November they are obtained from the Cochin backwaters also in large numbers. Berried and spent specimens are also caught from this area. The plankton collections made during the course of the present investigations seem to indicate that only the first larval stage described (Menon, *op. cit.*) is a surface dweller. The second stage is only very rarely noticed in the plankton. Does it imply that after the first stage the larvae abandon their planktonic habit and sink? The present author has observed while rearing the first larval stage in the laboratory that after the first moult and transformation into the second stage the larvae sink to the bottom of the container and continue to swim about there. The above inference seems to be justified in the light of this observation. At this stage the larva is found to be very voracious eating its own moult and even other larvae. Attempts to collect the later larval stages from the surface or bottom have not succeeded. Rearing experiments were also unsuccessful since the second stage did not survive long enough to moult into the next. It has however been reported from Singapore (Ling and Merican, *op. cit.*) that the larvae thrive well in a mixture of sea-water and fresh water. This probably shows that the larvae stay on in the backwaters until they reach about 10 or 15 mm. length. The smallest juvenile caught from up the Pampa river in February measured 21 mm. So after completing the larval life in the backwaters

the juveniles go up the river by December or early January. In February also fresh recruits arrive at the upper reaches of the Pampa. The specially designed sledge trawl when operated did not catch any juvenile of this species although other prawns of the same size were caught. The juveniles of *M. rosenbergii* are caught mostly in the *peru vala* a sort of shore seine operated in the rivers, which are dragged along from the middle of the stream and is hauled up towards the shore. In April 1960 one specimen of the species measureing 34 mm. was obtained in an improvised bottom net operated in a narrow channel east of Ramankari. It would therefore appear that the juveniles prefer to remain close to the banks of the rivers and channels hiding in holes and crevices and among submerged plants and seldom come to the middle of the stream. This is confirmed by actual observation on several occasions in such places from where they were caught with the help of a piece of cloth or with bare hands. As has already been reported (Raman, 1964) during the summer months the juveniles are seen concentrating in the deeper areas of the river near Pulikizh. They come down the river and enter the backwaters with the onset of the monsoon.

Sex Ratio

When the fishery starts in May or June at the various centres the males far outnumber the females. In 1961 when the fishery commenced early in March at Ramankari the females were in a minority up to June–July (Table IX). From August onwards females predominated and this condition prevailed in September and October as well. In November males once again become more numerous at this centre. At Kumarakom also the same trend was observed with the difference that the preponderance of males at the end of the season was not observed here.

Table IX

Sex ratio of the catches from Kumarakom and Ramankari during 1960–1963

Months	1960		1961		1962		1963	
	♂	♀	♂	♀	♂	♀	♂	♀
Kumarakom								
June	69·2	30·8	80·0	20·0	...	...	...	...
July	69·9	30·1	68·0	32·0	62·5	37·5	53·3	46·7
August	48·4	51·6	46·1	53·9	40·7	59·3	49·5	50·5
September	..	..	29·5	70·5	66·7	33·3	29·7	70·3
October	16·7	83·3	21·6	78·4	28·6	71·4	..	..
November	53·3	46·7	..	..	50·0	50·0	..	..
December	44·9	55·1	..	..	..	..	..	..
Ramankari								
March	..	..	95·0	5·0	...	...	...	...
April	..	..	89·4	10·6	...	...	67·4	32·6
May	97·2	2·8	85·9	14·1	...	..	..	..
June	67·8	32·2	90·0	10·0	73·1	26·9	60·9	39·1
July	65·8	34·2	51·4	48·6	...	..	41·8	58·2
August	50·6	49·4	35·6	64·4	...	...	23·6	76·4
September	54·3	45·7	31·6	68·4	...	...	41·7	58·3
October	52·9	47·1	29·8	70·2	48·5	51·5	..	..
November	..	..	..	..	...	...	70·0	30·0

Movements

The second dominance of males at Ramankari may be the result of the downward migration of females to the backwaters. The continued dominance of females at the backwater centres even in November and December indicate this. From September onwards males belonging to size groups between 150 and 250 mm. become very rare at the backwater centres. This may be partly due to the effect of continued fishing and partly due to a movement up the river. These sizes are caught from the centres up the river from November-December onwards (Table VII). During the monsoon months and up to September the species seems to be absent from all the centres above Pulikizh. At Pulikizh during the monsoon time also specimens are available. They are caught during experimental fishing in September and October. From November onwards some of the males belonging to the previous year's brood seem to be slowly moving upstream and by December they are available at all the centres in the upper reaches of the river. A few are usually caught from Pulikizh and Ranni in almost all the off-season months (Table VIII). It may be seen that the 150 mm. and 210 mm. groups among males which are moving up the river are represented in the catches of both these centres. Both sexes of the 0-year class are obtained at Pulikizh, but at Ranni males alone are met with. The latter sex seems to be more erratic in their movements and have a wider distribution. Perhaps, they are able to tolerate a wider range of ecological variations. They are present at all points along the Pampa during December to February. In March when the salinity goes up (even up to 18‰) some specimens are caught from the backwater centre at the river mouth. From April, however, they become very rare at the lowest centres. Later, in May with the first monsoon showers they are again available at these centres, most of the males caught ranging between 100 mm. and 160 mm.

The females on the other hand go up the river at the early juvenile stage and there seems to be a return movement from February onwards. Until then they are available only near Pulikizh. After reaching about 100 mm. they seem to be moving away from this area and are caught along with male specimens during March and April from certain centres in the river nearer to the backwaters. In May very few females are caught from the eastern centres Aranmula and Ranni. This was immediately after the first pre-monsoon showers. Perhaps, some of them may be going further up beyond Pulikizh area. With the onset of the monsoon all these are swept down into the extensive paddy fields and canals of Kuttanad and thence to the Vembanad lake.

Food and Feeding

M. rosenbergii is a bottom feeder and an omnivore. Detailed analysis of stomach contents was not attempted because all the specimens from the commercial fishery being caught with baits had stomachs filled with tapioca or coconut as the case may be. However, a few stomachs from the drag net catches were examined and were found to contain bottom debris and mud with large quantities of decaying organic matter. Fish scales and remnants of fish were met with in a few instances. The former may be accidentally swallowed along with the detritus from the bottom but the latter shows that the species eats fish and other organisms if obtained. Mary John (*op. cit.*) has also reported an omnivorous food habit for the species.

Moulting

To follow the moulting periodicity, the method used by Menon (1952) and George (1959) was tried. It is found that moulting takes place at irregular intervals—roughly one moulting for every 10 mm. of growth. The size frequency of soft individuals also supports this. Many of the freshly berried individuals are found to have just moulted. Perhaps, they are moulting prior to the extrusion of eggs as observed by Allen (1960) in the case of *Crangon allmani* Kinahan.

TOTAL LENGTH-CARAPACE LENGTH RELATIONSHIP

The total lengths (X) and carapace lengths (Y) of the two sexes were plotted to find out their relationships (Fig. 7). It is found that these body measurements have a straight line relationship.

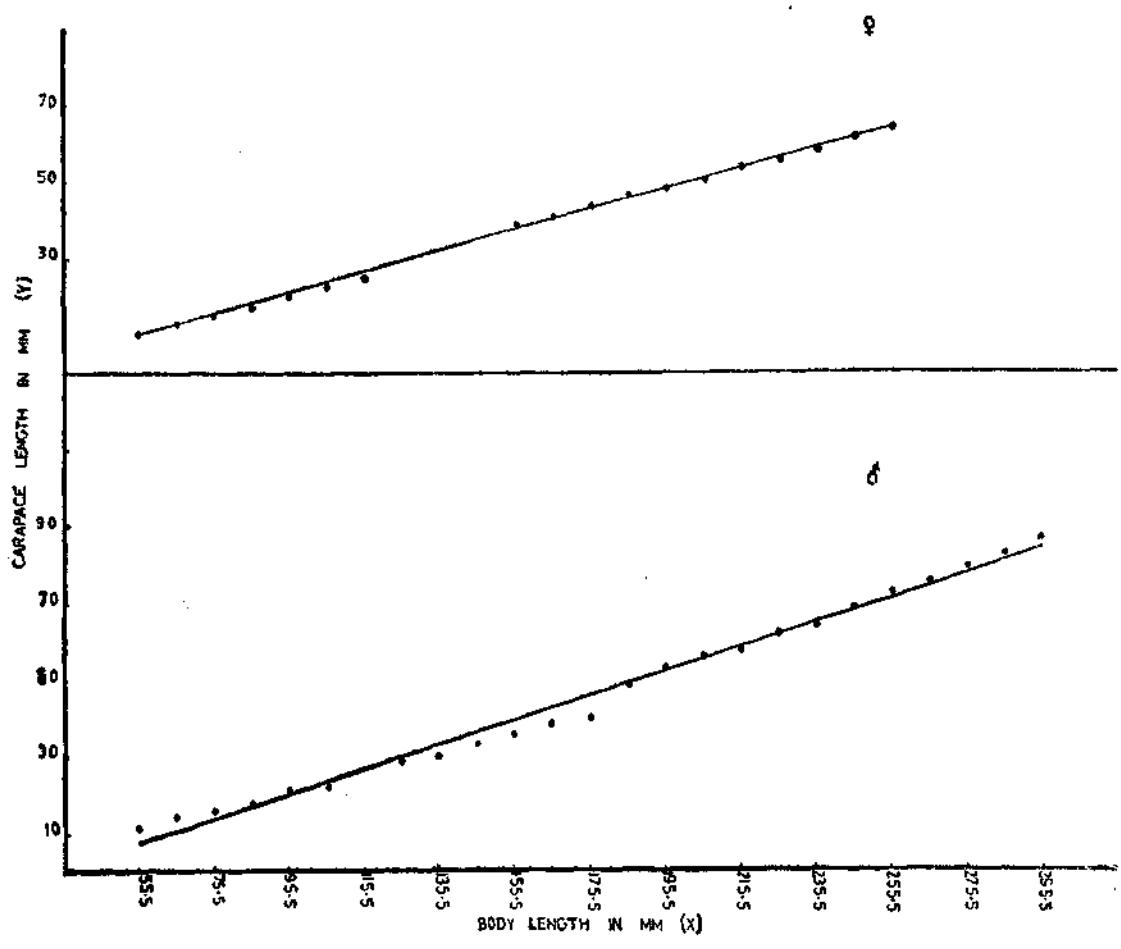

FIG. 7. Body length (X), carapace length (Y) relationship of male and female
——— Calculated line. . . . . Observed values.

The regression lines fitted by the method of least squares are as follows:

$$\left.\begin{aligned} Y &= 0{\cdot}32281\,X - 10{\cdot}81851 \\ X &= 3{\cdot}06401\,Y - 35{\cdot}08947 \end{aligned}\right\} \text{ Males}$$

$$\left.\begin{aligned} Y &= 0{\cdot}27892\,X - 5{\cdot}67957 \\ X &= 3{\cdot}58076\,Y - 20{\cdot}53643 \end{aligned}\right\} \text{ Females}$$

The coefficients of correlation "r" between the two lengths were found to be 0·99483 and 0·99983 for males and females respectively indicating the high relationship between the two quantities.

Discussion

The observations recorded indicate the probability of this species having a rather long breeding period extending over 6 months from July to December. The peak of the breeding activity is observed in October–November. Berried specimens are caught from Ramankari and Pulikizh during these months. All of them had orange-coloured eggs and it seems that they all come down to the brackish-water areas by the time the eggs turn grey and hatch out. Towards the end of the season even very small females are found to be berried. After spawning once at the peak of the breeding period for earlier those that are left uncaught are likely to remain in the backwaters and spawn again. There are indications of this in a second peak of availability of berried specimens in November in certain years. Fresh recruitments of juveniles arriving at the upper reaches even up to February–March also seem to support this view. Moreover spent and berried specimens are found to have well-developed ovaries even in November. Ling and Merican (*op. cit.*) suggest the possibility of two or more spawnings in the same season.

Juveniles and large males seem to be quite at home at the river mouths adjacent to the backwater even when the salinity is nearly 18‰ indicating that increased salinity alone is not the inducing factor for them to move up the river. Probably temperature may be an important factor influencing their movements. Mary John (*op. cit.*) has observed that the optimum temperature for its normal activity is from 29° to 34° C. When summer heat increases they are perhaps going up the rivers and remaining in deeper basins of the river systems. At these places the bottom is slushy with plenty of organic detritus which is their favourite food. When it rains occasionally during the dry months large numbers of them come down to the backwater regions. These up and down migrations of the species could be studied with more accuracy only by conducting mark recovery experiments.

The species is a fast growing one, females attaining 180–200 mm. in one year. In the case of males the modal size at 141–160 mm. when the fishery starts in March at Ramankari moves to 161–180 mm. by May after which the growth appears to be faster. From June to October the males grow about 80 mm., an average of 20 mm. per month. But during the off-season at the river centres the growth is comparatively slow and a few males which probably remain upstream during the early monsoon months come down only in September–October. They are stunted in their growth because of their longer sojourn at the upper river centres. These and a few of the others before reaching 270 mm. (modal group at the end of the season) return to the rivers by November and come down along with the next year's brood. They show modes at 230 mm. in May, 250 mm. in June and 270 mm. in July at Ramankari. Thus a good number of males are surviving for a second year, whereas in the case of females such a second year group is missing. Early in the season at all centres and towards the end of the season at the upper centres males are more in the catches. In the total fishery also the males are in a majority as could be expected from the presence of one and two-year old specimens among them. As mentioned in a previous section a part of the variations in sex ratio would seem to be related to these movements.

M. rosenbergii is a comparatively slow-moving species. Since it is being subjected to fishing at different stages of its life there is a likelihood of the stock becoming depleted at some time or other. Mary John (*op. cit.*) has pointed out this possibility and emphasised the need for the protection of the breeders. Though such an alarming tendency is not observed at present as shown by the catch per unit of effort data, it is quite essential to keep a close watch on the fishery in the years to come. A self-imposed closed season during October—November 1963 by the freezing industry is a welcome trial the results of which could be assessed in later years only.

It is feared that destruction of fry by small meshed nets like *peru vala* and *koru vala* in the upper reaches of the rivers during the summer months might adversely affect the prawn stocks at least in the long run. Gunter (1956) has stressed the need for protecting nursery areas.

It is also reported that while using copper sulphate for catching the riverine fishes by poisoning in the upper reaches of the rivers, good numbers of small prawns are also seen dying. A number of them might also be the juveniles of *M. rosenbergii*. Hence a closed season tried along with some measures for protecting the nursery areas during summer months may bring about the desired effect on the fishery.

Being a fast-growing species *M. rosenbergii* is an ideal prawn for culture. Naidu (1939) in a report on a survey of the fisheries of Bengal has stressed the importance of the freshwater lobster (*Palaemon*) and suggested that artificial hatcheries of the species may be of great value in augmenting the fisheries. Mary John (*op. cit.*) has suggested the establishment of hatcheries or sanctuaries for protecting berried females and young ones for conserving and developing the fisheries. Ling's studies in Malaya are aimed at making rearing of the species a profitable proposition. Further detailed studies would be necessary before undertaking culture of these prawns on a commercial basis.

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BIOLOGY AND FISHERY OF THE BALTIC SHRIMP (*LEANDER ADSPERSUS* VAR. *FABRICII*) ON THE COAST OF THE GERMAN DEMOCRATIC REPUBLIC

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ABSTRACT

The Baltic shrimp *Leander adspersus* var. *fabricii* lives along the total coast of the German Democratic Republic, but it is only in the Wismar Bay abundant enough to pay a little special fishery on it. Only in the months May–August considerable amounts are found in the shallow shore waters, when—during the ripening of the eggs and after the deposition of them—the females seek there for nutritious places. The shrimps are caught nearly exclusively with "Krabbenkorbe" fykes with a leader of network. Newly the leader is substituted by a chain of electric lamps. The annual catch averages 4–5 metric tons. It fluctuates considerably due to environment, short time of spawning, low rate of reproduction and short duration of life. The catches are sold exclusively fresh and cannot satisfy even the local demand.

BIOLOGY

THE Baltic shrimp (*Leander adspersus* var. *fabricii*), wrongly called "Krabbe" (crab), is found along the whole coast of the German Democratic Republic. It is most numerous and economically most important in Wismar Bay, a fertile area with very little influx of freshwater; towards the east it becomes more and more rare. Their stock is everywhere mixed with small numbers of the Common shrimp (*Crangon crangon*).

In the warmer season it appears in the shallower shore waters, where it can be caught. By day the shrimps keep hidden, mostly in dense stocks of sea-weed or algae or rather buried in the soft sea-bottom (sand), by night they swim about. In the colder season they seem to stay at greater depth and greater distance from the shore, but attempts to demonstrate that were not successful. It is possible that they are distributed loosely over large areas and so do not figure in the catches.

The migration to shallow shore water in summer is certainly for propagation. It is true that the females are impregnated before they migrate to these areas, probably in greater depth, but then they go into the more fertile shallow shore waters where they let the eggs ripen. The eggs seem again to be deposited in deeper water, probably in dense stocks of sea-weed, where the larvae can protect themselves from many predators or noxious environmental influences. After spawning the females return to the shallow water, where they again feed themselves into condition. The majority of males stay in deep water, after having impregnated the females. Only a few males follow the females into shallow water.

According to P. F. Meyer (1937) the spawning period of *Leander adspersus* var. *fabricii* in the German Democratic Republic lasts about 3½ months (from the middle of May to the end of August). Only during this time are larvae to be found there. The number of eggs produced in one spawning period depends on the size of the females (*see* Table). About 7% of all mature females, mostly the bigger, *i.e.*, the older ones, spawn twice a year.

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TABLE

The number of eggs in Leander adspersus *var.* fabricii *related to the size of females*
(after P. F. Meyer, 1937)

Size of females in cm.	Average number of eggs
4	1,000
5	1,300
6	1,800

IMPORTANCE FOR FISHERY

The catching of Baltic shrimps is a special fishery in the German Democratic Republic, practised only where the stock is abundant enough to make the yield rewarding. At present this is the case only in Wismar Bay, in the western part of the G.D.R. coast. This catch is utilised only for food of man. Of course shrimps are also caught on the whole G.D.R. coast when needed as bait for the long-lining of eel (*Anguilla anguilla*) and cod (*Gadus morhua callarias*), but this catch is not of great importance. The catch of undersized shrimps for fodder, as it is practised in the German Federal Republic along the coast of the North Sea, is not carried out in the German Democratic Republic. The Baltic shrimp has considerable importance as natural food for many useful species of fish, particularly for cod (*see* Fig. 1).

Only female shrimps are caught for food during their stay in the shallow shore water. The males are considerably smaller and stay mostly in deeper water. They remain mostly out of the scope of the fishing gear and—if coming into it—are not caught, because they pass easily through the meshes.

THE CUSTOMARY CATCH

The usual gear for catching shrimps for food is the "Krabbenkorb"; driftnets or drift seines ("Treibzeese") are less frequent. If shrimps are to be caught as bait, push nets and shore seines are used.

The "Krabbenkorb" (*see* Fig. 2) is a fyke net with rings, total length about 5 m. It has two funnels, two wings 2 m. long and a leading net reaching upon the dry shore. The entrance ring is flat at the bottom and 1 m. broad, it is 1·5 to 1·6 m. high. The leading net and the entrance ring should rise 20 cm. above the surface so that the shrimps cannot escape over it. The leading net reaches far into the vestibule and leads the shrimps into the first funnel.

All network is of cotton. The mesh-sizes are the following: in the leading net 10–12 mm., in the vestibule 10 mm., and in the pocket 8 mm. The width of the wooden rings decreases from 1·6 m. in diameter at the mouth to 0·6 m. near the pocket.

Since the Baltic shrimps swim about only in the night, the fyke nets are to be set in the evening and hauled in before daybreak. At dawn the shrimps would discover the openings in the funnels and escape.

The small mesh-sizes require repeated cleaning of the network; especially jellyfish (*Aurelia aurita*) frequent the area during the season and fill up the narrow meshes. The current of the

water is stopped and the net is set in vibration. This drives the shrimps away. Therefore the fisherman has to clean the fyke net several times during the night, if jellyfish are numerous, every other hour or even more often. For the same reason the fyke nets must not remain in the water by day when no shrimps are caught, but they must be hauled in every morning and set every evening. That makes this fishery—even with small catches—a heavy labour. In spite of the good prices paid for Baltic shrimps, this kind of fishery is not popular with the fisherman. As soon as another branch of fishery (gill-netting and long-lining for example) promises similar gains, shrimp fishing is often given up.

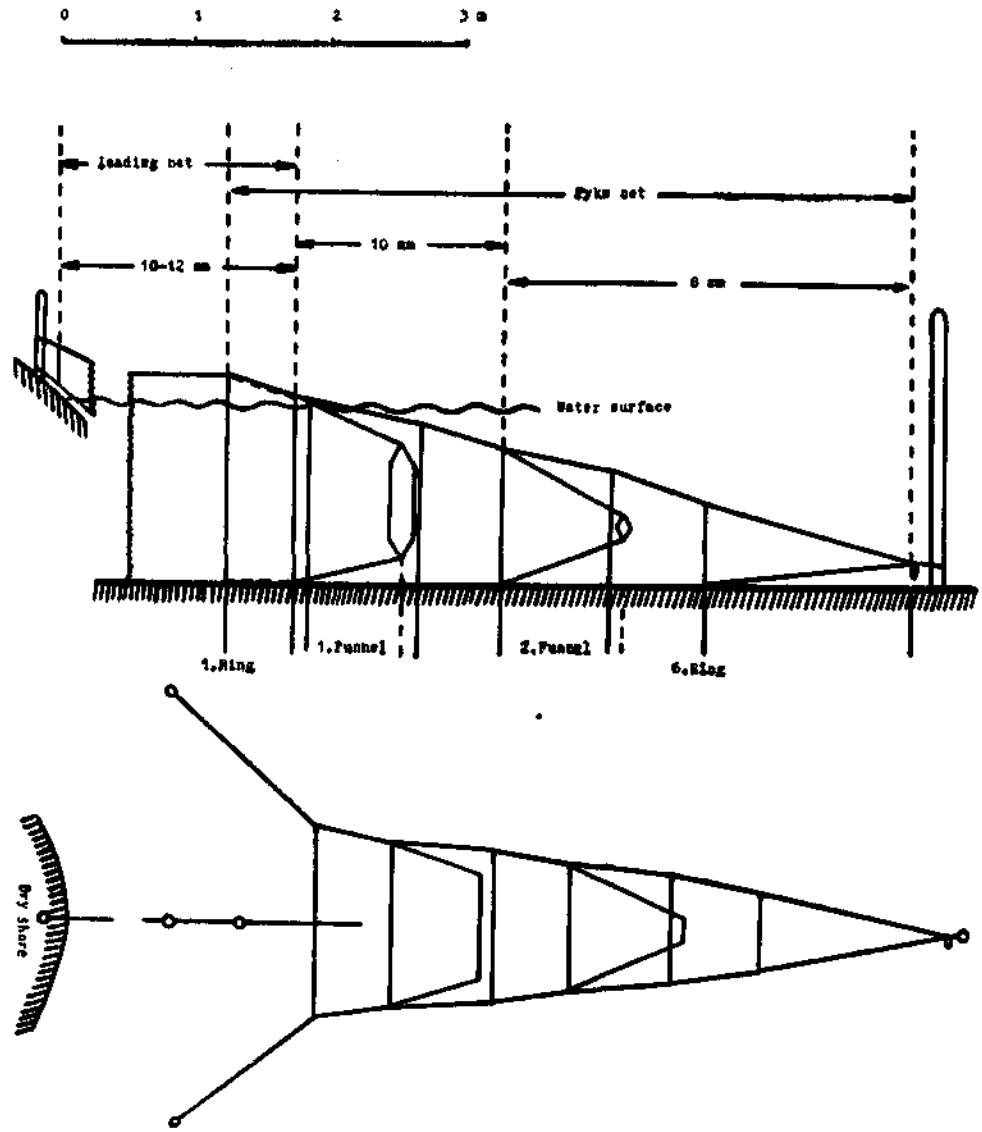

FIG. 2. Shrimp fyke ("Krabbenkorb") from Wismar. Top: Lateral view. Bottom: View from above (after Bobzin)

Therefore it is no wonder that by no means all of the fyke places in Wismar Bay totalling 40 are fished regularly during the season. The places where such a fishery is possible have been

established since decades (*see* Fig. 3). Because they naturally are not all equally favourable for the catch, they are every year again divided by lot among the fishermen, who all belong to the same co-operative.

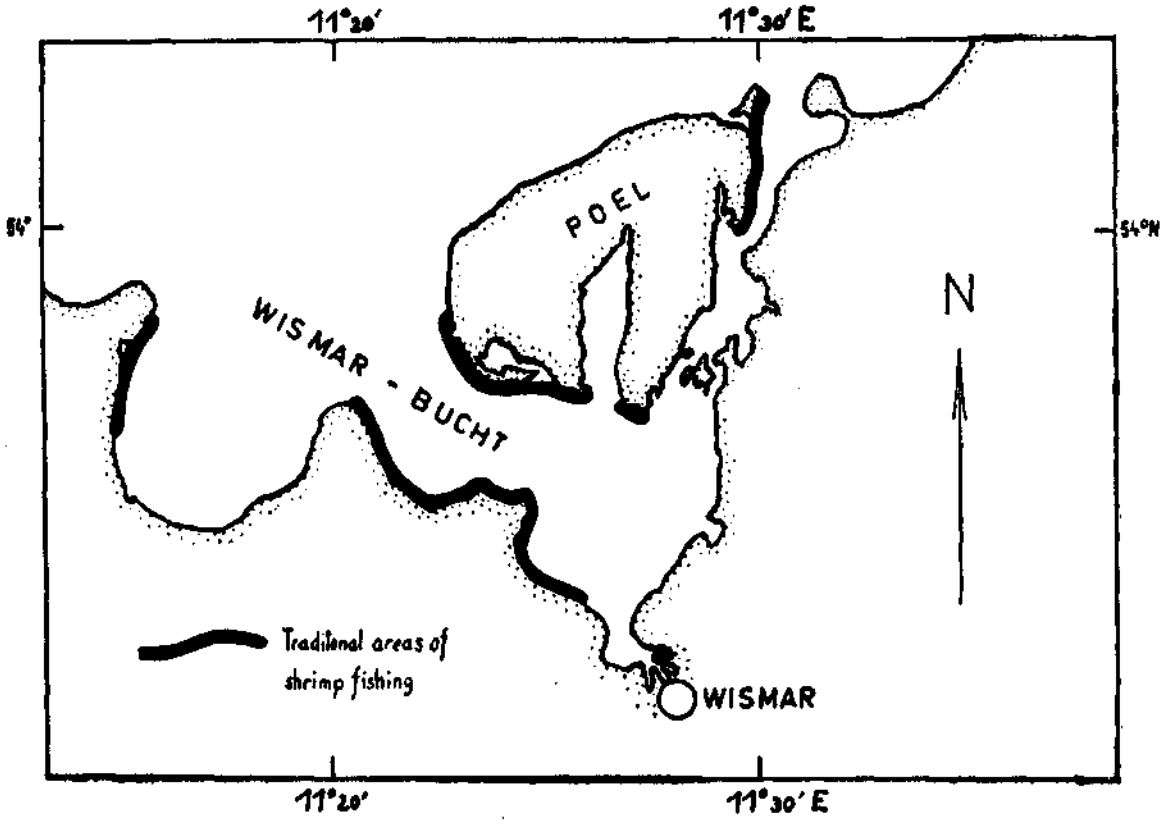

FIG. 3. The areas of the shrimp fishery in Wismar Bay

CATCH WITH ELECTRIC LIGHT

Recently Bräutigam (1958) has endeavoured to increase the catch rate of the fyke nets by using electric light. Having found that Baltic shrimps show a positive phototactic reaction, he replaced the leading net of the normal fykes by a chain of electric underwater lamps, setting the last lamp before the entrance of the fyke. The lamps and the leading-in cable hang on floats closely below the surface. The chain is anchored to the first lamp. The space between them is fixed according to the turbidity of water and the intensity of the light. An automatic switch-gear switches off the lamps in a certain chronological order. The first lamp is switched off first, some time later the second, then the third, and finally the fourth. When the fourth lamp is switched off, the first is lighted again, with the switching off the fifth, the second, and so on. Along the, at first lighted, chain of lamps a dark interval 3 lamps wide goes to the fyke. At the end of the fyke, opposite the lamp chain, a slightly brighter lamp shines all the time.

At the beginning of the catch, after nightfall, all the lamps are switched on. Due to the positive phototaxis the prowling shrimps coming into the range of a lamp remain in the scope of the chain. When the first lamp goes out some time later, the animals gathered here are allured

by the next and so on, until they arrive at the entrance of the fyke. When the last lamp of the chain is switched off, the shrimps make their way to the continuous lamp behind the fyke and fall into the gear.

The interval between the switching off of one lamp and the next must be long enough for the shrimps to locate the next lamp and swim to it. With a distance from lamp to lamp of 3–5 m. they need about 1–2 minutes. Most favourable was the use of 40-watt bulbs. The lamp chain should not exceed 50 m., because otherwise the shrimps would scatter easily.

The substitution of the leading net by a lamp chain has the following advantages:

1. Jellyfish pass the lamp chain without disturbing the catch.
2. The lamp chain need not reach up to the dry shore.
3. Lamp chains can be set in only 25% of the time needed for setting the leading net.
4. The labour needed for setting the gear is considerably reduced.
5. The catches increase.

Quantities of Catch

The annual catch of food shrimps in the German Democratic Republic amounts to about 4–5 (metric) tons. This quantity varies considerably according to hydrological and meteorological factors. There were not only years in which about three times as much was caught in the area (1934–36), but also periods when the shrimps had practically vanished at the beginning of the century. That is obviously due to the relatively low fertility and the short spawning period. Development and growth of the tender shrimp larvae are highly affected by environment factors. In the area the currents, temperatures, and salinity vary greatly. Each of these factors—and especially several together—may decimate the shrimp fry heavily. On the contrary, when during the spawning period favourable conditions prevail, an immense number of shrimps grow up. As Baltic shrimps probably live no longer than 4 years, the total stock varies. If these conditions prevail for several successive years, the stock either diminishes so that this fishery stops, or it increases so much that record catches are landed.

Utilization of Catch

In spite of relatively high prices there is at present much more demand for Baltic shrimps than the catches supply. They are marketed almost only at Wismar. Because like all crustaceans they decay faster than fish, they are landed immediately after the catch in the early morning coolness, instantly cooked, and put up for sale fresh on the same morning. They are not canned at all.

Prospects

The new gears developed by Bräutigam make it possible to fish more intensely by using more fykes, for light fykes can be set above greater depths and in shallow water without reaching up to the dry shore. However, the fishermen hesitate to fish more intensely, because they are troubled about the stock they need for bait too. This worry is no doubt exaggerated. But as the stock is very variable for many reasons—natural ones and not to be influenced by man—, one must warn against greater investments, because a normal amortisation is not certain. Provided that the stock increases noticeably which would be shown by a continuous increase of the catches per fyke over several years, the fishery could be intensified, *i.e.*, the number of fykes could be cautiously augmented. But there is no indication of an essentially greater importance of the shrimp fishery in the future.

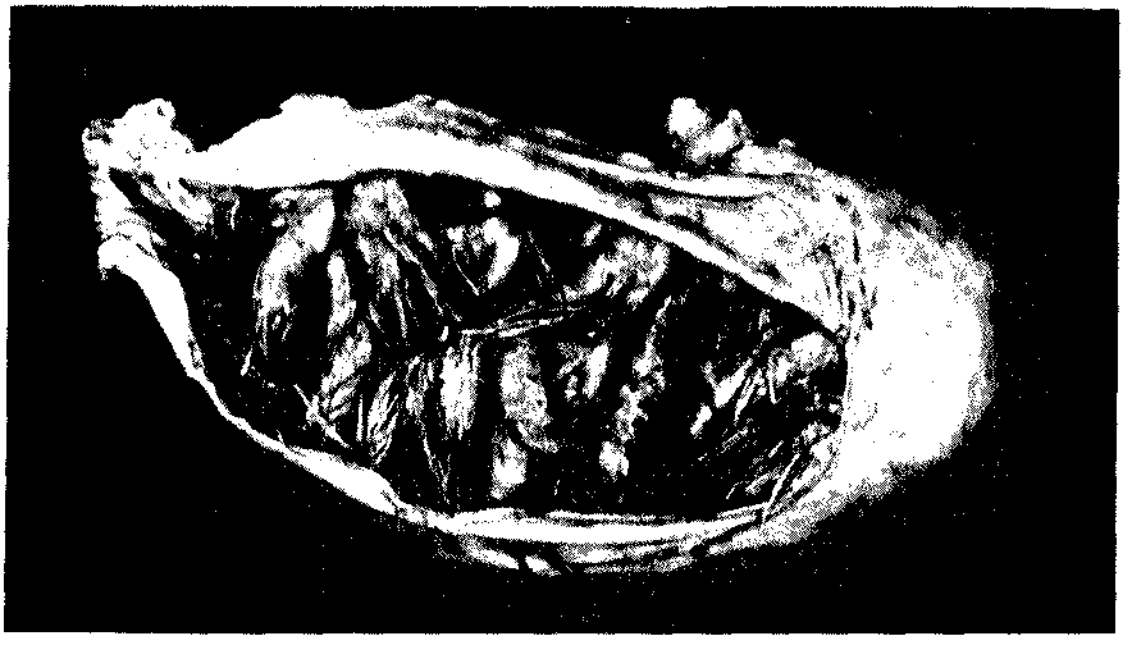

FIG. 1. Opened stomach of a cod (*Gadus morhua callarias*) caught in Wismar Bay, filled with swallowed shrimps (mostly Baltic shrimp, *Leander adspersus* var. *fabricii*) sporadic common shrimp, *Crangon crangon* (Jähnichen phot.)

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CONTRIBUCION AL CONOCIMIENTO DEL CAMARON DE RIO *CRYPHIOPS CAEMENTARIUS* (MOLINA), DECAPODA PALEOMONIDAE

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ABSTRACT

"Trabajo en el que se detalla el resultado de las siguientes investigaciones".

1. REPRODUCCION DEL CAMARON (*Cryphiops caementarius*) EN LA VIDA LIBRE

Periodo de reproducciôn.—Se dá a conocer el resultado de las investigaciones, sobra la presencia de hembras ovígeras a lo largo del río; con la finalidad de determinar los meses de mayor y menor reproducción, durante el año. Dato importante que nos ha permitido prohibir la pesca del Crustáceo por algunos meses, con la finalidad de cuidar la exterminación de la especie.

Número-de huevos.—Empleando métodos volumétricos y por cuenta directa, se ha podido determinar el número de huevos de cada hembra en relación directa con su longitud.

Areas de desove y crianza.—Observaciones que nos han confirmado que el desove se opera totalmente en el estuario de los ríos y la crianza tiene lugar en plena agua dulce de los mismos.

Edad de la primera maduración sexual.—Determinada a base de la captura de pequeños ejemplares hembras cargadas de huevos.

2. MIGRACION DEL CAMARON (*Cryphiops caementarius*)

Periodos sucesivos de los movimientos migratorios.—Con los caracteres de la migración anual, en la sentido mar río por los camarones juveniles; que por primera vez en su ciclo vital alcanzan el agua dulce de los ríos y las migraciones estacionales del camaron adulto en relación con la maduracion de sus órganos genitales y adquisición de su alimento.

Motivo de los movimientos migratorios.—Migracion instintiva y las caracteristicas de la migración mécanica ocasionada por el aumento del caudal de agua, habida en los ríos de la localidad en época de verano, como consecuencia de las lluvias del verano.

3. PESCA

Mètodos de pesca usados durante el año.

Peso de la cosecha por unidad de esfuerzo en las diferentes estaciones del año a lo largo del rìo.

Total de pesca habida anualmenta.

4. ALGUNOS ASPECTOS SOBRE LA CRIANZA DEL CAMARON EN CAUTIVIDAD

Adaptación del camarón a cautividad.—En lo que se demusetra que siendo el camarón de río (*Cryphiops caementarius*) una especie por excelencia migratoria, vive satisfactoriamente en cautividad.

Reproduccion en cautividad.—Con el conocimiento sobre la cantidad de huevos contenidas en las hembras de crianza y su comparación con las de la vida libre, número de veces que cada hembra deseva en cautividad, durante el ano en relacion con la temperatura ambiente y de los estanques, datos sobre edad de la madurez sexual en cautividad.

Desove y ecloción de los huevos en cautividad.—Dandole mayor importancia a la obtencion del estudo larval y a los trabajos experimentales que se vienen realizando con éstas.

Reproduccion De La Especie

1. *Condiciones generales*

(*a*) *Dimorfismo sexual*

Considerando de especial importancia el conocimiento de los hábitos reproductivos del camarón de río (*Cryphiops caementarius*) el autor ha efectuado muchas observaciones al respecto durante un período de tres años (1961, 1962 *y* 1963) en los ríos Majes-Camaná, Ocoña, Quilca y Tambo, del Departamento de Arequipa.

Conocido es el dimorfismo sexual existente en la especie, encontrándose los sexos separados, el poro genital en las hembras se abre en la cara interna del artejo basal del tercer par de patas i en el macho en el quinto. Los machos alcanzan mayor talla que las hembras, teniendo los primeros el segundo par de patas más desarrollados.

(*b*) *Caracteristicas de los huevos*

Las hembras maduras poseen huevos que cubren casi totalmente el abdomen. Los huevos recientes son de color rojo intenso, de forma esferica y de aproximadamente un milimetro de diámetro. Se encuentran adheridos entre si por una sustancia mucilaginosa, momento que es algo dificil separarlos del cuerpo del animal ó aislarlos uno del otoro ya que al desprenderse lo hacen formando racimos de más de 4 huevos. En un estadío más avanzado de maduración la coloración pasa del rojo intenso al rojo claro con lo que disminuye la cantidad de mucilago. Finalmente los huevos se tornan blanquecinos, distinguiéndose un punto oscuro casi en el centro, que corresponde a los ojos del embrión; es en este éstado de madurez que la sustanica mucilaginosa desaparece, desgranandose los huevos del abdomen de la hembra al menor movimiento que se le somete con tal fin.

La maduración de los huevos es simultanea y el desove total, operandose consiguientemente la eclosión de los huevos correspondiente a la hembra dentro de un corto tiempo, dando como resultado una larva del estadio Mysis (Observaciones originales del autor en laboratorio).

(*c*) *Numero de huevos*

Se ha efectuado recuento de huevos por el método volumétrico y, excepcionalmente, por cuenta directa. Los resultados indican que el número de huevos está en relación directa con el tamaño del animal. Así en un ejemplar de 12 cm. de longitud total y con 25 gramos de peso se encontró 61,500 huevos y en hembras de 3·8 cm. se hallarón 500 huevos.

Tabla I

Relación entre la longitud de las hembras y el numero de huevos

	cm.		huevos	
En ejemplares de	11 a	11·5	55,000 a	60,000
„ „	10	10·8	44,000	49,000
„ „	9	9·9	33,000	44,000
„ „	8	8·5	22,000	30,000
„ „	7	7·9	16,000	22,000
„ „	6	6·7	11,000	16,000
„ „	5	5·7	3,000	5,500
„ „	4	4·8	1,000	2,000

La especie alcanza madurez sexual, dentro del primer año de vida, ya que se encuentran hembras ovígeras desde una longitud de 3·5 cm. lo que demuestra que las hembras nacidas y que salen del estuario del río regresan ovígeras antes del primer año para dar lugar a nuevas generaciones.

(*d*) *Zona de desove*

Es indiscutible que la zona de desove corresponde al estuario del río, pero cuando las hembras no llegan a él por que algun ostaculo se lo impide ó por que los huevos han llegado a su completa madurez, desova en plena agua dulce; en donde la larva estadio Mysis, procedentes de la eclosión de los huevos no progresa, muriendo poco tiempo déspues, antes de pasar a camarón juvenil, tales experiencieas han sido confirmadas en los trabajos experimentales que sobre reproducción del camarón se vienen realizando en cautividad, por intermedio del Servicio de Pesquería del Ministerio de Agricultura y a cargo del autor.

Que la zona de desove corresponde al estuario del río, queda confirmada con la salida del camarón juvenil, de 15 mm. de longitud promedio, en el sentido mar—río durante todo el año. Esta migración presente en la desembocadura de los ríos y parte más baja de los mismos, hizo pensar desde un comienzo que el camaron es una especie que se reproduce durante todo el año, para su confirmación hubo que realizar observaciones sobre la presencia de hembras ovígeras a lo largo de los ríos y muy especialmente en el sistema río Majes-Camaná; el que fué dividido en 6 estaciones, en donde se llevarón adelante las observaciones a través de los años 61–63, caracterizandose cada una de ellas por ser lugares de fácil reconocimiento y acceso a ellas mediante diferentes vías de comunicación. Las caracteristicas de las mismas se dan a conocer a continuación:

Estacion N° 1, "*Chiflon*": Desembocadura del río y 1 kilometro de distancia en el sentido aguas arriba y de O. a 15 m. de altitud.

Estacion N° 2 "*Characta*": Terrenos de cultivo que forman la hacienda "Characta," a 120 m. de altitud y a 15 kilometros desde la desembocadura.

Estaction N° 3 "*Palo parado*": Correspondiente a la linea divisoria del río Majes (Provincia de Castilla) y el rio Camana (Provincia de Camana), a 250 m. de altitud y 30 kilometros desde la desembocadura.

Estacion N° 4 "*Punta Colorada*": Puente de fierro sobre el rio Majes, a 500 m. de altitud y 55 kilometros desde la desembocadura del río.

Estacion N° 5, "*Aplao*": Capital de la Provincia de Castilla, a 650 m. de altitud y a 80 kilometros desde la desembocadura del río.

Estacion N° 6, "*Andamayo*": Lugar de nacimiento del río Majes—Camaná, por la confluencia de los ríos Andamayo y Colca, a 1,100 m. de altitud y 130 kilometros desde la desembocadura del rio.

2. *Resultados obtenidos en las estaciones*

Del análisis de los resultados de las estaciones se desprende lo siguiente:

(*a*) Durante los meses de Diciembre, Enero y Febrero, existen hembras ovígeras a lo largo de todo el rio. Correspondiendo el menor porcentaje al mes de Diciembre.

(*b*) Que de Marzo a Junio el porcentaje de embras ovigeras decrece.

(*c*) De Julio a Diciembre el número de hembras ovígeras aumenta progresivamente, hasta cubrir todo el area de su distribución en el río.

(*d*) Que solamente es posible hallar hembras ovígeras durante el año, en las partes más bajas del río muy cerca a su desembocadura.

TABLA II

Porcentaje de hembras ovígeras durante el año (Promedio de los años 1961-63)

Meses	Estaciones					
	I	II	III	IV	V	VI
	%	%	%	%	%	%
Enero	95	95	100	100	100	100
Febrero	95	95	100	100	100	100
Marzo	80	20	0	0	0	0
Abril	15	0	0	0	0	0
Mayo	2	0	0	0	0	0
Junio	2	0	0	0	0	0
Julio	4	0	0	0	0	0
Agosto	10	2	0	0	0	0
Setiembre	20	3	0	0	0	0
Octubre	50	10	5	0	0	0
Noviembre	70	40	18	12	5	0
Diciembre	90	50	30	20	15	10

3. *Migración del camarón juvenil*

Anualmente los camarones hembras desovan en el estuario del río, correspondiendo su mayor porcentaje a la época del verano. Como consecuencia del desove, que es total y se efectua en corto tiempo (Experiencias realizadas en cautividad), aparece una larva del estadio Mysis la que pasa a camarón juvenil; el mismo que migra instintivamente durante el año en el sentido mar-río, preponderantemente ésta migración alcanza sus puntos más altos durante los meses de Abril a Julio, caracterizándose por tener el aspecto masivo en los primeros tramos del río, más ó menos 2 kilometros desde la desembocadura, lugar donde puede verse migrar contra la corriente filas interminables de pequeños camaroncitos; pero más alla de los 15 kilometros no es possible la constatación de éste hecho, pero sin embargo la migración continua por entre las piedras, plantas acuáticas ó raíces de los arbóles que crecen en ambas orillas del río. Este hecho está directamente relacionado con el tamño del animal, en los primeros tramos del río en donde llega alcanzar 16*a* 18 mm. de longitud no le permite entrar a las partes mas profundas, haciendo su migración muy por la orilla, sin embargo cuando logran alcanzar mayor tamaño toman mayor profundidad y la migración a simple vista parece detenerse, tal hecho ha sido confirmado a base de muestreos realizados con tal finalidad a diferente alturas del río.

La tabla dá el crecimiento del camarón conforme asciende el río que ha sido dividido en 6 estaciones y en cada una de ellas se han realizado muestreos consecutivos durante los años 1961, 1962 *y* 1963.

Anualmente nuevas generaciones de camaron juvenil salen del mar al río, sosteniendo asi constante la pesca comercial habida durante el año. Pero en los meses de Enero a Marzo, la migración río arriba de éstos ejemplares no es manifiesta debido al considerable aumento de agua, que impide en todo momento la migración directa de éstos pequeños ejemplares denominados camarón juvenil. Sin embargo y debido a la reotaxía intensa que le caracteriza a éstos crustáceos

hace que muchos individuos logren vencer las corrientes de agua llegando hasta muy cerca del limite de migración con una longitud de 30 mm. durante los primeros días del mes de Abril.

TABLA III

Variaciòn del tamaño-durante el movimiento migratorio del camaròn juvenil

Estacion	Lugar	Distancia desde el mar	Altitud	Longitud promedio
		km.	M.	mm.
I	Bocana	0 a 1	0 a 15	15
II	Characta	15	120	19
III	Palo parado	30	250	23
IV	Punta colorada	55	500	29
V	Aplao	80	620	31
VI	Andamayo	130	1,100	35

Cuando las aguas del rio han bajado, corrientemente ésto sucede al finalizar el mes de Marzo ó primeros dias del mes de Abril, empieza la migración de nuevas generaciones en el sentido mar río, dicha migración se continua hasta el mes de Diciembre, en forma periódica, pero la cantidad de camarón que sale mensualmente no es constante en el año, teniendo sus puntos más altos desde. Abril a Agosto, decrecinedo de Setiembre a Noviembre y notándose un lijero aumento durante el mes de Diciembre.

Estos datos han sido determinados a base de observaciones en el medio natural y más tarde para llegar a conclusiones concretas, se de terminó un lugar conocido muy junto a la desembocadura del río Majes-Camaná, lugar donde se hizo captura del camarón juvenil durante 12 meses usando el mismo método de captura y empleandose el mismo tiempo de trabajo (15 minutos)

La longitud promedio de los ejemplares capturados es de 15 mm. y de un peso de 0·1 gramo, determinado por el promedio de 100 ejemplares que dan siempre 10 gramos de peso, lo mismo que la longitud es determinada por la medición de 100 ejemplares.

No toda la población anual que sale por primera vez del mar al río llega en el mismo año hasta la parte final de migración, correspondiente a la localidad de Andamayo, a 1,100 metro de altitud y a 130 kilomteros desde la desembocadura del río. Sometido a una minuciosa observación el ciclo anual de migración, se encuentra que las nuevas migraciones que salen del mar al río durante los meses de Enero a Agosto, llegan hasta el limite final de migracion.

Las generaciones salidas de Setiembre a Diciembre no logran éste límite, debido al aumento de agua en el río en la época del verano. Por lo tanto existe en el río en un ciclo anual de migración del camarón juvenil, dos grupos y ellos son:

(1) Grupo migrante que llega en el mismo año de salida del mar hasta el límite final de migración y

(2) Grupo migrante que no logra llegar a la meta final de migración, en el mismo año de salida del mar al río.

El primer grupo.—Se caracteriza por que existe en él individuos que llegan al limite final de migración, quedandose en las partes altas del río approximadamente cuatro meses e individuos

TABLA IV

Cantidad de camaròn-juvenil capturado, en la parte baja del rìo Majes Ca-manâ en el año 1961

Meses	Cantidad de ejemplares capturados	Peso en gramos	Tiempo de trabajo
			minutos
Enero	3,00	300	15
Febrero	3,00	300	15
Marzo	3,00	300	15
Abril	40,000	4,000	15
Mayo	30,000	3,000	15
Junio	15,000	1,500	15
Julio	10,000	1,000	15
Agosto	5,000	500	15
Setiembre	3,000	300	15
Octubre	3,000	300	15
Noviembre	4,000	400	15
Diciembre	10,000	1,000	15

que solamente llegan a la meta final de migración para luego regresar de inmediato al mar durante el verano, por acciòn de las crecidas de agua habidas en el río, como consecuencia de las lluvias veraniegas.

Cuando los individuous del primer grupo que llegan a la meta final de migración y se quedan durante cuatro meses en las partes altas del río, les toca hacer su regreso río abajo lo hacen con una longitud de 7 a 8 cm. caracterizandose las hembras por ser totalmente ovígeras, el tamaño alcanzado está de acuerdo a los cuatro meses que han permanecido en el río. La pesca habida anualmente tiene influencia sobre los individuos de éste primer grupo, que son interceptados en su camino hacia el mar por las trampas fijas denominadas "izangas" y de regreso del mar al río por los "chaueos", solo unon pocos ejemplares que logran salvarse de ésta doble pesca habida durante el verano, logran llegar por segunda vez a la meta final de migración.

Los individuos que llegan a la meta final de migración y no se quedan en el río, sufren menos los efectos de ésta doble pesca habida anualmente en el verano; por que su tamaño alcanza solamente los 4 cm. lo que no permite ser camarón comerciable, pues nuestra reglementación en bien de la conservación de la especie, decreta que el tamaño comercial debe ser desde los 7 cm. de longitud total, como tal la totalidad de ellos llegan por segunda vez a la meta final de migración aproximadamente en el mes de Junio, con una longitud de 8 cm. Este hecho está corroborado con la presencia de los pescadores en las partes más altas del río, solamente a partir del mes de Julio.

El segundo grupo: Del que ya hemos hablado y que no logra llegar hasta la meta final de migración en el mismo año de salida del mar al río, regresa al mar con una longitud de 20 a 30 mm. quedandose en él hasta el término de las avenidas, al final de las cuales migra nuevamente al río, legando por primera vez a la meta final de migración aproximadamente en el mes de Agosto, con una longitud de 5 cm. conjuntamente con las nuevas generaciones que salen por primera vez de mar al río; cerrándose asi la cadena constante del ciclo migratorio del camerón juvenil que sale por primera vez del mar al río y regresa nuevamente a éste.

4. *Distribución y migración del camarón adulto*

El camarón es un animal migratorio, auque está presente durante todo el año a lo largo del río, su disponibilidad para la pesca fluctúa, siendo mucho mayor en primavera y verano que en el resto del año, especialmente en los meses de Abril, Mayo, Junio y Julio en que la pesca es baja a lo largo de los ríos.

Al estudiar inicialmente la migración del camarón el sistema río Andamayo—Colca—Majes —Camaná, fué examinado hasta una altura de 3,600 metros, determinándose que la distribución de este crustaceo es do 0. a 1,100 metros de altitud. Segun referencieas, excepcionalmente se encuentran especímenes hasta los 2,000 metros, pero en general debe tomarse la zona de Andamayo (1,100 metros de altitud) como el límite superior de distribución normal para el camarón en el río Majes—Camaná; debiendo existir alli una barrera ecológica asociada a la altura que determina dicho límite. Esta observación es confirmada con la distribución de los pescadores en el río.

Auque el camarón existe durante todo el año a lo large de toda el área de distribución, a mi jiuicio realiza dos clases de migraciones:

(*a*) Migraciones diurnas en sentido vertical hacia la orilla del río para la obtención de su alimento.

(*b*) Migraciones estacionales (río–Mar) en relaciön con el desarrollo de sus órganos genitales.

Las migraciones diarias están sincronizadas con los hábitos nocturnos de la especie, que sube a la superficie durante la noche en busqueda de alimento, hecho que es aprovechado para la pesca con candil ó luz.

Las migraciones estacionales se caracterizan por presentarse cada ano en época de verano; es el período en que la población adulta arrastrada por las fuertes corrientes de agua baja hacia el mar, donde las hembras ovígeras realizan el desove, después de lo cual surcan nuevamente el río.

La migraciön mécanica del río al mar empieza desde el momento en que el río aumenta su volumen de agua, como consecuencia directa de las fuertes lluvias del interior. Las fuertes decargas de agua habidas arrastran todo el camarôn al mar; período migratorio que suele durar todo el tiempo que el río permanece en pleno aumento. Este tipo de migración forzada la conocen bien los pescadores de la zona haciendo uso de las izangas (trampas fijas) para la captura de los camarones que son llevados hacia el mar. Poco tiempo después que las aguas del río empiezan a disminuir, comienza la migración instintiva mar–río, ésta migración consiste en un desplazamiento ascendente, en que las hembras que forman parte se encuentran ya totalmente desovadas; los pescadores aprovechan éste movimiento migratorio para capturar el camarón, usando el chauco (trampa fija). Es ésta migración más notoría en los primeros tramos del río sobre todo muy junto a la desembocadura.

Esta migración suele ser periódica desapareciendo cada vez que el río aumenta de volumen y comienza cuando nuevamente bajan las aguas; es decir que está de acuardo con la fluctuación veraniega del volumen del río.

Explotacion Del Camaron

1. *Condiciones generales*

Como se comprenderá fácilmente después de las discuciones anteriores sobre los desplazamientos migratorios del camarón, la densidad de la pesca fluctua durante el año, siendo ésta mayor en primavera y verano; alcanzando sus puntos más bajos durante el invierno. Pero en general la pesca habida durante el año alcanza los 100,000 kilos de camarones, extraidos de los ríos Ocoña, Majes-Camaná, únicos centros camaroneros de gran explotación en el Perú.

2. *Métodos de pesca*

Los métodos de pesca empleados en la zona para la captura del camarón son los siguientes:

(*a*) *Pesca con luz*

Método usado solamente durante las noches, en la época de estiaje y cuando las aguas son transparentes.

(*b*) *Pesca con cordel*

Consiste en una cuerda que pende de una caña rústica que en su extremo libre lleva ensartadas lombrices de tierra. Cuando el camarón traga la lombriz con parte del cardel, queda atrapado. Un pescador usa de 4 a 6 cañas, las cuales levanta alternativamente para extraer la pesca.

(*c*) *Pesca con atarraya*

La atarraya es usada tanto de día como de noche y en cualquier época del año; se ha demostrado que los lances con ésta red son más fructíferos en las partes más profundas, de allí que los pescadores la prefieran, sobre todo en los remansos del río, donde penetran los pescadores hasta la profundidad de un metro, realizando desde allí sus lances hacia las partes más hondas.

(*d*) *Pesca con isigua ó llica*

Este es un aparejo de pesca que en su parte anterior tiene un semicírculo de madera cuyos extremos están unidos por una gruesa cuerda de jebe, que por su elasticidad le es muy fácil adaptarse al pizo pedregoso del río; de esta estructura que constituye la boca se continúa una bolsa tejida, en forma de dedo de guante, con una malla cuyas aberturas estiradas son de 3 centímetros.

La pesca con esta aparejo consiste en atrapar los camarones cuando estos saltan al remover las piedras que el pescador encuentra a su paso. Esta clase de pesca se realiza en las zonas poco profundas del río. (Ver fotos N° 1 y 2).

(*e*) *Pesca con trampas fijas*

Las trampas fijas usadas por los pescadores son: La izanga y el chauco.

La pesca con izanga.—La izanga consiste en un cono construido con carrizo cuya boca tiene alrededor de 50 cm. de diámetro y se va adelgazando hacia el vértice su longitud alcanza 1·20 m. Para la pesca los camaroneros colocan una serie de izangas con la boca en el sentido contrario a la corriente, formando hileras continuas que cierran la mayor parte del río (Ver foto N° 3 y 4).

Por este método se capturan camarones de todo tamaño y tiene mayor rendimiento durante las avenidas del río; que es cuando los camarones bajan hacia el mar, tal como se ha expresado en la discusión de las migraciones.

La pesca con el chauco.—El chauco consiste en una canasta cónica, en cuya boca se ha insertado un embudo, hecho de caña, en forma tal que los camarones tengan facilidad para penetrar y gran dificultad para salir. (Ver foto N° 5). El uso de esta trampa se limita a la parte baja del río, durante la época del verano, y solamente en el momento que el camarón hace su migración en el sentido mar río. La trampa es colocado en hileras con la boca en el sentido de la corriente del río. (Ver foto N° 6, 7, 8 y 9). Un pescador por lo general durante la época de pesca (verano) posee de 2 a 3 hileras de chaucos, con un promedio de 4 unidades por hilera. Es conveniente hacer notar que el chauco solamente captura ejemplares que han cumplido con su función de reproducción.

CONCLUSIONES

Sobre reproducción y migración

1. Toda la población en el río efectua migraciónes.

2. Las hembras realizan una migración mecánica de desove hacia el mar durante la época de creciente del río, lo que frecuentemente corresponde de Enero a Marzo. Realizado su desove vuelve al río en los mismos meses, aunque algunos ejemplares que se retrasan realizan ésta migración de retorno durante el resto del año.

3. La especie se reproduce durante todo el año y es fertil antes de cumplir el primer año de vida.

4. De Enero a Febrero todas las hembras a lo largo de la zona de su distribucion son ovígeras.

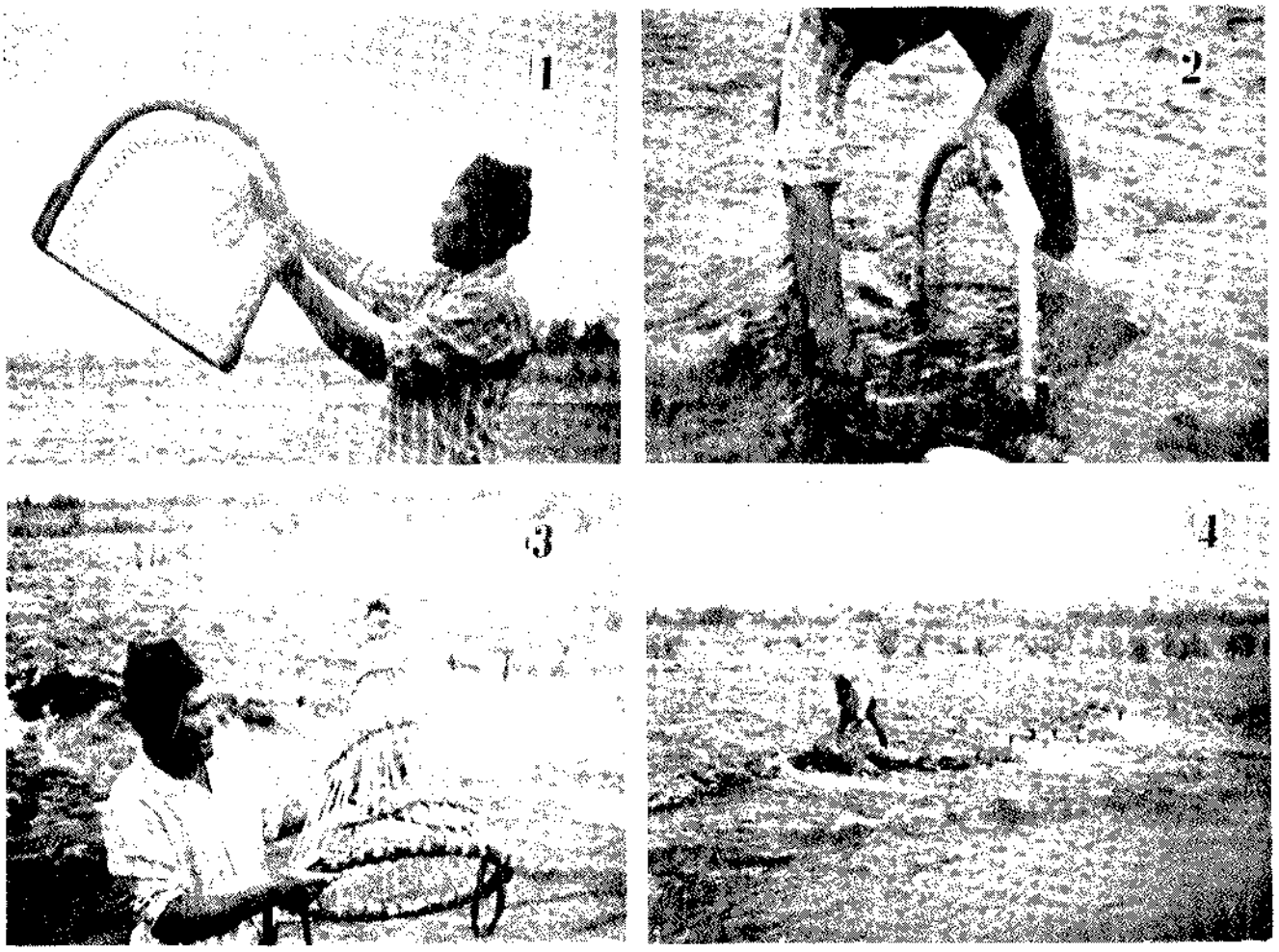
5. La mayor área de desove está en la zona en que las aguas del río se mezclan con las del mar.

6. El paso del estadio Mysis a camarón juvenil tiene lugar en el estuario del río, no en agua dulce.

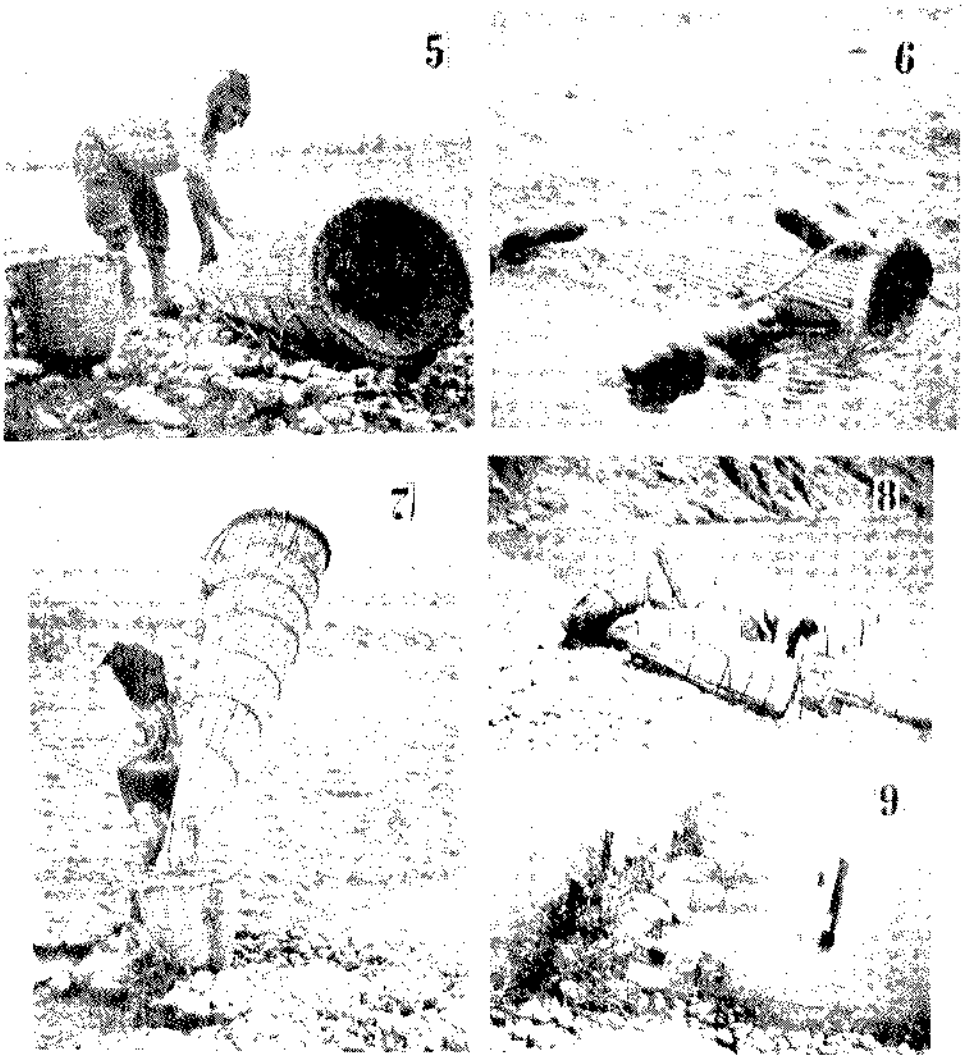
7. El número de huevos tiene una relación directa con el tamaño del animal.

Sobre la explotación del camarón

8. Anualmente los ríos camaroneros del Departamento de Arequipa, producen al rededor de 100,000 kilos de camarones.



Figs. 1-4. Fig. 1. Un pescador muestra la isigua Oyica. Fig. 2. El pescador de la foto No. 1, haciendo uso de la isigua en el río Majes-Camaná. Fig. 3. Un pescador muestra una izanga. Fig. 4. Un pescador trabajando con izangas en el río Majes-Camaná



FIGS. 5-9. Pescador mostrando un chauco. "la porte anterior corresponde a la boca". Fig. 6. Manera de colocar el chauco en el agua. Fig. 7. Un pescador vaciando un chauco, luego de sacarlo del agua Foto. corr. al río Mares-Cumaná. Fig. 8. Grupo de chaucos que un pescador. Trata de colar en el río, muy- cerca de la desembocadura. Foto corr. al río Ocona. Fig. 9. Fila de más de 3 chaucos colocados en el río, poco antes de su desembo cadura al mar. Foto corr. al río Ocona

OBSERVATIONS ON THE BREEDING AND SEASONAL ABUNDANCE OF TEN SPECIES OF PLANKTONIC COPEPODS OF THE GULF OF MANNAR*

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ABSTRACT

The quantitative biology of the following ten species of planktonic copepods is included in the present study: *Pseudodiaptomus aurivilli, Calanopia thompsoni, Acartia erythraea, Paracalanus aculeatus, P. parvus, Calanopia aurivilli, Acrocalanus gibber, A. monachus, Euterpina acutifrons* and *Oithona rigida.*

There have been three principal aims: (*a*) determination of the breeding seasons of different copepods; (*b*) estimation of quantitative seasonal distribution and (*c*) determination, if possible, of the number of broods in a year and the longevity of broods. The data obtained during the present studies on these subjects are presented, and compared with earlier works and points of interest are discussed.

Based upon the breeding habits, the planktonic copepods of the Gulf of Mannar are divided into three groups: those having a single, well-defined breeding season; those having more than one breeding season and those having irregular breeding periods. It may be added that this division is purely tentative for it is hard to explain why organisms living under similar environmental conditions should have different breeding habits.

INTRODUCTION

THERE have been three principal objectives for the present investigations: (*a*) determination of the breeding seasons of different copepods; (*b*) estimation of quantitative seasonal distribution of different species; and (*c*) determination, if possible, of the number of broods in a year and the longevity of broods. It may be stated that some useful informations have been obtained on the general pattern of breeding, quantitative variations of different species throughout the year and the succession of their life-cycles. The investigations were confined to adults and copepodites only. The correct identification of the naupliar stages is an extremely difficult task as the collections invariably contain various developmental stages.

Ten species which constitute the more common forms of the area investigated have been included in the present study. From the point of view of total abundance *Acartia erythraea* could be said to be the most important species though in tropical waters it is difficult to regard any single species as a dominant item of the plankton. Some species are found throughout the year without much seasonal variations while some others display great fluctuations. Digby (1950) in his excellent studies on the biology of small planktonic copepods off the Plymouth area derived his conclusions on following three types of evidences: (i) comparative abundance of different species; (ii) their percentage distribution; and (iii) the size of the adults. He has also pointed out the drawbacks of each of these considerations. Nevertheless, a study of these factors forms an important prerequisite to an understanding of their biology as it reveals many important facts.

MATERIAL AND METHODS

The present study is based on the examination of eighty-eight horizontal surface plankton hauls collected in the Gulf of Mannar, each of fifteen minutes duration. These hauls were made

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from May 1959 to December 1960. All the collections were made between 5–30 and 6–30 A.M. Half meter organdie nets with mesh size of 0·230 mm. were employed in all the collections which were preserved immediately after the haul. On several occasions duplicate hauls were also made. These were used for comparing the two sets of readings. The routine collections were made at station A and the duplicate samples at station B, the details of which can be seen in Ummerkutty (1967).

For laboratory analysis the total catch was subsampled as follows: The entire quantity was transferred to a wide-mouthed bottle and diluted upto 250 c.c. by adding formalin. A subsample of 2 c.c. was taken out by means of a graduated pipette. All organisms contained in this example were counted under a binocular microscope by employing a plankton counting chamber.

Breeding Periods

Pseudodiaptomus aurivilli Cleve

Large numbers of adult males, females and copepodites swarmed the surface waters in the months of December–January 1959–60; this was to some extent accompanied and later on

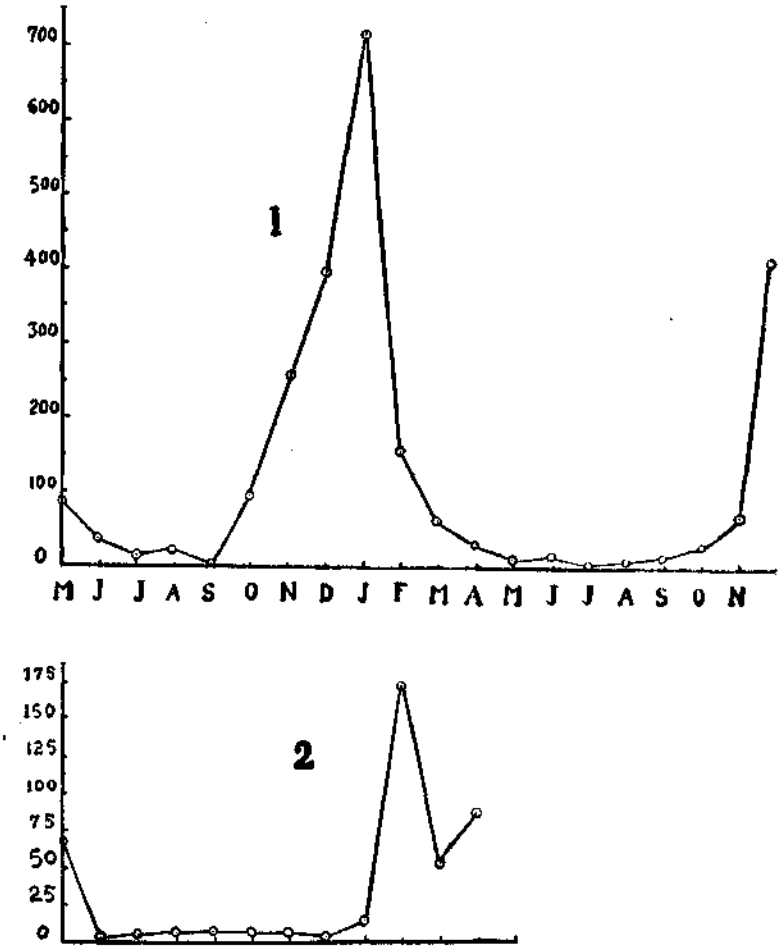
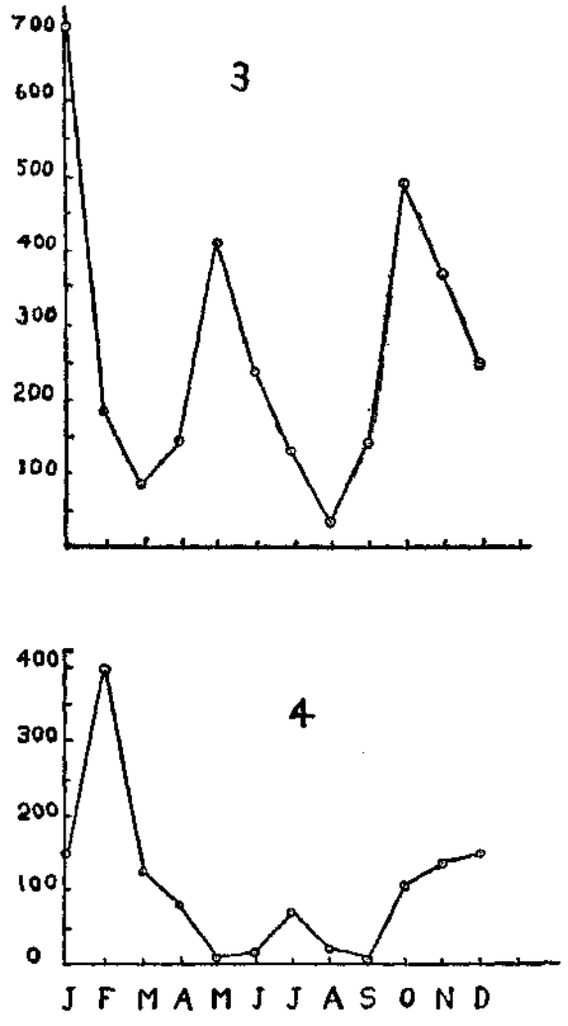


Fig. 1–2. Distribution of total population (adults and copepodites) of different species of copepods in the Gulf of Mannar during 1960. Fig. 1, *Pseudodiaptomus aurivilli*, Fig. 2, *Calanopia thompsoni*,

followed by large number of naupliar stages. The abundance was maintained in February though a steep reduction was noticed from the January level. A clear and gradual declination was observed during subsequent months and in July the species virtually disappeared. The data for next four months (August–November) display a gradual increase in the population. It is interesting to note that the level in December was almost the same as for the same month of the preceding year (Fig. 1).

A close study of the data available for 1959 revealed that in the month of May a fair number of individuals, more than half of which were adults were caught. This was followed by a declination in June, July and August and in September the species was at its minimum of occurrence. The months of October and November witnessed an abrupt upward change in this species which compares well with the condition found in 1960.



FIGS. 3–4. Distribution of total population (adults and copepodites) of different species of copepods in the Gulf of Mannar during 1960. Fig. 3. *Acartia erythraea*. Fig. 4. *Paracalanus aculeatus*.

The percentage distribution of adults throws more light on the breeding pattern of this species. August–September 1959 and July–August 1960 were the periods of lowest abundance of the species. During these periods only adults were caught. For the few months following this low peak the population consisted chiefly of adults. By the end of November both in 1959 and in 1960 good numbers of adult females were observed to carry eggs and this was followed by a sudden increase of early stages in the population in December and January. This suggests that intensive spawning takes place during the months of December–January. As young stages were also found during subsequent months, it appears that the breeding of stray individuals or isolated late spawners continue till about February.

Calanopia thompsoni A. Scott.

This species shows a great similarity to the earlier species in its distributional pattern except that during the non-peak period its abundance becomes very insignificant. It also has similar peaks during the months of September–January (Fig. 2), with, however, a fall in December. During May–June a fair number of first to third copepodites are present. In July and August these stages are replaced by fourth and fifth stages. The adults begin to appear in small numbers in August, and from September onwards they increase steadily and attain the maximum in January. The early copepodites of these species are seen in the months of September which signifies the commencement of breeding season. During subsequent months when intensive spawning recurs, the life-cycle passes in quick succession. In February and March the early stages begin to disappear, thus indicating the completion of breeding season. In these months the species is represented predominantly by late copepodites and adults.

Although occurring in relatively small numbers, *Calanopia thompsoni* appears to have some importance by virtue of its large size. If weight alone is taken as a criterion, the contribution of this species during the peak period to the total biomass will be found to be quite substantial.

Acartia erythraea Giesbrecht

This is one of the commonest species of this area and is found almost throughout the year. However, during the peaks of October and January, because of the swarming of so many other copepods, its comparative importance is reduced. There are two well-defined peak periods of abundance for this species, one in April–May and the other in October–January. During the latter peak, however, the population suffers a minor declination in November (Fig. 3). A study of the percentage distribution of the various stages show that the setback in November is due to a lower rate of recruitment of new copepodite population.

Kartha (1959) found two distinct peaks for this species first in March–April and the other in November–January, with an additional smaller peak in September. During the year 1960 these sequential changes appear to have shifted forward by one month. The first maximum is found in April–May, extending even upto first half of June. The smaller peak noticed by Kartha in September is found to occur in October and almost entirely merges with the second large peak of the year. The facts that during the year 1954 no such intermediate peak was noticed by Kartha and that even when present the peak is extremely small suggest that this smaller peak may better be considered in continuation of the all-round increase of the species during the colder months of the year.

Paracalanus aculeatus Giesbrecht

This species was found at its maximum during January–March whence it decreases gradually. The lowest number was observed in May. During June–July another peak was found to occur. But while in 1959 this latter peak was conspicuous it turned out to be quite insignificant in 1960 (Fig. 4). In September the species reached the second minimum and during this month the popula tion consisted chiefly of the copepodites. By October, however, all the young stages have moulte

either into fifth stage or adults. Incidentally this was the month when the adult population recorded its greatest percentage of abundance. This not only shows that the breeding has practically ceased a month or so earlier, but may also indicate that the next active breeding season of the species is in the offing.

Sewell (1929) has made the suggestion that it is probable that the abundance of this species and of the following is more or less mutually exclusive. He found that when *P. parvus* was dominant in a particular locality *P. aculeatus* was almost entirely absent or present only in small numbers. The reverse situation of abundance of *P. aculeatus* and an absence of *P. parvus* was also noticed.

Paracalanus parvus Claus

Kartha (*loc. cit.*) noted great variations in the trend of seasonal changes of this species. Both in 1952 and in 1953 he observed only a single prolonged breeding period with its maximum in December–January. In 1954 he found a second increase with breeding activity during April-May. This was, according to him, mainly responsible for the total copepod peak in May–June. The data available for 1960 present a picture almost intermediate to these two extremes (Fig. 5). The species reaches the maximum in November–January months. A second peak which comparatively is quite small and insignificant is found in May–June. A third increase occurs in September, just prior to the most intensive breeding period of the year. It is probable that active breeding starts early in September, and continues upto January or February. The steep reduction found in October is mainly due to a lesser percentage of adults.

Besides the main peak during the colder months, the presence of a second peak is reported for 1954 (Kartha, *loc. cit.*). Its occurrence in 1960 as well indicates that it is probably a regular feature of the species. Even in 1953 Kartha's figure shows a minor peak (Kartha, *loc. cit.*, Fig. 3, *b*) which is not mentioned in the text and which resemble the second peak observed in 1960. The correspondence of the present data with these earlier reports thus is not a mere coincidence.

Calanopia aurivilli Cleve

Generally the maximal occurrence of this species is during the months of October–December. The lowest numbers are found in May and August. There is a slight increase during the intervening months of June and July.

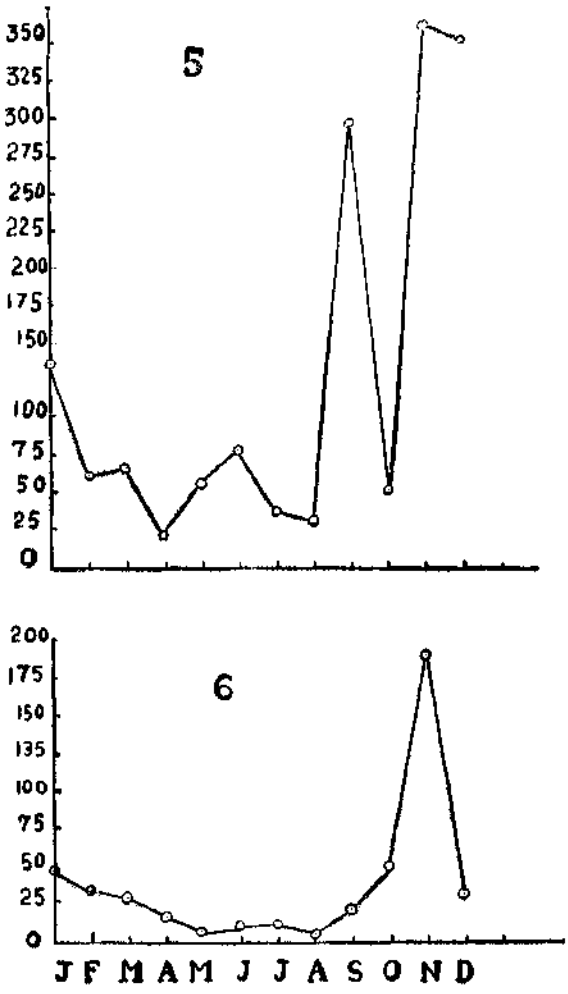
By September the species starts increasing in number. This process goes on steadily until November when the species attains its annual maximum (Fig. 6). That November is the most active breeding month is shown by the percentage distribution of the adults and copepodites. The latter which formed only forty-two per cent of the total population in September now swarm the water, constituting about seventy-eight per cent. Further while in September the early copepodites (I–III) were entirely absent, in subsequent months they contributed a major share in the total plankton.

Although small, the June–July peak also may indicate a clear breeding period. From April to June practically there was no new recruitment of early copepodites. But in July there is a sudden appearance of these stages, forming about sixty per cent of the total population of this species. By August all the young ones moult to higher stages and by September the population predominantly attains adulthood, and this marks the beginning of another active breeding period.

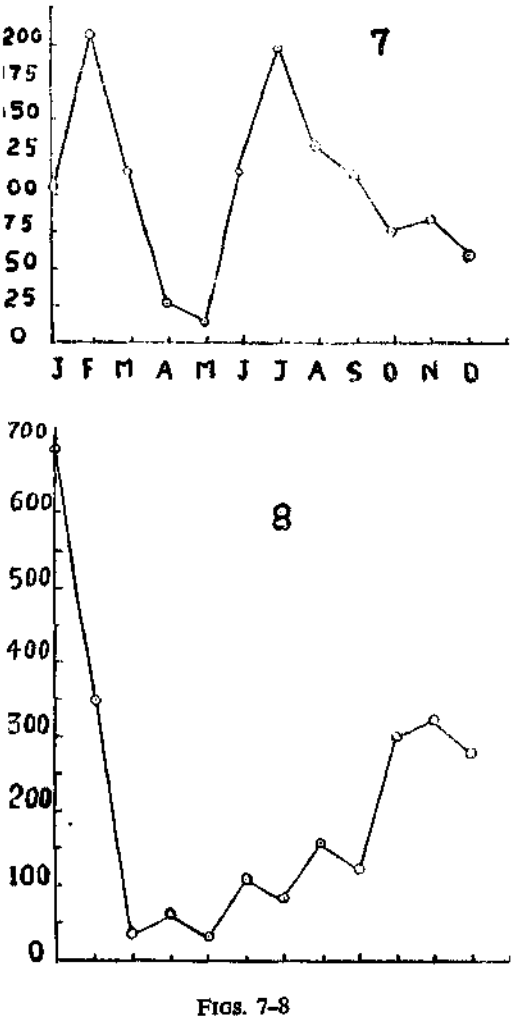
Acrocalanus gibber Giesbrecht

Kartha (*loc. cit.*) treated three species of this genus together and stated that in the Gulf of Mannar there "was a fairly good population from June to August in 1952 with a peak in August;

and July–September in 1953". He further stated that "in 1954 there was a peak of short duration in May". The present observations differ from these records. It may be because of the fact that in the earlier account these different species were pooled and dealt with together.



Figs. 5–6



FIGS. 7–8

FIGS. 5–6. Distribution of total population (adults and copepodites) of different species of copepods in the Gulf of Mannar during 1960. Fig. 5. *P. parvus*. Fig. 6. *Calanopia aurivilli*.

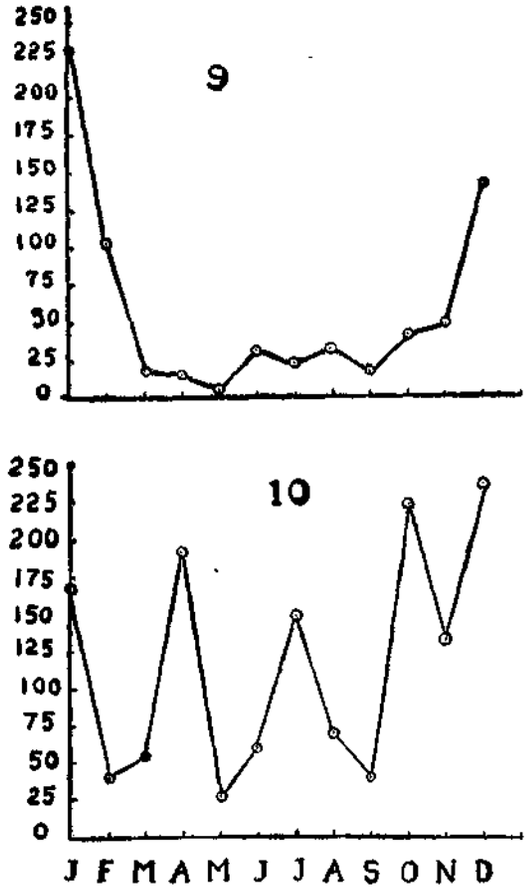
FIGS. 7–8. Distribution of total population (adults and copepodites) of different species of copepods in the Gulf of Mannar during 1960. Fig. 7. *Acrocalanus gibber*. Fig. 8. *A. monachus*.

A. gibber displays two major peaks in the year, the first in January–February, extending upto March and the second in June–July, extending upto August. There are clear gaps between the intervening periods (Fig. 7). However, a percentage distribution of different copepodites and adults reveals little information as to any change in the rate of breeding between different seasons. It is interesting to note that the peaks observed for this species correspond to those recorded for *Calanopia aurivilli* and *Paracalanus parvus*, the only difference being that the June–July peak is larger and the winter peak is shifted more towards the colder months.

Acrocalanus monachus Giesbrecht

The only definite thing that could be said about the distributional pattern of this species for the year 1960 is that there was an enormous increase of the population during the months of November–February, attaining the maximum in January (Fig. 8). After February there was a steep reduction, reaching the minimum in March. From then onwards small fluctuating peaks were observed, almost at intervals of two months until October when the species displayed a gradual increase. A study of the percentage distribution of various copepodites and adults does not reveal much except that in December the adult population reaches its maximum. The annual maximum population observed in February is due to active breeding of these adults.

A. monachus is a small species and it is possible that the sampling of the early copepodites is inadequate. It is also possible that during the laboratory analysis some of the copepodites could have been mixed up with those of a related species, *A. gracilis*. The latter is a large species and occurs only occasionally. However, when both species occur together, and especially when the population is dominated by the early copepodites, the correct identification becomes a difficult task.



FIGS. 9–10. Distribution of total population (adults and copepodites) of different species of copepods in the Gulf of Mannar during 1960. Fig. 9. *Euterpina acutifrons*. Fig. 10. *Oithona rigida*.

Euterpina acutifrons (Dana)

According to Kartha (*loc. cit.*) this species occurs throughout the year, with slight variations in its abundance and with an over-all increase during the cold months. Only in 1954 he observed an additional peak during May–August. There is general agreement between the present data and the earlier accounts. The species started a steady increase in October and the tendency is continued upto January whence it takes a reverse direction. During March–October the species undergoes considerable fluctuations (Fig. 9), the yearly minimal level being recorded in the month of May. However, it is surprising that during this month the population was composed mainly by the copepodites especially the earlier ones and that the largest percentage of the adults was found to occur during the preceding month of April.

Oithona rigida Giesbrecht

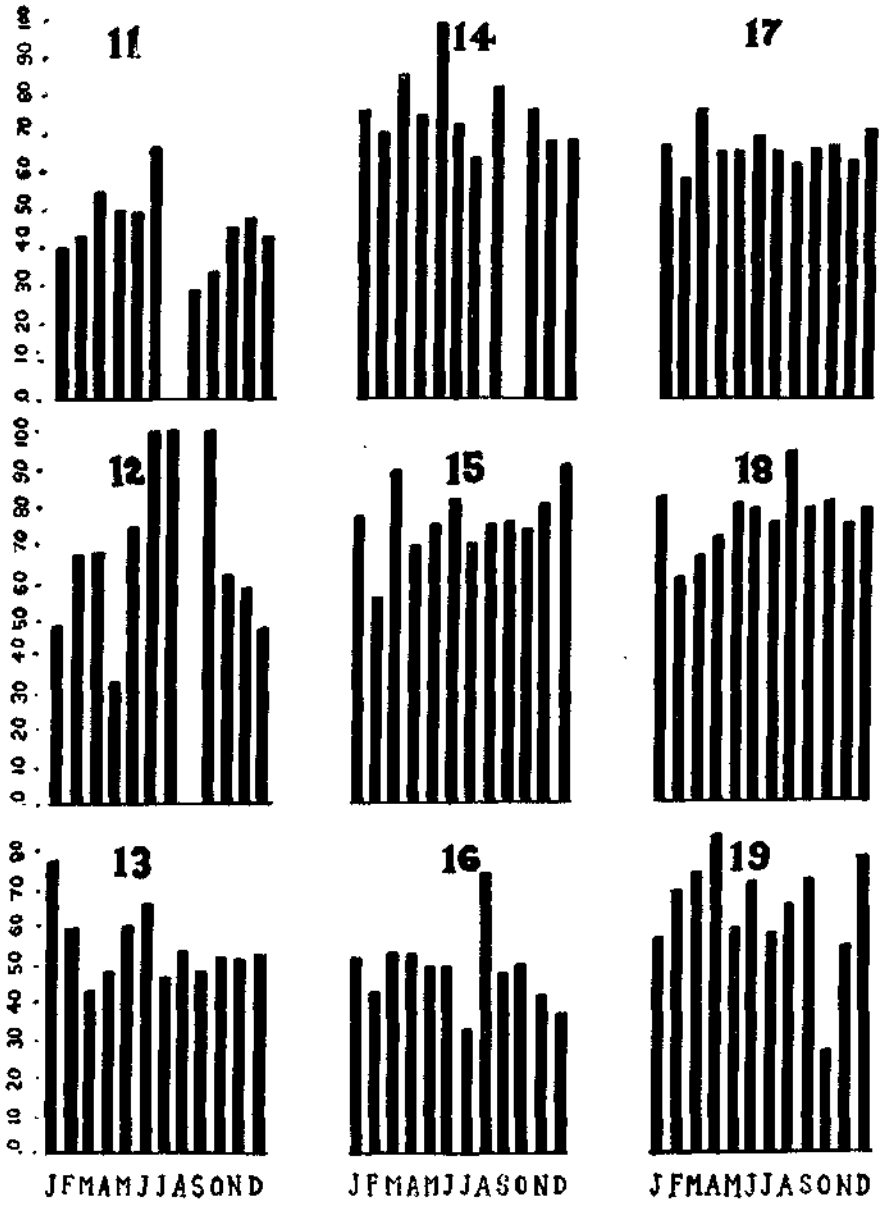
Kartha (*loc. cit.*) found that the species of the genus *Oithona* showed irregularity in its distribution from year to year with, however, a constant peak in September. There is good agreement between the present findings and the earlier records. The present species attains its annual maximum during the months of December–January. Other peaks are observed almost at equal intervals in March–April, June–July and September–October (Fig. 10).

The four peaks observed in the present investigations correspond to those reported by Kartha, especially for the years 1953 and 1954. The present data differ from those of the year 1952 in that the peaks recorded in March–April and June–July in that year are considerably insignificant. It appears that this is a prolonged spawner, but with distinct periods of active breeding which are intercepted by short intervals of lesser reproductive activity.

Quantitative Distribution

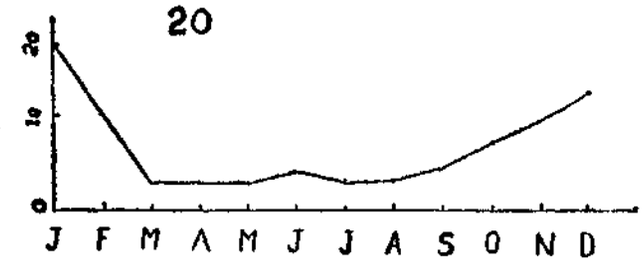
The copepod population as represented by the ten species noted above in the Gulf of Mannar is the highest during the coldest months of the year, November–February (Figs. 11–19). By the end of February or March, almost all the species record varying degrees of declination (Figs. 20–21). In several species the decrease is constant during the summer months and a reversal towards the other direction is marked in the beginning of August or September whence the increase in their numbers becomes steady. By taking all species together it appears that the copepods show a unimodal pattern of distribution. However, this picture is obscured if we examine individual species separately. Not only do several of them show more than one peak in a year, but the peaks of different species are not often synchronised. In all species, however, one of the annual peaks corresponds with cold months of the year, thus resulting in an over-all increase of the copepod population during that season. Prasad (1954 and 1956) found that although the copepod population showed an increase in October there was a reduction in November before attaining a subsequent increase resulting in a peak in December–February. Kartha (*loc. cit.*) obtained more or less similar informations. However, Prasad and Kartha (*loc. cit.*) have clearly demonstrated that a close relationship exists between the breeding of copepods and the diatom cycles and that treated in a general way "the maximum breeding in the Gulf of Mannar is during September to March". It is probable that the reduction of population obtained in November during certain years is not due to any complete break in the reproductive activities but may be due to a slowing down of the new recruitments of nauplii and copepodites after the completion of an initial generation. In several species (*P. aurivilli, C. thompsoni, A. erythraea, P. parvus, A. gibber, O. rigida*) this disjunction is seen in the winter peak. But in several others (*P. aculeatus, C. aurivilli, A. monachus, E. acutifrons*) the increase initiated during September or October is steady and continuous, attaining a single prolonged annual maximum. Prasad (1954) who first observed dicyclicity in the distribution of copepods in the Gulf of Mannar offered the following explanation: "It is possible that while in other localities the maximum occurrence of one or more species may overlap, there may be still others whose maxima fall in such a way as to fill the gaps and present an over-all unimodal distribution. A

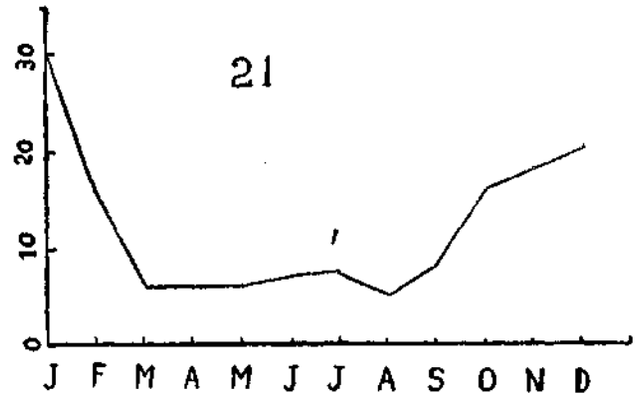
similar phenomenon may not be taking place here thereby resulting in an apparent reduction in population level and a bimodal curve."



FIGS. 11–19. Percentage distribution of adult females in the different species of copepods in the Gulf of Mannar during 1960. Fig. 11. *Pseudodiaptomus aurivilli.* Fig. 12. *Calanopia thompsoni.* Fig. 13. *Acartia erythraea.* Fig. 14. *Paracalanus aculeatus.* Fig. 15. *P. parvus.* Fig. 16. *Calanopia aurivilli.* Fig. 17. *Acrocalanus gibber.* Fig. 18. *A. monachus.* Fig. 19. *Oithona rigida.*

If individual species are considered separately it is found that the annual maximal peaks coincide with the most active breeding periods. It has been observed that the breeding activity is a continuous process in great many of the species and takes place almost throughout the year. Only in a few species (*e.g., P. aurivilli*) there is a cessation of spawning activities during the periods of minimal occurrence. However, in all the continuous spawners there is great reduction in the rate of production and the succession of broods during the non-peak periods. It appears that during these periods different naupliar and copepodite stages take longer durations than those during the peak periods when because of the highly favourable environmental conditions the reproductive activities are accelerated and that the life-cycles are spent in quicker succession.





FIGS. 20-21. Fig. 20. Distribution of total adult copepods of the ten species studied in the Gulf of Mannar during 1960. Fig. 21. Distribution of total copepod population (adults and copepodites) of the ten species studied in the Gulf of Mannar during 1960.

The relative difference in the distribution of the two sexes of adult animal do not exhibit any particularly interesting trend except that in some species the females tend to dominate almost always while in others a fifty-fifty ratio is roughly maintained. In species with strongly defined annual peaks (*e.g., P. aurivilli, C. thompsoni*) the males slightly outnumber the females during the breeding periods. It is also interesting to note that in these species the females form a greater proportion of the adult population during the periods of minimal occurrence. Among the late copepodites, the ratio of sexes is monotonously uniform, each sex equalling the other. A sex-wise analysis of the earlier copepodites is not possible as in these cases there is apparently no external character for sexual determination.

Annual Number of Broods and Their Longevity

Pseudodiaptomus aurivilli and *Labidocera bangalencis* have been reared in the laboratory for studying the stages of their life-cycles (Ummerkutty, 1965). The methods adopted for rearing was to select specimens of a particular stage and allow to moult to the next stage. In this way, by repeated observations on different stages a continuity of all stages could be established. In some cases the specimens survived longer than one moult, thus giving actual indication of the time required by the organism to moult from one stage to the other. However, the time taken by plankton organisms to moult in captivity to next higher stage may not be the same as in their natural environment. None of the nauplii and the early copepodities which underwent more than one consecutive moult in the laboratory took more than 2–3 or rarely 4 days for the process. The late copepodities hardly lived for four days after their first captive moult. Probably the duration required for the next moult is longer in these cases but may not exceed 6 or 7 days. Giving an average of three days for the naupliar and four or five days for the copepodite development it is found that a nauplius freshly hatched and reared under captive conditions could attain adulthood in five or six weeks. This could possibly depend on the optimum conditions of the environment.

There are many types of evidences to show that the period required for completion of the entire life-cycle is much shorter during the propitious colder months. It has been found both in the earlier studies (ch. Prasad, 1954 and 1956; Kartha, 1959) and also in the present investigations that for several species (*A. erythraea, P. parvus*, etc.) the winter increase is interrupted after a month or so before reaching the maximal peak. If this interruption is accepted as a break in the reproductive activity it can be seen that during the favourable periods of colder months the entire life-cycle requires four to five weeks for its completion.

During the non-peak periods the life activities in most of the species are slackened and although breeding takes place, the rate of production of new stocks appear to be at a much lower rate and the nauplii and the copepodites appear to last for longer durations. *Oithona rigida* which shows several peaks in a year provides a fine example. The breeding in this species is continuous. As noted earlier the species reaches its maximal abundance during December-January. Following this period there is a month of recuperation before the species launches on the next generation. The latter lasts exactly for two months before attaining maturity and for preparing the species to start on a new generation. The colder months, however, present a different picture. During this period two or more successful generations are completed in rather quick series within a period of three to four months, the generations sometimes being interrupted only by short periods of lesser reproductive activity.

It is possible that species with one annual maximum should have two or three broods during the entire active breeding period and one or two during the rest of the year. The species with two or more maximal periods would certainly have additional broods. Prasad and Kartha (*loc. cit.*) observed: "In the temperate waters the usual number of broods is three or four and in cold waters this appears to be reduced to one. It is not unlikely that in the tropical waters there are more number of broods than in the temperate and cold waters".

General Remarks

Breeding habits of copepods of the Gulf of Mannar appear to be divisible into three groups: (1) Those breeding throughout the year with irregular variations in the frequencies so that their population includes not only adults but also various copepodites. All these are caught irrespective of any seasons. *Acrocalanus monachus* and *Oithona rigida* exemplify this group. (2) Those breeding throughout the year but with distinct peaks during certain months so that although the various copepodites and the adults of the species are available in every month, yet their percentage abundance displays considerable differences. Several species fall into this group: *Acartia erythraea,*

Paracalanus aculeatus, P. parvus, Calanopia aurivilli, Acrocalanus gibber and possibly *Euterpina acutifrons.* (3) Those breeding only during certain seasons. Among the species studied *Pseudodiaptomus aurivilli* and *Calanopia thompsoni* come under this group.

This grouping of copepods on the basis of breeding habits is made with some reservations and should be regarded as tentative. In the first instance it is questionable why species residing under similar environmental conditions should have differential breeding seasons. It will not be out of place to suggest that the availability of food may serve as an important factor in controlling the breeding behaviour of copepods in tropical waters. The synchronisation of diatom outbursts and naupliar development of marine invertebrates has clearly been demonstrated (Ussing, 1938; Marshall and Orr, 1952; Barnes, 1957; Prasad and Kartha, 1959). Those species with clear seasonal spawning habits could be said to be under the strong influence of regular periodicities of phytoplankton. The breeding of other copepods, irrespective of the season, could be due to the fact that in tropical waters phytoplankton may be available almost throughout the year in varying quantities. This latter suggestion is, again, illustrated by *Tortanus gracilis* and *T. forcipatus* both of which are predatory and feed on nauplii and other minute creatures. These species are not very common in this area, but whenever present they are represented not only by adults but also by copepodites, indicating a continued breeding throughout the year. As the naupliar diet is invariably present throughout the year those copepods do not find any scarcity of food. They, therefore, breed all the year round.

The temperature variation in the Gulf of Mannar have recently been discussed by Prasad (1957) who noted that temperature is maintained more or less at a uniform level throughout the year except during some months corresponding to the calendar winter when there is an abrupt reduction. The earlier parts of these colder months represent the biological spring of this area with a great bloom of phytoplankton and the latter part the biological summer with the greatest number of zooplankton. The coincidence of the breeding of copepods with this part of the year is, therefore, natural. However, why several species should have another significant peak period during the months of June-July, extending even upto August is not clear. This is particularly interesting in view of the fact that during this period active breeding of copepods occurs in the Palk Bay (Prasad and Kartha, *loc. cit.*).

A final word may be added about the continuity of the species throughout the year. In temperate and cold waters several earlier workers have noticed (for a review *see* Digby, 1950 and Marshall and Orr, 1955) that species with well-defined seasonal breeding disappear almost altogether during the unfavourable periods. In such cases it is held that either these species migrate at lower depths during the unfavourable conditions or they never disappear completely from the water column, but merely are scarce enough to become noticed. In tropical waters the breeding appears to be a continuous process and only the intensity differs from season to season. The influence exerted by the immediate favourability or unfavourability of the environment is manifested in the breeding behaviour of the copepods in the form of seasonal rhythm.

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DISCUSSION

DR. B. RASMUSSEN: There are no differences in the breeding period in most of the species of copepods mentioned, though in some there are these differences. Why?

Food can be said to be the important factor for abundance of some of the copepods and some relation can be established for these species while in some others there is no such relation.

DR. J. H. WICKSTEAD: The studies on *Calanus* have bot been completed in Plymouth Lab.

DR. S. KRISHNASWAMY: I think we should stop thinking in terms of relating the phytoplankton bloom, etc. to the abundance of copepods, because Darwinian orthodoxy will not allow so many species to breed in one and same period.

DR. V. HANSEN: There are 3 species of copepods living in the North Atlantic and these species as they migrate up towards the surface from the depths as great as 600 meters they breed step by step (turn by turn), and I feel in such cases where the environment is more or less the same, we should look for other parameters or mechanisms for such kind of differential breeding seasons.

DR. V. H.: How isolated is this area, Gulf of Mannar?

DR. S. JONES: Beyond the islands, there is oceanic connection which ranges in depth upto about 1,000 fathoms.

DR. S. KRISHNASWAMY: The differential breeding season may be due to the liberation of certain amino-acids by the bloom of phytoplankton which may trigger the breeding, setting and growth of the larvae.

DR. B. RASMUSSEN: It cannot be considered that all the animals should be influenced in same manner by the environmental factors. It may be that some animals may or do behave independently or differently.

DISTRIBUTION OF SEX RATIOS OF PENAEID PRAWNS IN THE TRAWL FISHERY OFF COCHIN*

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ABSTRACT

Sex ratio data of four species of penaeid prawns *Metapenaeus dobsoni, Penaeus indicus, Parapeneopsis stylifera* and *Metapenaeus affinis* in the trawl fishery catches of Cochin for 1962 and 1963 are analysed statistically and it is found that in the former three species the distributions of the sexes are significantly different from what could be accounted for by binomial theory and in *Metapenaeus affinis* alone the sexes are more or less evenly distributed throughout the year. It is suggested that the differential sex ratios in the fishing grounds may be brought about by the segregated sex movements for breeding.

IN sex ratio studies in which monthly samples are collected and analysed for sex ratio estimation, different monthly samples may give different estimates of sex ratio. It is possible that either the sex ratios are distributed according to the binomial theory and the apparent difference in the monthly sex ratios are due to sampling fluctuations or the sex ratios are not distributed according to the binomial theory due to an actual change in the concentration of the sexes.

Sex ratios of the four species of penaeid prawns, *viz., Metapenaeus dobsoni, Metapenaeus affinis, Penaeus indicus* and *Parapeneopsis stylifera* in the commercial trawl fishery in Cochin area for the years 1962 and 1963 have been analysed in order to determine whether or not they were distributed binomially. Tables I *a* to *d* give the sex ratios of the different species during the different months of off-shore catches. From the tables it is evident that the ratio of males vary considerably in different months in most of the species. To test if the variation in the monthly sex ratios could be expected from binomial theory or not, x^2-statistics given below was calculated:

$$x^2 = \frac{\sum\left(\frac{x_i^2}{n_i}\right) - \frac{(\Sigma x_i)^2}{\Sigma n_i}}{pq}$$

where x_i is the number of males in the "i"-th month, n_i is the total number of observations in the "i"-th month, $p = \Sigma x_i / \Sigma n_i$ (Cochran, 1954) and $q = (1-p)$. The x^2 values of each species with the associated degrees of freedom are given in Table II separately for 1962 and 1963. Significance tests at a probability level of 0·01 show that the variations in sex ratios in different months in the case of the three species *M. dobsoni, P. stylifera* and *P. indicus* were significantly different from what could be accounted for by binomial distribution. But the variation in monthly sex ratios in the case of *M. affinis* was not found to be significantly different from the expected binomial ratios.

If the sex ratios are distributed according to the binomial theory, the estimate of variance of sample estimate of the sex ratio is given by $v(p) = pq/n$, where p is the sample estimate of male ratio, $q = 1 - p$ measuring the estimate of female ratio and 'n' the sample size. This formula is not valid if the distribution is not binomial, unless individual prawns are sampled at random. In actual practice cluster sampling is resorted to. In this case Cochran (1953) has given the following formula for estimation of variance of p.

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TABLE I

Showing the sex ratios of the different species for 1962 and 1963

Months	1962			1963		
	Sample size	Males	Ratio	Sample size	Males	Ratio
		(*a*) *M. dobsoni*				
January ..	993	428	0·43	1,047	519	0·49
February ..	1,057	466	0·44	1,222	432	0·35
March ..	1,743	553	0·32	997	389	0·39
April ..	919	416	0·45	1,009	385	0·38
May ..	1,127	536	0·48	1,069	456	0·43
June ..	846	553	0·65	50	39	0·78
November ..	271	150	0·55	167	98	0·59
December ..	390	247	0·63	196	94	0·48
		(*b*) *M. affinis*				
January ..	205	109	0·53	287	132	0·46
February ..	200	103	0·51	331	187	0·56
March ..	323	178	0·55	297	131	0·44
April ..	55	18	0·33	384	204	0·53
May ..	545	265	0·49	377	189	0·50
June ..	285	152	0·53	97	41	0·42
September ..	1	1	1·00	..	..	..
October ..	442	217	0·49	15	7	0·47
November ..	446	223	0·50	97	49	0·50
December ..	635	324	0·51	44	27	0·61
		(*c*) *P. stylifera*				
January ...	33	9	0·27	41	17	0·41
February ..	43	8	0·19	29	16	0·55
March ..	108	47	0·43	141	65	0·46
April ...	49	25	0·51	251	32	0·13
May ...	401	174	0·43	31	13	0·42
June ...	818	423	0·52	24	10	0·42
September ..	515	238	0·46	..	..	...
October ..	778	419	0·54	125	80	0·64
November ...	574	348	0·61	177	118	0·67
December ..	326	170	0·52	18	14	0·78
		(*d*) *P. indicus*				
January ...	247	144	0·58	82	50	0·61
February ...	115	82	0·71	46	30	0·65
March ..	40	22	0·55	15	6	0·40
April ..	2	1	0·50	143	71	0·49
May ..	9	5	0·55	84	28	0·33
June ..	18	9	0·50	...	...	...
October ..	2	2	1·00	..	..	...
November ..	5	1	0·20	..	..	...
December ..	153	117	0·76	8	2	0·25

TABLE II

Showing the values of x^2 for different species for 1962 and 1963

Species	1962			1963		
	Degree of freedom	Value of x^2	Significant or not	Degree of freedom	Value of x^2	Significant or not
M. dobsoni ..	7	333·519	Significant	7	110·740	Significant
M. affinis ..	9	14·892	Non-significant	8	17·752	Non-significant
P. stylifera ..	9	66·082	Significant	8	29·566	Significant
P. indicus ..	8	22·273	Significant	5	20·118	Significant

$$v'(p) = \frac{1}{k(k-1)\bar{n}^2}(\Sigma x_i^2 + p^2 \Sigma n_i^2 - 2p \Sigma x_i n_i)$$

where k is the number of clusters sampled. Table III gives the value of $v(p)$ and $v'(p)$ in the case of all the species studied.

TABLE III

Showing the values of v (p) *and* v' (p) *for different species for* 1962 *and* 1963

Species	1962		1963	
	$v(p)$	$v'(p)$	$v(p)$	$v'(p)$
M. dobsoni ..	0·0000338	0·001967	0·0000423	0·000574
M. affinis ..	0·0000798	0·00077	0·0001295	0·000338
P. stylifera ..	0·0000686	0·000451	0·000295	0·001305
P. indicus ..	0·0003859	0·005584	0·000661	0·006130

For all the species it is found that $v'(p)$ is greater than $v(p)$. This shows that the two sexes are distributed in greater patchiness in different months than expected by binomial theory.

x^2 tests have shown that the same sex ratio is not maintained throughout the fishing season in the case of the three species *M. dobsoni*, *P. stylifera* and *P. indicus*. Menon (1957) studying the inshore prawn fishery of Cochin area observed the occurrence of difference in the sex ratios of all these species as well as *M. affinis* especially in the larger size groups. It is possible that the difference in sex ratios observed may be due to an actual change brought about byinshore-off shore movements of these prawns as suggested by Menon (*op. cit.*). A close examination of Table I *a* will reveal that in the case of *M. dobsoni* the ratio of males is high in the fishing grounds in the months June and November–December. In other words females are less abundant here during these months. According to George (1962) these are the months of peak breeding season for this species in this area. Hence it is possible that this difference in sex ratio may be due to the movement of females in larger numbers to deeper waters for spawning. In the other species *P. stylifera* and *P. indicus* also the differential sex ratio can be explained to be due to breeding movements. In *P. stylifera* the female ratio is less in the exploited ground, as can be seen from Table I *c*, in October to December which is the peak breeding season of this species on the Malabar Coast as observed by Menon (1953). In the case of *P. indicus* the peak breeding months in Cochin area is November–December and February (George, 1962) when females are noticed to be less in the trawl catches (Table I *d*). However, it is interesting to note that in the case of *M. affinis* alone the x^2 value is non-significant thereby indicating that this species does not appear to segregate by sex in the trawling area. This apparent difference in this particular species may be due to the fact that the breeding of this species does not take place anywhere near the present area exploited by the trawl fishery, so that segregated movements for breeding does not take place in this ground. The insignificant number of post-larvae of this species in comparison to the others entering the backwaters near the fishing area further strengthen this point of view.

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NOTE ON GROWTH AND PROTANDRIC HERMAPHRODITISM IN THE DEEP SEA PRAWN, *PANDALUS BOREALIS*

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ABSTRACT

The deep sea prawn (*Pandalus borealis*) is a boreal species, in the Atlantic distributed from the Arctic Ocean to the waters off Scandinavia. This species is a protandric hermaphrodite, *i.e.*, the youngs are males which later change into females. In the north Atlantic the prawn shows great variations in growth and age of sexual maturing. In the far north the prawn matures into females when 5-year old, in the south when 2, 5-year old. The temperature surroundings seem to be the regulatory factor for growth and maturing. An year-class of prawns upon maturing may split into two fractions, one slow-growing retaining the male characters, the other fast-growing turning into females. The length distribution of such a divided year-class then shows two maxima.

THE deep sea prawn is a boreal species with a northern distribution (Fig. 1 & 2). This crustacean has a very complex life-history. Through the investigations by various authors in the 1930'ies it was

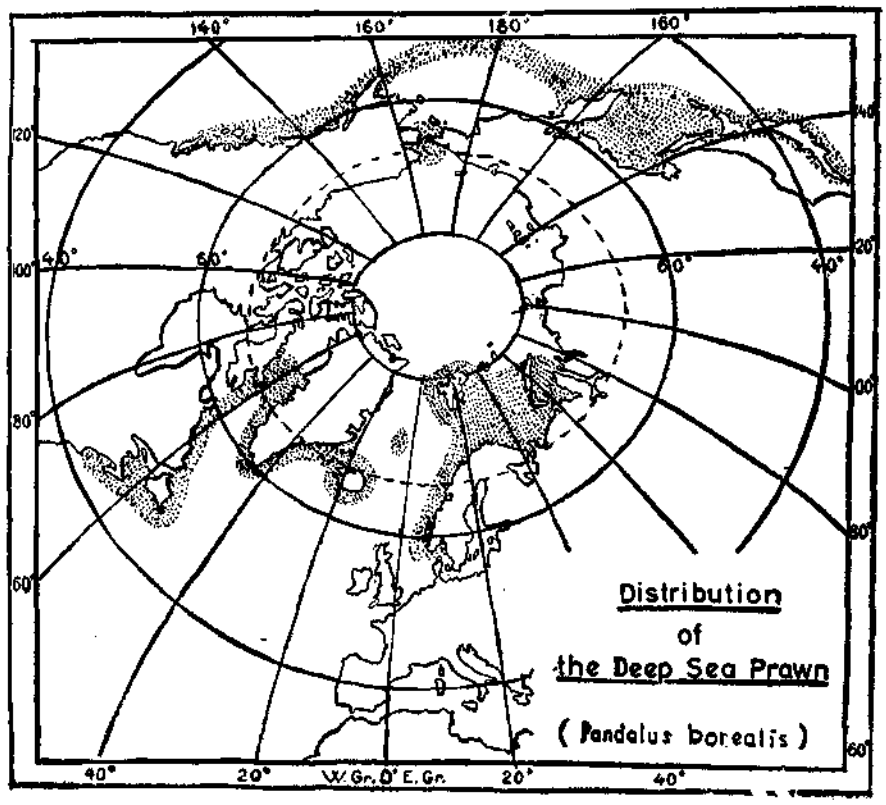

FIG. 1. Distribution of the Deep Sea Prawn, *Pandalus borealis*

discovered that the deep sea prawn was a protandric hermaphrodite, *i.e.*, this species had the ability to change its sex in such a manner that in early life the prawn acted as male and later on changed its sex and acted as female. Early investigations further indicated that the growth and sexual maturing of the prawn were largely uniform in all areas of its distribution, as for instance, on the Pacific Coast of Canada as well as in the Atlantic where the prawn stock off the Scandinavian countries were investigated. The general biological picture was that the deep sea prawn functioned as active male when 1, 5 years of age at a size of 90 mm, then changed its sex and spawned as female when 2, 5 years of age at a size of about 120 mm. Subsequent investigations by the present author proved, however, that the growth rate and the sexual development of the deep sea prawn in the Arctic regions of the Atlantic Ocean were much slower than in any of the areas previously investigated. For instance, in Spitsbergen waters (78° N. lat.) the prawn did not mature as males till 3 years of age, acted as male also in the fourth year and did not reach the female stage till 5 years old. The hypothesis was naturally born that the great difference found in the life-histories of these widely separated prawn populations was largely due to environmental factors. If such were the case several questions presented themselves. For instance, did there really exist a graded geographical variation in the growth and sexual development of the prawn in conformity with the theory that the farther north the prawns were found, or the colder the environment, the slower the growth and maturing? And if this were found to be the case, by which characters would such a graded variation be expressed in the different prawn populations?

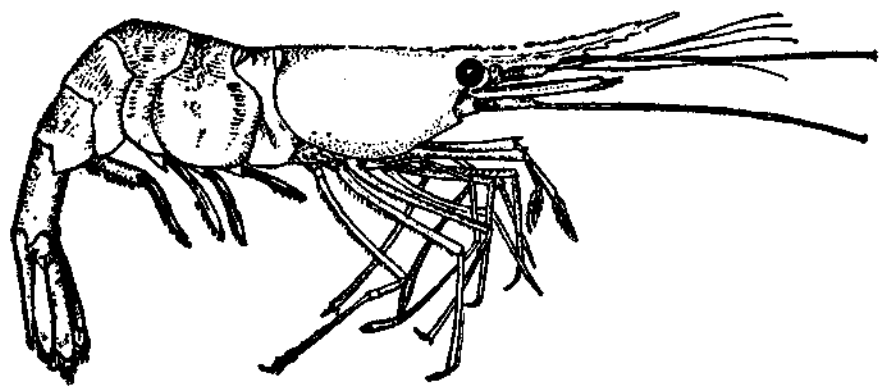

FIG. 2. The deep sea prawn (*Pandalus borealis*)

To answer these questions it was natural to pursue the investigations on the deep sea prawn on the hypothesis that in different latitudes from south to north we might be able to find prawn populations which by their pattern of growth and sexual development would form natural intermediate links between the prawns in the southern and northern area of distribution. Such investigations were carried out during the 1940' ies and the results emphasized the fact that it was necessary to revise any previous conception that the life-history of the deep sea prawn should be largely uniform in its whole area of distribution. Our investigations proved that the cycle of growth and maturing in the deep sea prawn varied not only from one locality to another, but also from brood to brood born in different years in one and the same locality. We also found indicated the basic rules for the reaction of the prawns towards changes in the environment.

The investigations proved that decreasing temperatures in the sea caused slower growth and retarded maturing in the deep sea prawn. This means that in the North Atlantic we will generally find more slow-growing and slow-maturing prawns the farther north we go. In Norway many prawn fields are situated in the so-called "threshold fjords," *i.e.*, deep inlets with a shallow barrier at the entrance. In these fjords we often find lower temperatures and salinities near the bottom than what is the case on prawn fields situated in open sea outside. The prawns in these threshold fjords can without regard to geographic latitude show a life-history approaching that of the slow-growing prawns in Arctic waters.

Also in respect to spawning of the deep sea prawn we find features which seems to conform to a certain pattern. In the southern part of the area of distribution the deep sea prawn spawns in October–November, the females carrying their eggs for about 5 months till they hatch the following March–April. However, in the extreme north (78° N. lat.) spawning takes place 3 months earlier than in the south, and the eggs hatch 2 months later the following spring, the ovigerous period in the Arctic thus lasting for about 9 months. Along the coast of Norway we find intermediate lengths of the ovigerous period, 7–8 months in Northern Norway decreasing to 6 months further south. The general rule seems to be that the colder the environment, the earlier spawning and the longer the ovigerous period.

In ordinary circumstances all individuals of a prawn population in the southern area of distribution have the tendency to spawn as active males at a size of about 90 mm. and age 1, 5 years, and as active females at a size of about 120 mm. and age 2, 5 years. But going succinctly northwards the prawns mature as respectively males and females much later in life. It is significant that in spite of the great difference in age when maturing, the size respectively of the males and females is largely the same in the different localities. There is obviously an intimate connection between the process of sexual maturing and the rate of growth in the different areas. The basic principle seems to be that a particular prawn population, or a single year-class, having a high rate of growth produce sexually mature males and females earlier in life than does a slow-growing population. The number of individuals within an age group maturing as respectively males and females is determined not so much by the age as by the size attained of the individual prawns.

The growth of the deep sea prawn has been studied by measuring the length of the individuals from samples collected at suitable intervals (Petersen's method). At the same time the prawns have been sorted as to sexual stage. A year-class of prawns 1, 5 years old may show a size distribution as shown in Fig. 3 "A", containing prawns 75–100 mm. in length with a mean size of 88 mm. This size group of prawns contain active males in late autumn. In Fig. 3 "B" a division of the age group has just taken place, one part having attained transitional characters into females, the other part retaining the male characters. The division of the age group does not occur at a sharply defined size. The male fraction and the transitionals form two separate groups which overlap in size. During the subsequent months the two fractions show a steadily increasing difference in mean size caused by the difference in rate of growth of the two (Fig. 3, "C, D, E").

The principle governing the mechanism of this division within an age group seems to be that the largest individuals of a size group will change into females, while the smaller prawns remain males. The very smallest individuals of a size group may even form a third fraction on the extreme left consisting of immature prawns. The division of an age group into different sex categories is closely connected with the attainment of a more or less definite size level. If for instance an age group has attained a mean size of about 80 mm. in autumn only a few individuals will mature as females. If, however, the mean size attained by the age group is 100–110 mm. perhaps 25–75% become females. Age groups of a mean size of 120 mm. in autumn will generally consist of females only. The lengths stated only indicate the trend of the sexual development.

The general rule seems to be that the largest males of an age group undergo the transformation into females first. The transition animals have in the following months an accelerated growth while those which remain males have a restricted growth. As a natural consequence we find after a while that for example a group of 2, 5 year old prawns can consist of two distinct size groups, one consisting of small males and the other of large females, but both of identical age (Fig. 3 "E"). If not closely followed they could normally have been mistaken as two different age groups.

Environment, rate of growth, and sexual maturing are closely connected factors which find their expression in the varied life-histories of the deep sea prawn in the many localities between the Arctic Ocean and southern Norway. The prawn can sustain life and multiply within a wide range of temperatures, submitting to local conditions, growing and maturing in conformity to laws laid down by nature. In temperate surroundings the deep sea prawn grows fast and matures early, in

the cold waters of the far north the prawn grows slowly and matures late in life, while in between we find prawn populations which in their life-history show intermediate links between the two

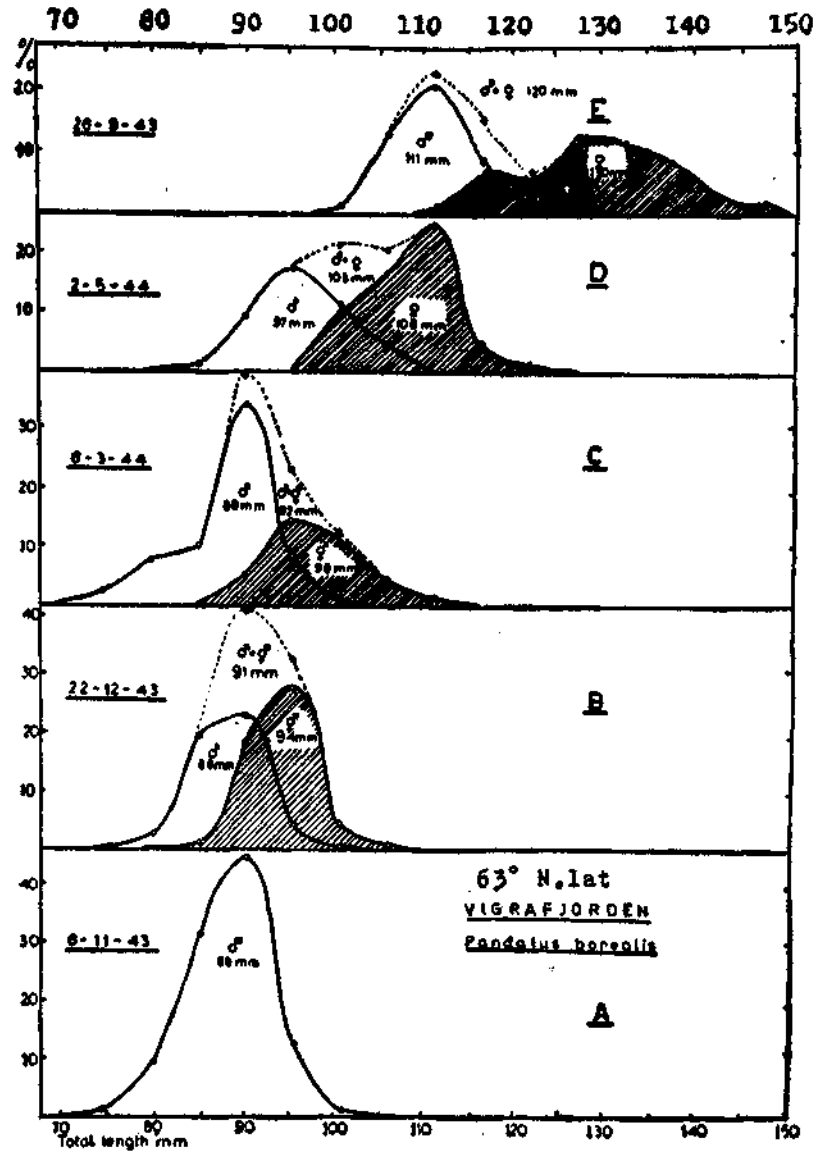

FIG. 3. Group of male prawns (A), the separation of a female fraction (B), and the subsequent growth of both fractions (C.D.E.)

extremes. Examples of this variation is shown in Fig. 4. From one growth type to another we find a natural transition expressed by a varied sexual division within the different age groups.

The variations in growth and maturing of the deep sea prawn will naturally influence the productivity and the renewal of the prawn stocks on the different fishing grounds, and thus also effect the commercial prawn fishery. In localities where the prawns have a slow rate of growth they will

become ovigerous relatively late in life, and produce few broods within a limited period of time, while in localities where the rate of growth is fast more broods are produced within the same period. If a prawn field with a high reproductive ability should be overfished the stock will recuperate in a short space of time, while localities with low reproductive rate would need a longer time to become remunerative again.

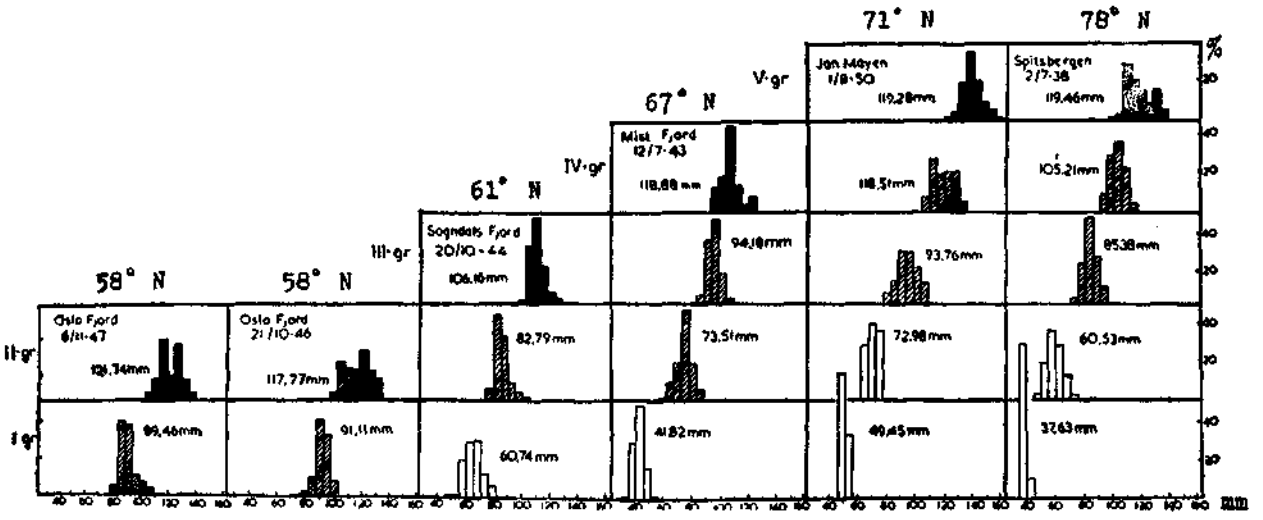

FIG. 4. The variations in age, size, and sexual development of the deep sea prawn in various localities along the Norwegian coast and in Arctic waters. White: youngs. Shaded: males. Black: females

The practical results of the investigations on the deep sea prawn indicate that certain prawn fields, particularly in Arctic waters, hardly can stand the same fishing intensity as those in southern areas. This biological aspect must be taken into consideration if protective measures should be contemplated.

DISCUSSION

Dr. J. H. Wickstead: Is the transition of males into females inevitable?

Dr. B. Rasmussen: We never get big males, or prawns being born as females. All males do turn into females at certain stage of growth.

Dr. J. H. W.: What about ecology of this prawn?

Dr. B. R.: These prawns are phototactic and they live on the bottom. When light fails to reach the bottom in the afternoon the prawns move up from the bottom. There is also migration due to spawning, which is preceded by shedding off their hard shells and as a protection they go away from the usual ground to the rocky bottom for hiding. Also cold current coming in can drive away the prawns for months together.

Dr. J. H. W.: Do the eggs hatch at the surface?

Dr. B. R.: We find them in the upper surface, *i.e.*, 100 meters from the surface in the ocean, though not exactly at the surface.

Dr. S. Jones: What is the maximum depth of occurrence of this prawn?

Dr. B. R.: About 600 fathoms.

Dr. A. L. Rice: What is the variation in temperature in winter? Whether temperature fall has anything to do with maturing?

Dr. B. R.: Variation in temperature is very little in winter; it seems to be due to the great depth and also due to the effect of the Gulf stream. A certain drop in temperature has no effect on the breeding but low temperatures in far north retards maturation.

Mr. K. H. Mohamed: What changes take place in gonads?

Dr. B. R.: The testes entirely change into ovaries and there is no vestigeal testes left.

Mr. P. Vedavyasa Rao: Whether there are any differences in the growth rate between the sexes?

Dr. B. R.: Yes. When they become females, the growth rate is very slow, because soon they spawn the eggs which are to be carried between the pleopods for about 5 months till the eggs hatch.

Mr. K. N. Sankolli: Are there other examples of such protandric prawns?

Dr. B. R.: Yes. There is another species *Pandalus montagui*. Probably there are other species mentioned in literature that I am not of aware.

Dr. A. L. Rice: What is the factor affecting this change in sex?

Dr. B. R.: Probably the only factor is growth rate and attainment of a certain size.

ON THE PROBLEM OF REPRODUCTION MECHANISM RELEVANT TO STOCK ASSESSMENT OF KING CRAB

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ABSTRACT

In the king crab fisheries, off the western Kamchatka, young male crabs have been caught mingled with commercial size crabs. The young are legally prohibited from catching. In the previous report of the writer, he intended to show some dynamical problems relevant to catching the young male. Conclusions are following: (*a*) indices of abundances of commercial size crabs have no correlation with those of the young, and (*b*) catching the young seems not to be effectual in cannery production from the standpoint of population dynamics.

The biological patterns of life-cycle of king crabs of the young as well as of the commercial size were not taken into account in the above analysis. The writer, here in this report, intends to analyse relationships between the abundances of king crab resource off the western Kamchatka and the density distributions of the young male crabs by age, based upon the more biologically significant information which are broken down by season and area not only from data of Japanese fisheries but also of Russian. Though age determination is not so precise yet, abundances of the young by age are estimated and introduced into analysis.

INTRODUCTION

IN the king crab (*Paralithodes camtschatica*) fisheries off the western Kamchatka, young male crabs have been caught mingled with commercial-sized crabs, although the young are legally prohibited from catching. In the previous report of the writer, he attempted to show some dynamical problems relevant to catching the young male. The conclusions are as follows: (1) indices of abundance of commercial-size crabs have no correlation with those of the young, (2) catching the young seems not to be effectual in cannery production from the standpoint of population dynamics, and (3) it is, however, reasonable to use them for canning if the young be fallen to death to the bottom of the net.

The biological patterns of life-cycle of king crabs, the young as well as the commercial-size, were not taken into account in the above analysis. The writer, here in this report, intends to analyse relationships between the abundances of king crab resource off the western Kamchatka and the density distributions of the young crabs by age, based more on the biologically significant information which are broken down by season and by area not only from data of Japanese fisheries but also from those of Russian fisheries. Though age determination is not so precise yet, abundances off the young by age are determined by trial and introduced into analysis.

SECULAR VARIATIONS OF DENSITY DISTRIBUTIONS OF YOUNG MALE CRABS COLLECTED BY JAPANESE AND RUSSIAN FISHERIES

Young male crabs which have carapaces less than 13 cm. length are prohibited from being fished, but a great part of them are most likely to be mature. That is why they are taken by gill nets as they migrate in the same way as commercial-size crabs do off the western Kamchatka. An index of abundance of the young can be obtained from the catch per unit effort. This can be calculated from records of scarting net; not however, from commercial fisheries where the young

caught should be released into the sea. Indices of abundances by region thus obtained are shown in Table I. There are four regions in the fishing ground off the western Kamchatka. Fishing seasons are classified into three, which are determined by the different phases in the life-cycle of king crab. They are the phase approaching the coast, the spawning phase and the migrating phase to feed after spawning. Figures in Table I are indices only in spawning season which is the best season in representing an index of abundance.

TABLE I

Variations in indices of abundances of young male crabs by year and by region in the spawning season, from data collected by Japanese scarting nets

Year	Region			
	Kafran	North	Middle	South
1958	4,644	9,843	1,220	..
1959	13,474	1,142	1,155	..
1960	8,411	2,681	1,273	..
1961	10,594	3,119	2,738	..
1962	4,835	402	234	..

Indices of abundance of commercial-size crabs are calculated from both commercial nets and scarting nets. They are shown in Table II. Correlations are found between indices from scarting net and from commercial net. Therefore it is reasonable to accept to adopt the indices from scarting net as indices of abundance.

TABLE II

Variations in indices of commercial-size crab's stock calculated from scarting nets of Japan and from commercial nets of Japan and Russia

Year	Scarting net					Commercial net	
	Kafran	North	Middle	South	Total	Japan	Russia
1958	5,267	3,669	942	..	9,878	6·7	11·6
1959	19,411	2,222	2,042	..	23,675	8·8	12·8
1960	8,984	8,048	2,058	..	19,090	11·6	13·2
1961	12,682	3,346	2,896	..	18,923	11·7	14·3
1962	6,234	775	807	..	7,816	11·6	16·2

Russian research vessels also collect data on young crabs by trawl nets and the results about the index of abundance by region are shown in Table III.

It has been discussed to put forth the view that we cannot find out correlations between indices of abundance of the young and of the commercial-size. In the next step of analysis, we have to discover the reasons why there are no correlations. It occurs to the writer that there are three reasons to cause such a non-coincidence, in spite of the necessity of there being correlations from the biological standpoint. The first one is that young crabs distribute in different grounds from commercial-size crabs. The second is that grounds to be scarted or investigated are not same as those

TABLE III

Variations in indices of densities of younger crabs caught by trawl nets of Russian research vessels

Year	Region					Mean
	Hiryuzof	Northern Sanctuary	Ycha	Korpakof	Kiftiku	
1957	229	496	231	78	3	194
1958	346	127	45	79	41	68
1959	95	174	99	16	5	79
1960	25	22	22	48	47	29
1961	36	63	30	38	7	28
1962	73	51	26	15	1	20

to be operated by commercial vessels. The third is that age composition is not considered though the young consist of three or more age groups. In the successive sections the writer tries to discuss the third point. The other points are also important but it is impossible to derive conclusion here because of insufficiency or lack of data.

AGE COMPOSITION OF YOUNG MALE CRABS CAUGHT

The method of age determination of crabs is not clarified completely yet, but we can estimate the age composition roughly from width of carapace. Estimated age composition is shown in Table IV, represented in per cent. by year and by region in the spawning season.

TABLE IV

Age compositions in per cent. of younger male crab by region, in the spawning season

Region	Kafran				Northern				Middle				Southern			
Maturity	Immature	Mature			Immature	Mature			Immature	Mature			Immature	Mature		
Year \ Age	4	5	6	7	4	5	6	7	4	5	6	7	4	5	6	7
1958	16	44	23	17	2	15	38	45	0	6	35	59	0	0	0	100
1959	7	28	32	27	0	19	45	36	0	13	38	49	..	..	..	..
1960	5	47	27	21	1	33	38	28	0	10	29	61	0	6	22	72
1961	0	17	50	33	0	18	46	36	0	10	34	56	0	1	49	50
1962	0	21	57	22	1	19	42	38	0	10	34	56	..	..	..	..

Indices of abundance of young crabs are known as indicated in Table I. So we can calculate the indices by age from Table I and Table IV combined. Results thus obtained are shown in Table V.

TABLE V

Indices of abundances of young crabs by age

Year \ Age	5	6	7
	(*a*) Kafran		
1958	2,043	1,068	789
1959	3,773	4,312	3,638
1960	3,953	2,272	1,766
1961	1,801	5,297	3,496
1962	1,015	2,756	1,064
	(*b*) Northern		
1958	1,476	3,740	4,429
1959	217	514	411
1960	885	1,019	751
1961	561	1,435	1,123
1962	76	169	153
	(*c*) Middle		
1958	73	427	720
1959	150	439	566
1960	127	369	777
1961	274	931	1,533
1962	23	80	131

Graphical representations of annual changes of indices by year-class are revealed in Fig. 1, which indicates that the same trend is absent in annual variations within any year-class and in any region.

ABUNDANCE OF COMMERCIAL-SIZE CRABS AND THEIR RELATION TO YOUNG MALE CRABS BY AGE

In recent years indices of abundance of the young male seem to decrease year-by-year as indicated in Table I. Especially the decreases are remarkable for the year 1962 and in the northern and middle regions. As described in the previous report and also in the above sections of the present report, no correlation has been found either between indices of the young male and those of commercial-size in the succeeding years or among the indices of the young male by age for the same year-class. In this section an attempt has been made to establish whether or not there is a relationship between indices of the young male by age and the commercial-size in the succeeding years.

Although commercial-size crabs consist of many age groups, their age compositions are not taken into consideration because age determination is more difficult here than in the young.

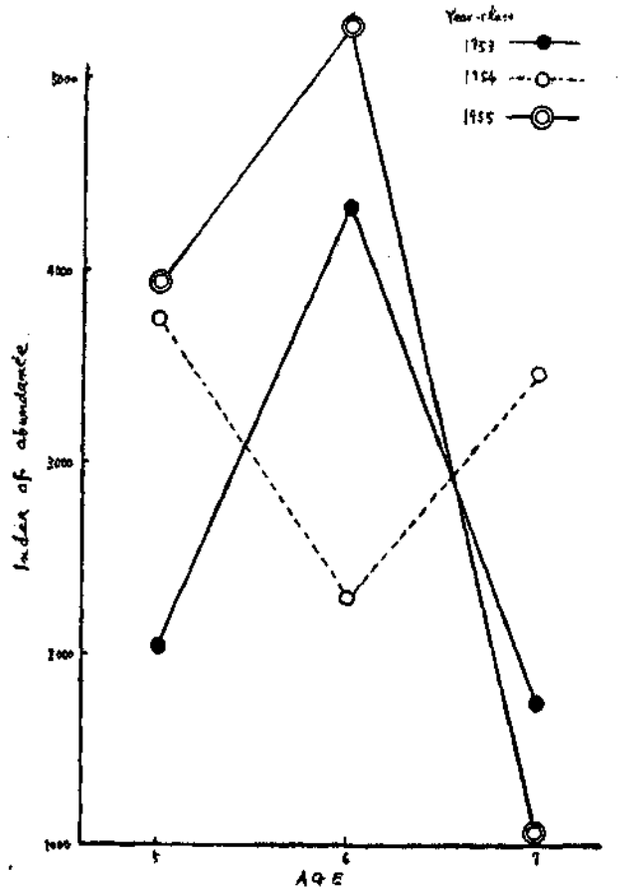

FIG. 1*a*. Annual changes of indices by year-class

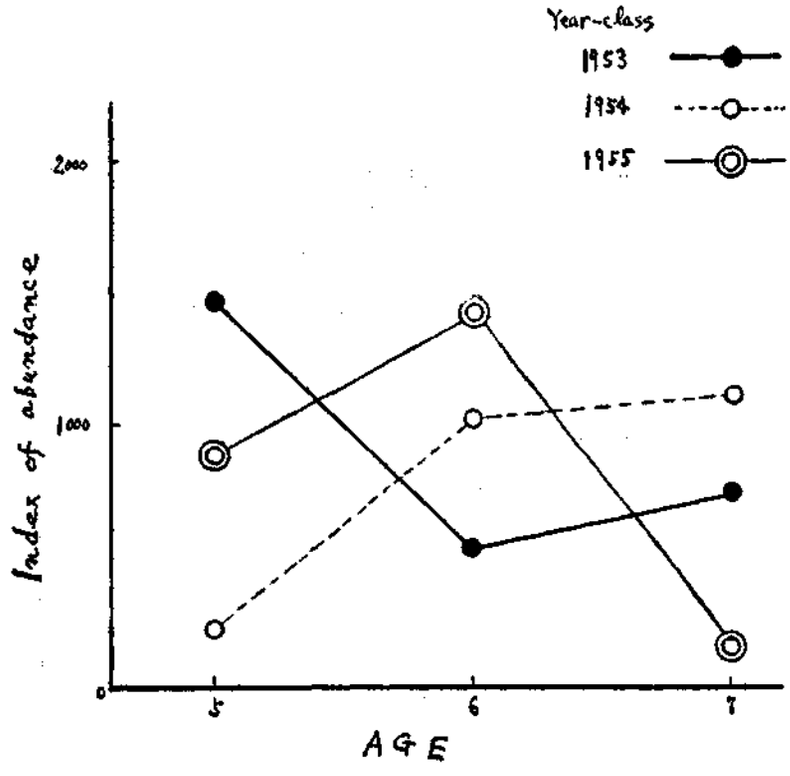

FIG. 1 *b*. Annual changes of indices by year-class

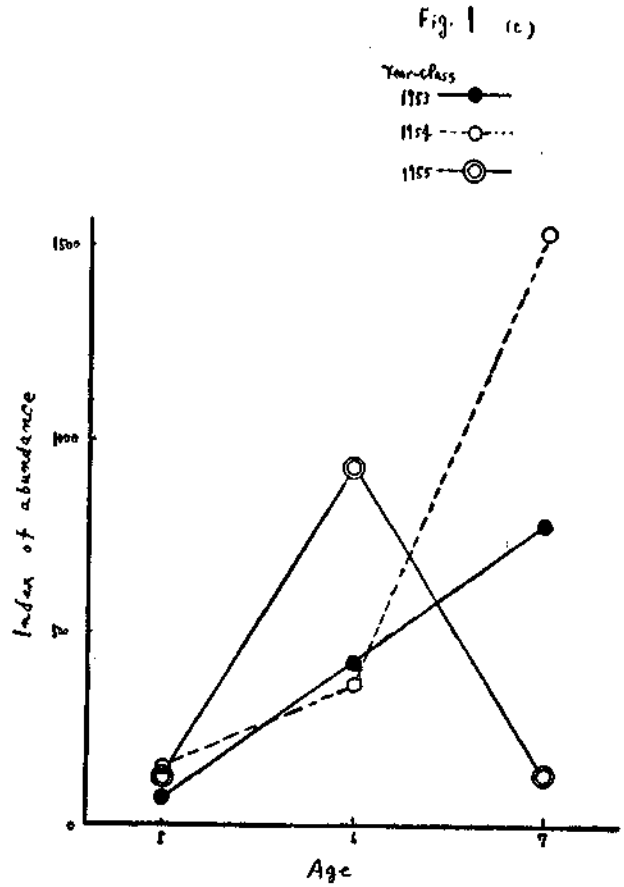

FIG. 1 *c*. Annual changes of indices by year class

Commercial-size crab's indices are compared with those of 7-year group in the preceding year which are indicated in Table V. Scatter diagrams are shown in Fig. 2.

Generally speaking the quantity of the adults could be expected to be larger when the quantity of the young is large. However, from the scatter diagram (Fig. 2) no positive and significant correlations could be found. On the contrary, they seem to be negatively correlative. Such a result would allow the following inferences about catching the young, its effects on commercial fisheries and mechanism of reproduction. First, it can be assumed that young male crabs segregate from commercial-size crabs. Therefore, indices of abundances of the young are not significant and representative, because they were calculated from data of scarting nets operated in commercial fishing grounds. In other words, scarting nets do not cover the overall grounds of the younger. Secondly, if a negative correlation would be true, the real amount of the young seem to be almost the same year by year. The catchable stock of the young is only a part of the true amount and therefore the remnant which will recruit next year is negatively correlative. That is, when indices of the young caught by scarting nets is small, recruitment for next year is abundant, and *vice versa*. Thirdly, if it would be true that there is no correlation between both abundances, the reason for this suggestion remains unknown. Perhaps unknown factors influence natural mortality in different degrees year by year.

However, the present findings are different from those described in the previous report in spite of adopting all available biological and other data. In a word, apparent indices of both stock size

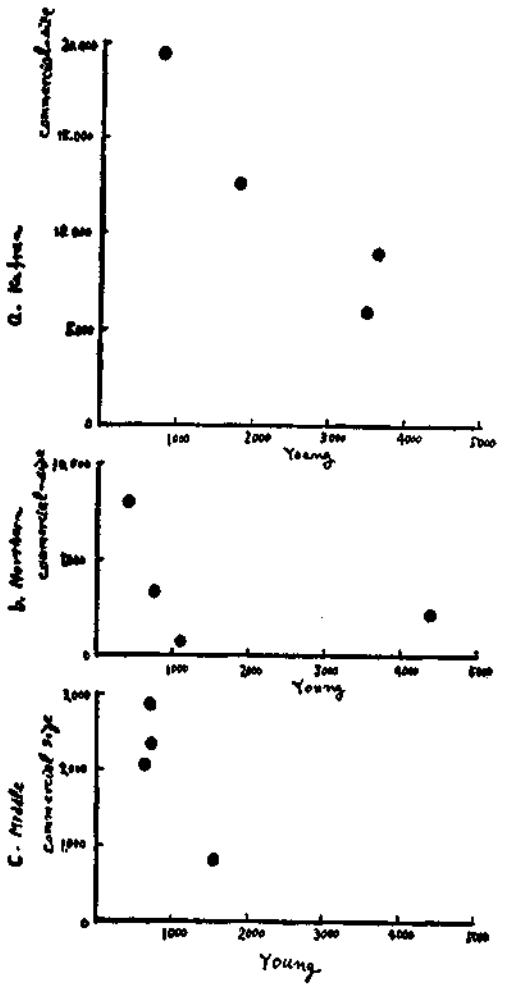

FIG. 2. Relationhips of stock indices between 7-age group crabs and commercial-size crabs. (*a*) Kafrau district, (*b*) Northern district, (*c*) Middle district

are indifferent with each other. This is very important in predicting the future state of king crabs. Based upon results obtained, it is impossible to predict amounts of commercial-size crabs from information available about young crabs.

CONCLUSION AND DISCUSSIONS

Generally speaking, information on abundance of young stage of aquatic resources is very important and useful in order to predict the future state of the population and to manage the fisheries on the level of optimum regulations. Aiming at the same prospect for king crabs exploited off the western Kamchatka, the writer has tried to obtain relationships between abundance of commercial-size crabs and those of young male crabs in this report. All available biological and other data, that have been treated here are broken down into ages, seasons and regions from both Japanese and Russian investigations. Results here obtained are not same as expected, but rather contrary to what are expected. Information clarified here and results obtained by analysis are as follows:

(1) Secular variations of density distribution of young male crabs by region in the spawning season as evidenced from the data collected by Japanese scarting nets as well as by trawl nets of Russian research vessels (*see* Tables I to III).

(2) Age composition of young male crabs caught, indices of stock sizes of the young by year-class and by region (*see* Tables IV and V).

(3) Comparing indices of stock size of the young with those of commercial-size crabs, we cannot find a positive correlation, but in some cases they seem to be negatively correlative. This finding may allow several inferences about survival process of the young and reproduction mechanism of king crabs.

(4) In future study, it is necessary to treat the problem through under-estimation of age composition of commercial-size crabs as well as by developing the method of estimation of true index of the young.

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THE MORPHOMETRY OF SEXUALLY MATURE INSTARS IN THE CRAB *PORTUNUS SANGUINOLENTUS* (HERBST) (BRACHYURA: PORTUNIDAE)*

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ABSTRACT

Morphometric and morphological criteria are established for the determination of two sexually mature instars in females and three in males of *Portunus sanguinolentus* (= *Neptunus sanguinolentus*), a commercially important species of the Indo-West Pacific fauna. Data were obtained from two years of collection at selected stations in Kaneohe Bay, Oahu, Hawaii. Morphometric and morphological changes were ascertained from crabs which molted in captivity. Criteria of sexual maturity in males were verified by breeding experiments.

Crabs of the last female juvenile instar had a mean carapace length of 42·9 mm. and underwent the pubertal molt to the first mature instar with a mean length of 50·2 mm. followed by a molt to the second mature and terminal instar with a mean length of 56·6 mm. In the males, sexual maturity was less apparent; spermatozoa and spermatophores were observed in portions of the reproductive tract before the remainder of the tract was functional. The most reliable external indicator of sexual maturity in males was the coloration of the chelae which are ox-blood red in mature instars. Mean lengths of three sexually mature male instars were 43·9, 52·4 and 61·1 mm. respectively.

RELATIVELY little is known about the life-history of the edible Indo-Pacific crab *Portunus sanguinolentus* (Herbst). This paper reports on a portion of an overall study of the reproductive aspects of the biology of this species (*see* also Ryan, 1967 *a*, 1967 *b*). Knowledge of the distinguishing characteristics and size relations of sexually mature individuals is of particular importance in the study of commercially important crustaceans. Such knowledge may be utilized in further studies on the life-history of a species and aid in the development of its fishery. In this report, the distinguishing morphological features, instar number, and morphometric relationships are determined for the last juvenile and the sexually mature instars of *P. sanguinolentus* in Kaneohe Bay, Island of Oahu, Hawaii.

Much of the literature concerning *P. sanguinolentus* in the Indo-West Pacific is taxonomic in nature or records its distribution in a 'particular' region. Some work on its life-history in the Indian Ocean has been reported, principally by Menon (1952) on the life-history of the species along the Malabar Coast of India. Notes on its life-history are also given by Prasad and Tampi (1952, 1953) along with two other portunid species, *P. pelagicus* and *Scylla serrata*. Chhapgar (1956) included *P. sanguinolentus* in a study of breeding in several species of Indian crabs. Earlier, Naidu (1955) had described the first zoeal stage.

In the classic life-history studies of crabs, many give descriptions of sexually mature characters but few present morphological features to accompany morphometric data of instar sizes. Since growth in crustaceans only occurs immediately after ecdysis, the growth record of any individual consists of a series of steps, each step representing a stage or instar. The number of instars is thought to be fairly consistent for each species and individuals which have reached a particular instar are considered to be in the same stage of their life-history (Tyler and Cargo, 1963).

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* The data upon which this paper is based is a part of a thesis to be submitted to the Graduate School, University of Hawaii, in partial fulfilment of the degree of Doctor of Philosophy. Contribution No. 217, Hawaii Marine Laboratory (Present name: Hawaii Institute of Marine Biology).

There are a number of methods of determining growth and instar number in crabs, each with attendant difficulties. MacKay and Weymouth (1935) point out some of the difficulties in determining the number of instars in crabs. Some workers (Démeusy, 1958; Van Engel, 1958, etc.) report success in rearing individuals from the first crab stage and recording the number of instars in this manner. Size frequencies in large numbers of crabs are considered by MacKay and Weymouth (1935) to be satisfactory estimates of only the early crab stages because there is considerable overlapping of size. Caution against the use of captive molts is pointed out by MacKay and Weymouth (1935) and Hiatt (1948) who found that the effects of captivity adversely influence size increases at ecdysis. Since tags are either lost at molt or impair molt, tagging studies can only yield negative evidence.

However, if morphological features are extant in a species which identify one or more instars, then careful before and after molt measurement data of crabs caught just before molt may be used to complement measurement data of field collections of the identified instars. In such a way, four male instars and three female instars are compared morphometrically in *P. sanguinolentus* in this study.

Taxonomy and Distribution

Taxonomy of the genus *Portunus* is complicated by the fact that the generic name was used for two distinctly differing genera of crabs. The confusion was cleared by Opinion 394 of the International Commission of Zoological Nomenclature (1956) in which the name was retained for the genus *Portunus* Weber, 1795. The decision rejected the names *Lupa* and *Neptunus*, both of which appear in the synonomy as generic names for *Portunus sanguinolentus*. Crabs of the family Portunidae are widely distributed in temperate and tropical seas. Portunids are distinguished by having the dactyls of their 5th pereiopods enlarged and flattened which facilitate swimming. In the Indo-Pacific, the genus *Portunus* generally includes those of the family which have nine antero-lateral spines, the last of which is enlarged. *P. sanguinolentus* (Fig. 3 A) may be distinguished from all other species of the genus in its range by the presence of three large blood red spots on the posterior border of the carapace. For a complete description and synonomy, one is referred to the work of Stephenson and Campbell (1959).

P. sanguinolentus is widely distributed in the Indo-West Pacific. From Hawaii, the range of the species extends to Japan, China, Australia, India and East Africa (Forest and Guinot, 1962), although its absence is noted from many island chains. The species was early reported from the Adriatic, presumably introduced through the Suez Canal (Peters, Panning and Schnakenback, 1933). In many areas, it supports a modest fishery, particularly in Australia (Hale, 1927), India (Rai, 1933; Menon, 1952) and Hawaii.

Methods of Research

The crabs used in this study were collected by traps from the waters of Kaneohe Bay, Hawaii, during the period from January 1962 to June 1964. The traps were made of galvanized woven wire and similar in design to an Atlantic lobster pot. They were baited with trash fish, usually tuna heads, and placed in tandem in water 5–15 M. deep. During this period, the traps were down almost constantly. As the crabs were brought to the laboratory for study, they were kept in floating cages. Each cage was approximately 1 M. square and 1·5 M. deep. Many of the crabs were collected while in early or late pre-molt stages. During this study 233 females and 138 males molted in the live cars.

The crabs were observed daily and as the day of molt occurred, individuals were moved to isolation cages where ecdysis occurred and were kept there for 5–7 days before measurements were taken for comparison with those of the exuvia. However, only the measurements of those which

molted within five days after capture were selected for the morphometric portions of this study. The other crabs were utilized for comparative purposes or breeding experiments.

Measurements were made with dividing calipers and compared with a measuring board graduated to the nearest 0·5 mm. In the literature, crab measurements are usually expressed as carapace width or length. For several reasons, carapace length was used as the reference measurement. Gray and Newcombe (1938) and Tyler and Cargo (1963) considered length the better measurement in *Callinectes sapidus* which has a similar carapace outline. The carapace width could often not be taken with accuracy since the distal points of the 9th antero-lateral spines were broken. Also it is considerably more efficient to measure length than width in an active live crab. Carapace length is defined as the straight-line distance from the notch in the front to the posterior border of the carapace and does not include the curvature of the carapace. Colors were compared with the standard colors of Ridgeway (1912).

In order to obviate a consideration of many populations or size differences due to environmental effects, all trapping stations were within a semicircular end of Kaneohe Bay, the open outer edge of which is partially obstructed by Coconut Island upon which the Marine Laboratory is located. Maximum distance between trapping stations was approximately 2 km. Continuous water temperatures were recorded at the Laboratory next to the live cars. Mean monthly temperatures during this period varied from 23·7 to 27·7° C. Water temperatures of the open Bay were only taken occasionally and never varied more than 1° from that at the Laboratory dock. Although there was a slight peak in molt frequency during summer months (May to August), ecdysis commonly occurred at all months of the year.

Results and Discussion

Sexual Dimorphism

Sexual dimorphism in *P. sanguinolentus* is similar to that of other crabs. Sex is readily distinguished in larger individuals by the shape of the abdomen which is narrow and has the shape of a 'T' in males, while that of females is wide and its segments freely articulated. Sex is not readily distinguished, however, in early crab stages without microscopic examination. As Shen (1935), Hiatt (1948) and others have found, it is impossible to distinugish sex by abdominal shape in smaller crab stages. It was observed, from the first crab stage, that female *P. sanguinolentus* could be recognized by the presence of the paired oviduct openings which appear on the sternites of the 6th thoracic segment, lateral to the abdomen. In progressively larger juvenile females, these "move" beside and then under the abdomen as the abdomen widens in larger instars and the sternal depression similarly widens to accommodate it. The openings are particularly noticeable in small females which are collected from silty bottoms and the silt-filled openings contrast with the white undersurfaces of the crab. Additional sexual differences were noted in the coloration of the chelae and carapace, setation of abdominal appendages, placement of gonoduct openings, etc. These are discussed below.

Molt of Puberty

Males.—In crabs there are certain morphological features which are present in full expression at sexual maturity. These include not only ones which are associated with copulation itself but also others which are recognized as secondary sex characters. In the case of certain ones, *e.g.*, abdominal shape, their presence may be noted before maturity is reached, whereas in others, the conditions appear at a single molt. This molt was first designated as the molt of puberty by Perez (1929). Morphological features of the latter category may be determined by comparison of larger reproducing crabs with juveniles. These may be further verified when juvenile crabs are kept in captivity through the molt at which these features are attained.

Pubertal changes in males include the color of the chelae and other pereiopods, lengths of the pereiopods and lengths of the first pleopods relative to the sternites in the sternal depression. The

most accurate external determinant of sexual maturity in male *P. sanguinolentus* is the color of the chelae. Such color difference is known for *Callinectes sapidus*, a similar portunid, as an example of sexual dimorphism (Hopkins, 1963) but no mention is made in the literature that male *Callinectes* acquire the color in one molt although this author's unpublished observations show this to be the case in *Callinectes* as well as in *P. sanguinolentus*. Similar observations probably could be made for many other species.

The distinctive color of the male chelae is located principally on the inner surface of the dactylus and propodus (Fig. 3 B). In juveniles of both sexes, the color of the inner surface of the fixed finger is white with an amber spot at the base of the teeth. The proximal half of the dactylus is colored oxblood red. A mottled area of the same oxblood red is found on the inner surface of the proximal region of the propodus near its articulation with the carpus. At the molt of puberty, verified by breeding experiments, a patch or spot of oxblood red appeared on the inner surface of the fixed finger of the propodus. The patch or spot is not of consistent shape. It may exist as one or more transverse or horizontal bands. At the next molt, the color extends completely over the inner surface of both the dactylus and propodus. This sequence of color change through three instars was observed without variation, except in regenerated chelae, in 27 individuals and one or more of the molts observed in 96 individuals. The three color phases of the male chelae are hereafter designated "white", "spot" and "full" (Fig. 3 B). There is one more molt following the one in which the full color is reached (or full-1 and full-2). The last two instars are morphologically indistinguishable.

Although the size and shape of the colored spot varied from individual to individual, in no case did a white individual molt to full-1. The degree of color varied somewhat, approximating the colors burnt lake to oxblood red (Ridgeway, 1912). Crabs kept in captivity for extended periods usually had washed-out colors. There was one aspect of the color change which indicated that it may be under hormonal controls associated with onset of sexual maturity. If a white clawed male regenerated an automized chela, at the next molt, the regenerated chela was full colored or one phase ahead of the unregenerated cheliped which had the spot. At the molt following, both chelae were full.

Puberty in males may also be indicated by the size of the first pleopods. Prior to onset of maturity, the first pleopods gradually increase in length at the molts of the juvenile instars (Shen, 1935). The first pleopods of white crabs do not extend beyond the suture between the 6th and 7th sternites. After molt from the white condition, *i.e.*, in spot, full-1 and full-2, the pleopod extends to the hooks in the center of the 6th sternite. At the same molt at which the chelae attain the spot the 2nd and 3rd pereiopods also attain a purplish color on their anterior surfaces.

The absolute test of sexual maturity in males is copulation with impregnation of spermatophores into the seminal receptacles of the female. Many authors (Hiatt, 1948; Butler, 1960, etc.) have examined the reproductive systems of males and considered the presence of spermatozoa and spermatophores to be criteria of sexual maturity. In male *P. sanguinolentus*, spermatozoa and spermatophores are found in the testis and anterior part of the vas deferens of males in the white instar. Fifteen attempts were made to induce white males to copulate with newly molted females. None effected copulation. In six cases, these molted to the spot instar several days later, after which they copulated when presented to newly molted females. Spermatophores were found in the receptacles of the female in each case. The presence of spermatozoa in juvenile males has also been reported for oxyrhynchous crabs by Hartnoll (1963).

Females.—Onset of sexual maturity is explicit in female crabs. In contrast with males, passage of a female through the pubertal molt is indicated by gross morphological changes, particularly of the abdomen and accessory reproductive structures. The prominence of these changes at onset of sexual maturity in females led to the concept of the pubertal molt by Perez (1929). Because of the distinctness of sexual maturity in females, it is easier to calculate the number of mature instars. In female crabs, as in males, this number varies from species to species. In oxyrhynchous crabs

(Hartnoll, 1963), the pubertal molt is that of the terminal instar. While within cancroid crabs and in different species of the family Portunidae, the pubertal molt in females may be followed by one, two or several instars.

The most prominent pubertal change in female *P. sanguinolentus* is the change from a triangular abdomen to one of semicircular outline. All of the abdominal segments become freely articulated and are bordered by short stiff setae. When a female approaches the pubertal molt or a molt from one mature instar to the next, the dorsal surfaces of the abdominal segments assume a dark blue-gray color. After molt, this color gradually disappears as the principal layer of the exoskeleton becomes fully calcified and the abdomen appears similar to the other white undersurfaces of the crab.

When the abdomen of the female is lifted, there are other structures which readily indicate maturity. The oviduct openings, slit-like in a juvenile, are rounded soft ovals in the exoskeleton with distinct lips of soft cuticle. In juvenile females, and in males, the abdomen is held tightly against the sternum by a pair of hooks on the sternites of the 6th thoracic segment. Another change associated with reproductive functions accompanying the pubertal molt is that of the setation of the abdominal appendages. At this molt, the pleopodal endopodites attain their clusters of long silky setae on each segment. The eggs become attached to these at ovulation. The pinnate setae of the pleopodal exopodites are short and in two single rows on opposite sides of the appendage. Female *P. sanguinolentus* are carried by an adult male before molt and copulation usually occurs within a few minutes after the female extracts herself from the exuvia.

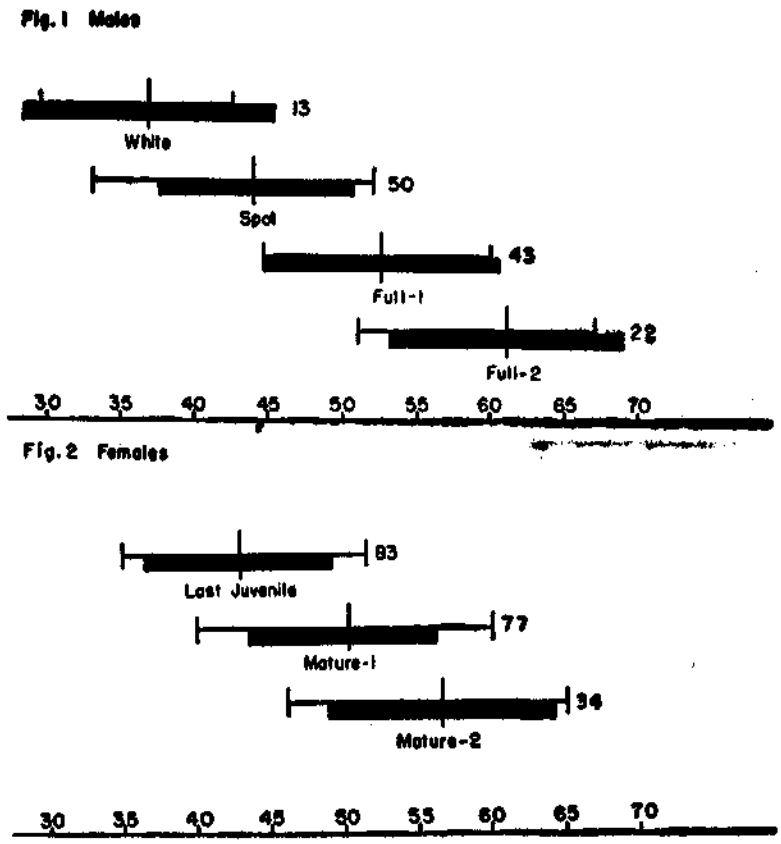
Evidence of these morphological features of sexual maturity may be detected in pre-molt juveniles two weeks or so before molt actually occurs. Particularly prominent of these is the coloration of the abdomen and the new oviduct openings whose outlines may be seen surrounding the small slits of the juvenile female. The golden color of the pleopodal setae may also be seen through the exoskeleton prior to molt.

In contrast with *Callinectes sapidus*, a similar protunid, the pubertal molt in female *P. sanguinolentus* does not occur as the final molt. Data presented below show that there is one more molt which precedes the second mature or terminal instar. Similarly two mature instars were noted by Drach (1933) for *Macropipus puber* (= *Portunus puber*) based solely upon morphometric data. It is possible to distinguish if a female is in the first or second mature instar. The 6th abdominal segment of the latter has more rounded borders although this roundness is difficult to define. Specifically, a difference is noted in the width of the 4th and 5th abdominal segments which become sufficiently widened in the second mature instar to cover the lateral borders of the 8th thoracic sternites (Fig. 3 C, D). This condition was observed in 58 females which molted from one mature instar to the next while in captivity.

Morphometry of Sexually Mature Instars

Males.—Carapace measuement data of the last four male instars are summarized in Table I. As shown in this table, there is a wide range of size within each instar. The range may be almost 30% of the mean size. Crabs of the last juvenile instar range in size from 29·5 to 42·5 mm. long (mean 36·9), those of the spot instar from 36·0 to 49·5 mm. (mean 44·0 mm.), those of the first full instar from 44·0 to 59·5 (mean 53·9), those of the second full color instar from 51·0 to 67·0 mm. (mean 61·1 mm.). In the case of the last instar, the measurement data are only those of crabs which molted in captivity. The other instars provided opportunity for comparison of length data from captive molts with field collections of crabs in the same instar. In this way, spot crabs which molted from white exuvia could be compared with spot exuvia which molted to full-1 and so on. In each of these group comparisons there was not a significant difference in the means.

Overlapping of size ranges for these four male instars is shown graphically in Fig. 1. To be noted is that in each instar, except the last, crabs of mean length are of sizes similar to larger indi-



FIGS. 1 and 2. Comparison of size ranges of last juvenile and mature instars of *P. sanguinolentus*. Carapace lengths, mm. Fig. 1. Males. Fig. 2. Females. Based upon data of Tables I and II. Heavy line indicates size range within 2 std. dev. ± mean (center crossline). Numbers of individuals at right.

viduals of the preceding instar and smaller ones of the instar following. Overlapping is still present when one attempts to interject statistical probability into estimates of instar size. If the size range of two standard deviations ± the mean is used ($p = 0{\cdot}05$), there is still overlapping. This emphasizes the difficulty of gauging instar number on size groups alone.

In his note on *P. sanguinolentus*, Menon (1952) estimated the number of instars based upon size frequencies. Unfortunately, the data were not differentiated according to sex. From his data, he concluded that there were seven instars represented in crabs larger than 40 mm. but cautioned against accepting this number without rearing studies.

The possibility exists that the full colored crabs which molted in the live cars may include more than one instar. Evidence that this is not the case and that there are only two full color instars may be concluded from several aspects of the data. First, the difference in the length data of full colored crabs which molted from spot crabs is not significantly different from the length data of full color exuvia. If the full colored exuvia measurement data include more than one instar, the range of size would have been greater and the mean size would have been significantly larger than that of full-1 crabs which molted from spot exuvia. Secondly, the coefficient of variation of full color

TABLE I

Carapace length data—Male instars of P. sanguinolentus

Instar group		No. Indiv.	Size range	Mean	Coef. var.	Remarks
			mm.	mm.	%	
White	1	13	29·5–42·5	36·9	8·4	Molted to Spot (2)
Spot	2	13	33·0–49·5	43·4	8·1	From White (1)
	3	16	38·5–52·0	44·3	7·8	Molt not successful
	4	21	36·0–49·5	44·0	7·5	Molted to Full-1 (5)
Full-1	5	21	46·5–56·5	51·9	6·9	From Spot (4)
	6	22	44·5–59·5	53·9	6·6	Molted to Full-2 (7)
Full-2	7	22	51·0–67·0	61·1	6·4	From Full-1 (6)

TABLE II

Carapace length data—Female instars of P. sanguinolentus

Instar group		No. Indiv.	Size range	Mean	Coef. var.	Remarks
			mm.	mm.	%	
Last Juv.	1	29	35·0–51·5	43·4	8·8	Experimentals
	2	28	37·0–47·0	42·3	6·8	Unsuccessful Molts
	3	26	37·0–48·0	42·9	7·2	Molt to Mature-1 (4)
Mature-1	4	26	46·0–56·5	51·2	5·6	From Last Juv. (3)
	5	20	41·0–60·0	49·6	7·6	Unsuccessful Molts
	6	33	41·0–55·5	49·7	7·7	Molt to Mature-2 (7)
Mature-2	7	33	47·0–63·5	56·6	7·3	From Mature-1 (6)

exuvia was only 8·1%. In all other instars of both sexes, the coefficient of variation was less than 10%. Similar coefficients of variation of less than 10% are reported for length data in each of two female instars of *Callinectes sapidus* by Tyler and Cargo (1963).

Females.—Length data of three female instars is given in Table II and the data graphically portrayed in Fig. 2. Analysis of the data gives much the same results as in males. The range of carapace length of the last juvenile instar which molted to the first mature instar was from 35·0 to 51·5 mm. (mean 42·9 mm.). Crabs of the first mature instar ranged from 40·0 to 60·0 mm. (mean 50·2 mm.) and crabs of the last instar from 46·0 to 65·0 mm. (mean 56·6 mm.). Overlapping of size was even greater in females than in males. In females, crabs of the last juvenile instar were larger than the smallest of the second mature instar.

It was supposed that the 58 individuals which molted in the cages from one sexually mature instar to the next might have actually included more than one instar. Evidence that this is not the case is found in several considerations of the data. The mean length of 24 individuals which had undergone the pubertal molt in captivity was 51·1 mm. after ecdysis. The mean length of 28 individuals which were collected in the field just prior to molt from one sexually mature instar to the next was 50·1 mm. When these groups were compared by the group comparison method of Snedecor (1956), the difference between the groups was not significantly different. The coefficient

of variation of the mature exuvia was 7·7% which was within the usual size for a single instar in this species.

Measurements of ovigerous females collected in the field were not of sufficient number to substantiate these conclusions of sizes and numbers of instars. Approximately 1,500 crabs were collected during the period of this study and of these only 26 were ovigerous. Unfortunately, it was not always recorded whether these were in the first or second mature instar. The mean lengths of those classified as first or second mature instar were within the size ranges of crabs which molted in captivity.

Acknowledgements

Credit is due to Dr. L. E. Cronin, Director, Chesapeake Biological Laboratory, for suggesting the need of such a study in *Callinectes sapidus*; preliminary work done under his direction there stimulated the choice of this problem after the author's enrolment at the University of Hawaii. Since this research was begun in 1959 and all specimens and data were destroyed when fire levelled the Hawaii Marine Laboratory in December 1961, the author is especially indebted to several for help and encouragement while the research was completely redone. He wishes to acknowledge: A grant-in-aid by the University of Hawaii; provision for space and use of boats and equipment by the Hawaii Marine Laboratory; free choice of his catches of crabs by Mr. Lester Zukeran; the help and encouragement by his wife, Ione, during this difficult period, and many others too numerous to include here.

Summary and Conclusions

1. A pubertal molt is demonstrable in male *P. sanguinolentus* based upon an external morphological criterion, color of the chelar propodus. Only crabs with the oxblood red color on the inner surface of the chelar propodus effect copulation.

2. Three sexually mature instars follow the last juvenile male instar. The last two of which are morphologically indistinguishable. In Kaneohe Bay, Hawaii, approximate mean carapace lengths of these are 43·9 mm. 52·4 mm. and 61·1 mm., respectively.

3. The last juvenile female instar is followed by two sexually mature instars which are distinguished on the basis of abdominal width and shape.

4. Approximate mean carapace lengths of the two mature female instars are 50·2 mm. and 56·6 mm. in Kaneohe Bay, Hawaii.

5. In both sexes, there is considerable overlapping of size which prevents instar identification of individuals upon the basis of size alone.

6. Males reach sexual maturity at a smaller size than females, possibly one instar ahead of females.

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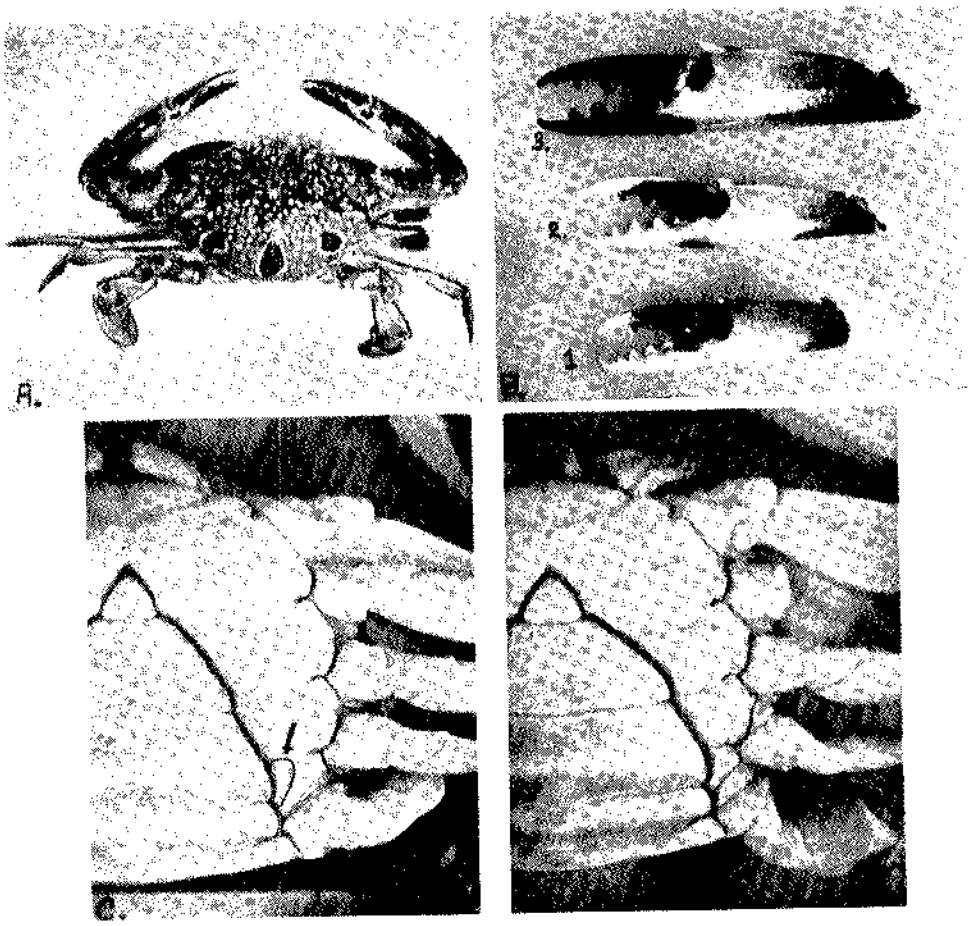

FIG. 3. (A) Adult male *P. sanguinolentus*, length 52·0 mm. (B) Color phases of male chelae: (1) white, (2) spot, (3) full. (C) Ventral view, female first mature instar, arrow points to sternite of 8th thoracic segment (outlined by India ink), carapace length 49·5 mm. (D) Ventral view, female second mature instar, sternite of 8th thoracic segment covered, carapace length 54·0 mm.

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FACTORS AFFECTING EGG-HATCHING IN *STREPTOCEPHALUS SEALI* (BRANCHIOPODA, ANOSTRACA)

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ABSTRACT

The influence of several environmental factors on the hatching of *S. seali* eggs was investigated in an attempt to account for the varying patterns of hatching noted under field conditions. Factors studied included constant and regularly cycled water temperatures, water depth, dissolved oxygen content of the hatching medium, and degree of desiccation of eggs. The optimum hatching temperature was determined to be 21° C., with a significantly increased percentage hatch noted in cultures based at 21° C. but regularly cycled over a range of 19–23° C. during a 10-hour period each day. Varying water depths (5–30 cm.) did not affect hatching, nor did dissolved oxygen concentrations within the range 0·88–8·00 ppm. Below 0·88 ppm a marked decrease in hatching percentage was noted. Eggs stored at various relative humidities (range: 0–100%) exhibited a direct correlation in total hatch and an inverse correlation in hatching time. The role of these factors in the natural habitat is discussed.

INTRODUCTION: STATEMENT OF PROBLEM

INVESTIGATIONS of the varied patterns of seasonal occurrence and population development of the anostracan fauna of temporary pond habitats have received increased attention in recent years. Among the more comprehensive of such studies have been those of Hall (1959 *a*, *b*, *c*, 1961) and Nourisson (1958, 1959, 1960, 1961, 1964) on *Chirocephalus diaphanus* Prévost. Both investigators have emphasized the role of multiple factors in egg-hatching including temperature, desiccation, and osmotic changes of the medium. Hall has placed particular stress on inhibition of development resulting from deep immersion of the eggs; he regards this as a factor of critical importance in retarding or preventing the hatching of eggs deposited by an adult population of *C. diaphanus* until an interval of drying followed by reflooding of the habitat has occurred. Nourisson on the other hand has concluded the direct influence of deep immersion of eggs to be of little importance; he has demonstrated that fluctuating water temperatures exercise a controlling influence, particularly low temperatures which drastically retard egg development and high temperatures (*ca* 25° C) which induce diapause at as little as 6 hours exposure per day.

Prophet (1963 *a*) has studied the factors, including conditions affecting hatching, which control the distribution of several species of Anostraca in the south-western plains of Kansas and Oklahoma. He noted that several pools contained *Eubranchipus serratus* Forbes during winter and that the same basins contained *Streptocephalus seali* Ryder in summer, an analogous situation to the occurrence of *Eubranchipus holmani* (Ryder) and *S. seali* in certain Louisiana habitats to be described in the present study. His investigations of factors affecting egg-hatching in five species of fairy shrimps (Prophet, 1963 *b*) demonstrated that a temperature of 10° C. was unfavourable for *S. seali* hatching, although *E. serratus* eggs hatched freely at 6° C. but not at temperatures of 15° C. or above. Prophet also noted that hatching stimulation resulted from short periods of drying, or from dilution of the hatching medium of eggs previously aged in habitat water.

I have been concerned with the problem, particularly as it applies to field populations of *S. seali* in south-east Louisiana. The species is known to occur during every month of the year in this region, the adults tolerating temperature extremes from near-freezing to as high as 42° C. (Moore,

1955). Continuing field investigations have revealed, however, certain peculiarities in the seasonal pattern of development of field populations. Exposed habitats such as ditches and unsheltered basins which are subject to wide diurnal temperature fluctuations may support populations of *S. seali* at any season, their occurrence being primarily dependent upon the frequency with which the habitat dries and refills (Moore, 1955). On the other hand sheltered forest pools, in which the diurnal temperature range is much smaller, usually exhibit *S. seali* populations only during the warmer months. During winter floodings these habitats normally support single-species populations of a second anostracan, *E. holmani*, a stenothermal species which cannot tolerate prolonged exposure to temperatures much in excess of 20° C. At one time I was of the opinion that interspecies competition led to the elimination of *S. seali* from the sheltered forest pools during periods of winter fill (Moore, 1959 *a*). More recently my studies showed, as did Prophet's (1963 *b*), that *S. seali* eggs hatch poorly or not at all at low temperatures and I have concluded (Moore, 1963) that this species probably shows no significant hatch in the shaded basins during the winter months. The problem of why such eggs fail to hatch after habitat temperatures have attained favourable levels, sometimes several weeks following initial flooding of the basin, has remained a matter of conjecture.

The present study was undertaken primarily to shed light on the latter problem. In the course of the investigations a detailed consideration of the role of temperature on the hatching of *S. seali* eggs was undertaken. Other factors investigated included the influence of depth of immersion of eggs, degree of desiccation of eggs, and the role of dissolved oxygen of the medium in the hatching process. I am indebted to the National Science Foundation (G-19365) for support of these studies.

Methods: Egg Processing and Hatching Procedures

In previously published studies (Moore, 1957, 1959 *b*) I have emphasized the considerable variation in hatchability that may exist between different lots of eggs of *S. seali*. Since this variation was noted under identical culture conditions, it was apparently due to differential viability of the eggs themselves, traceable either to inherent factors (*e.g.*, fertility) or to the different conditions under which they were collected, processed, and stored. The length of the egg storage period is one such condition. For example a group of 2,600 eggs, collected within 24 hours after deposition, was divided into 100 egg lots and sealed in 2 ml. ampules of habitat water. One to 4 ampules were tested each month for the ensuing year. A rapid and regular increase in hatchability was recorded to a maximum of 96% after four months storage; thereafter hatchability declined slowly and somewhat irregularly to the level of only 6% after 12 months storage. While this experiment demonstrates a correlation between egg viability and length of the storage period it should be emphasized that other lots of eggs, similarly processed and stored, sometimes retained a high level of viability for much longer periods. I have noted (Moore, 1959 *b*, p. 59) an instance in which *S. seali* eggs hatched after two years' storage. A single ampule of eggs from this same collection was recently tested after having been in storage for over 6 years; 11 of 72 eggs produced living nauplii, for a hatching percentage of 15·3. This is the longest period of egg diapause on record for a species of the genus *Streptocephalus*, although Mattox and Velardo (1950) found that eggs of the conchostracan, *Caenestheriella gynecia*, hatched after 8 years' wet storage in darkness.

To minimize as far as possible the influence of uncontrolled variables in the collection, processing, and storage of *S. seali* eggs used in hatching studies a standard method of egg preparation was adopted and closely adhered to in all experiments. Specifically, the possible presence of inviable eggs from some females was compensated for by combining eggs from several individuals. Field-collected adult shrimp were transferred as groups of 3–6 "mated pairs" to 400 ml. beakers of habitat water which were inspected at regular intervals and the deposited eggs collected, pooled, and immediately processed. The processing involved washing the eggs in 2 or 3 changes of clean habitat water to eliminate detritus, after which the eggs were counted out in lots of 100 into 2 ml. Neutraglas ampules of habitat water. The ampules were then sealed with a propane torch and stored at room

temperatures. Even with these precautions it was found that some variation was recorded in percentage hatch of eggs. For example, 5 ampules of 100 eggs each, processed from the same pooled lot and held in storage for 2 months, were divided into 50-egg aliquots and hatched under identical conditions. Total hatch from each of the 5 ampules ranged between 80% and 92%, the mean hatch was 87·4%, the standard deviation 4·4%. As a convenient "rule of thumb" it seemed reasonable to consider hatching percentage differences of twice this standard deviation (approximately 10%) as a criterion indicative of probable significance in those experiments employing eggs from the same collection under different hatching conditions. Since certain experiments, especially those testing the influence of temperature and dissolved oxygen, utilized eggs from different sources and of various ages the further precaution was observed here of dividing the contents of a given ampule into 2 equal lots, of which one (the control lot) was hatched under standard room conditions while the experimental lot was subjected to the test conditions. The "adjusted percentage hatch" based on a comparison of the hatchability of the experimental and control subjects was then calculated.

In routine hatching trials, eggs were recounted from the storage ampules into 400 ml. Pyrex beakers of demineralized autoclaved tap-water and loosely covered with a glass plate. The beakers were normally filled to a depth of 6 cm., a volume of *ca* 300 ml. Newly deposited and wet-stored eggs are denser than water and sink to the bottom of the beaker. The control hatching beakers were subject to small fluctuations in room temperature (recorded by thermograph) and to light changes ranging from normal room illumination during the day to complete darkness at night. The study of temperature in hatching involved the use of 2 Precision low temperature incubators in which the hatching beakers were in constant darkness. The control lots of eggs for these studies were hatched at room temperature in beakers covered with aluminium foil to exclude light, thus eliminating any possible bias due to differential illumination.

Hatching beakers were inspected regularly, at least once in every 24-hour period. Newly hatched nauplii were removed by pipette, counted, and recorded as either "alive", "hatching" (egg shell broken and the larva emerging, enveloped in the hatching membrane), or "dead". The periodic inspection of the hatching beakers was continued for at least a week; in certain experiments they were observed for over a month before discarding. Special egg processing and hatching procedures involved in some of the experiments will be described in subsequent sections.

Results

1. *The Influence of Constant and Fluctuating Water Temperature*

The influence of environmental water temperatures on the hatching of *Anostraca* eggs has been studied by several investigators as indicated in an earlier section of this report. Aside from a few scattered observations, however, the only data pertaining to *S. seali* are those of Prophet (1963 *b*) who reported constant temperatures of 10° C. and 32° C. to be unfavourable for hatching while 20° C. was favourable. In the present study, wet-stored *S. seali* eggs were tested in Precision low temperature incubators in which the temperature varied not more than $\pm$ 0·5° C. as monitored by recording thermographs. Approximately equal numbers of eggs from the same ampules were tested in darkness at room temperatures to obtain an index of the potential viability of the various lots. Room temperature extremes of 20–26° C. were recorded during the course of these experiments, but did not fluctuate more than 2–3° C. during any one hatching trial. For the experimental series, seven constant temperatures within the range of 10° C.–28° C. were tested; the results are summarized in Table I.

The greatest percentage hatch (45) was noted at 21° C.; furthermore, on the basis of potential hatchability as indicated by the controls, this temperature also represented the optimum. Hatching percentages dropped rapidly on either side of the optimum, particularly at higher temperatures, with virtually negligible hatch occurring at 28° C. and only slightly more at 10° C.

TABLE I

The influence of constant temperatures on hatching of eggs of Streptocephalus seali

Temperature	No. of experiments	Total No. of eggs	No. of eggs hatched	% hatch	Adjusted % hatch*
10° C.	4	377	12	3·2	5·4
Room controls	4	377	223	59·0	
13° C.	3	250	69	28·0	38·9
Room controls	3	249	178	72·0	
15° C.	1	75	22	29·0	30·5
Room controls	2	150	143	95·0	
17° C.	2	120	30	25·0	48·0
Room controls	3	155	81	52·0	
21° C.	3	148	66	45·0	72·6
Room controls	3	144	90	62·0	
25° C.	4	340	29	9·0	22·5
Room controls	4	278	110	40·0	
28° C.	4	193	1	0·5	1·0
Room controls	4	193	96	50·0	

* "Adjusted percentage hatch" in this and other tables represents percentage hatch at experimental temperature divided by percentage hatch of room temperature controls.

It will be noted that even at the optimum constant temperature of 21° C. the hatch was only about 73% of that of the same egg lots tested at room temperature. The only apparent variable in the two cases was the slight daily temperature fluctuations to which the control lots were subjected. To test the possibly stimulating effect of such fluctuations a number of experiments were carried out in which the incubator temperatures were cycled according to a predetermined daily pattern. In some experiments a temperature range similar to that to which the room temperature controls were exposed was attempted; in others the wider fluctuations characteristic of the natural habitats during both the summer and winter seasons were simulated. In actual practice the incubator was set at a certain base temperature and, at a given time each day, the thermostat was manually reset to a predetermined point. The incubator temperature rose gradually to the new temperature which was maintained for several hours, after which the thermostat was reset to the original base temperature. Actual water temperatures in the hatching beakers were continuously recorded by means of a thermograph with a remote sensing bulb. The results of representative experiments are summarized in Table II.

TABLE II

The influence of fluctuating temperatures on hatching of eggs of Streptocephalus seali

Base temperature	Altered temperature and period	No. of experiments	Total No. of eggs	No. of eggs hatched	% hatch	Adjusted % hatch
	hrs./day					
10° C. raised to 25° C.	9	4	347	0*	0*	0·0
Room controls	..	4	286	119	42	
10° C. raised to 27° C.	9	4	193	13	7	9·7
Room controls	..	4	193	141	72	
23° C. raised to 28° C.	9	2	120	17	14	26·9
Room controls	..	2	155	81	52	
21° C. varied to 19–23° C.	10	3	150	98	65	84·2
Room controls	..	3	149	113	76	

* 286 of these unhatched eggs were recovered and resealed in ampules for 7 days. When retested at room temperatures, a hatch of 108 larvae (40·3%) was recorded, approximately that of the corresponding control eggs.

These results would appear to support the hypothesis that fluctuating water temperatures within the range of 19–23° C. are more conducive to hatching of *S. sealii* eggs than is a constant temperature within this range. Note that the apparent optimum constant temperature of 21° C. produced an adjusted percentage hatch of only 72·6 (Table I) as compared with 84·2% when a base temperature of 21° C. was varied by approximately ± 2° C. during a 10-hour period each day (Table II). Only when a base temperature of 10° C. was employed did daily elevation to 25° C. or higher fail to stimulate an increased hatch. In fact, eggs cycled through a range of 10–25° C. during a 9-hour period each day did not hatch at all (Table II) although their viability was demonstrated when the same eggs, returned to room temperatures, hatched in normal numbers. When cycled through a range of 10–27° C., a small hatch occurred.

2. *The Influence of Low Dissolved Oxygen Content of the Hatching Medium*

To examine the possible inhibitory effect of low dissolved oxygen concentrations on hatching of *S. sealii* eggs, tests were carried out employing 300 ml. glass-stoppered Pyrex bottles as hatching vessels and a reservoir bottle of demineralized water, partially deoxygenated under aspirator-produced vacuum, as hatching medium. The water was transferred by nitrogen pressure from the reservoir to the hatching bottles and to sample bottles for dissolved oxygen determinations which were made by the standard Winkler technique. The same water, reaerated and in open beakers, was employed with control lots of eggs from the same ampules to determine potential viability from which the adjusted percentage hatch could be calculated. All tests were run under similar room conditions of temperature and illumination.

Eggs were tested at a wide variety of oxygen concentrations ranging from 0·5 ppm, the lowest concentration obtainable by the deoxygenation method employed, to near-saturation (*ca* 8·0 ppm). Significant differences in adjusted percentage hatch were noted only at the lower range of dissolved oxygen concentrations, consequently only data pertaining to concentrations of 2·5 ppm or lower are presented in Table III.

TABLE III

The influence of dissolved oxygen content of the medium on hatching of eggs of Streptocephalus sealii

Dissolved oxygen content (at start)	No. of experiments	No. of eggs tested	No. of eggs hatched	% hatch	Adjusted % hatch
0·5 ppm ..	3	150	0	0	0
Reaerated control ..	3	145	114	72	
0·6 ppm ..	1	50	5	10	11·7
Reaerated control ..	1	49	42	86	
0·7 ppm ..	2	100	17	17	39·5
Reaerated control ..	2	100	43	43	
0·9 ppm ..	3	150	118	79	92·3
Reaerated control ..	3	150	128	85	
1·3 ppm ..	3	150	114	76	103·6
Reaerated control ..	3	150	110	73	
2·5 ppm ..	2	100	93	93	111·1
Reaerated control ..	2	100	82	82	

There appears to be little evidence of inhibition of hatching at oxygen concentrations as low as 0·9 ppm. Below this concentration there is a rapid drop to an adjusted percentage hatch of 39·5 at 0·7 ppm and 11·7 at 0·6 ppm; at 0·5 ppm no hatching occurs. The hypothesis that low dissolved oxygen concentrations developing in the pond substrate would act to reduce or prevent hatching of *S. seali* eggs is thus supported, although the threshold of such inhibition is unexpectedly low—less than 1·0 ppm.

A corollary observation of probable significance relates to the period of survival of the newly-hatched nauplii in the sealed hatching bottles. These bottles were inspected at 6-hour intervals. At oxygen concentrations of 2·5 p.p.m. or lower a majority of the larvae were dead; at higher concentrations, on the other hand, most larvae survived. Apparently *S. seali* eggs will hatch under environmental conditions of low oxygen concentration which are unsuitable for continued survival of the nauplii.

3. *The Influence of Water Depth*

The studies of Hall (1959 *c*) on *Chirocephalus diaphanus* have apparently demonstrated an inverse relationship between the depth of water overlying the eggs of this species and their rate of hatching. Hall reported measurable inhibition at depths of 5 cm. and almost complete cessation of development at depths of 15 cm. and over. Since my routine hatching procedure involved immersion of the eggs of *S. seali* to depths of *ca* 6 cm., it was deemed necessary to test whether this resulted in any inhibition of hatching. Preliminary trials in beakers utilizing several water depths within the range 3–9 cm. failed to disclose any significant differences in total hatch or rate of hatching. Since, however, these experiments involved different total volumes of water, a technique was devised to eliminate this variable and at the same time to permit water depths similar to those in the natural habitat to be tested.

Hydrometer cylinders, 36 × 5 cm., having a total capacity of 600 ml., were employed. A frame of glass rod hooked over the rim of the cylinder permitted a small watch-glass to be immersed to any desired depth between 0–36 cm. Counted eggs were carefully pipetted into the watch-glass; hatched larvae were periodically removed by means of a long capillary pipette. Four ampules of *ca* 100 eggs each were used, the contents of each ampule being equally divided into 2 lots which were tested for hatchability at 2 depths. The results of this experiment are summarized in Table IV.

TABLE IV

The influence of depth of immersion on hatching of eggs of Streptocephalus seali

Ampule	Total No. of eggs	Percentage hatch at various depths 5 cm.	10 cm.	20 cm.	30 cm.
A	101	84	..	..	92
B	102	80	..	..	78
C	100	—	94	90	...
D	100	—	96	82	..
(Mean)	..	(82)	(95)	(86)	(85)

While the mean percentage hatch at 10 cm. depth was unexpectedly large, the values for 5, 20 and 30 cm. were well within the limits of normal variation in hatchability. Furthermore, hatching at all depths occurred within the first 48 hours of immersion with no indication of inhibition at any particular depth. It is concluded that water depths to 30 cm. do not exercise any significant inhibitory influence on hatching of the eggs of *S. seali*.

4. *Influence of Storage Humidity on the Viability of* S. seali *eggs*

Various investigators, as previously noted, have reported on the hatchability of dried eggs of this and other species of *Anostraca*. Such eggs were presumably "air-dried" and stored at ambient temperatures and humidities. The following experiment was designed to investigate the effect of subjecting *S. seali* eggs to various predetermined relative humidity levels at constant temperature for a uniform storage period; to determine, in other words, whether varying degrees of desiccation of *S. seali* eggs would result in differential hatch.

Newly deposited eggs were counted into shell vials, all free water was pipetted off, and the open vials were stored in desiccators charged with various water-sulphuric acid mixtures with vapor pressures providing relative humidity levels of 0%, 30%, 60% and 100% respectively at 20° C. The desiccators with the contained eggs were maintained at this temperature in a Precision low temperature incubator. After storage periods of 40–60 days the eggs were tested for hatchability according to standard procedures. A total of 2,000 eggs were so tested; 4 lots of 100 stored at each of the relative humidities cited, *plus* 4 control lots of 100, wet-stored in 2 ml. ampules of habitat water at 20° C. for the same periods. Hatching beakers were regularly inspected at least three times a day for the first 3 days and once or twice daily thereafter for a total of 14 days. Since no hatching occurred after the tenth day, data are presented for a 10-day period only.

Table V summarizes total hatching percentages of eggs stored at the various relative humidity levels and demonstrates a direct correlation between the two. It is interesting that eggs stored in a saturated atmosphere (100% R.H.) exhibited a higher percentage hatch than the wet-stored "controls". Storage at 0% R.H., on the other hand, resulted in negligible hatch.

TABLE V

The influence of storage humidity on hatching of eggs of Streptocephalus seali

Egg storage conditions	No. of experiments	No. of eggs tested	No. of eggs Hatch	% hatch
Habitat water (controls) ..	4	400	151	38
100% R.H. ..	4	400	265	66
60% R.H. ..	4	400	143	36
30% R.H. ..	4	400	118	30
0% R.H. ..	4	400	5	1·3

Of equal importance is the relationship between storage humidity and time to hatching after immersion of the eggs in hatching medium. These data are presented in graphic form in Fig. 1. As expected, the wet-stored "controls" and eggs stored in a saturated atmosphere commenced hatching within 18 hours after immersion, continued at a high rate, and completed their hatching within 2–3 days. Eggs stored at lower relative humidities showed a progressively increasing interval to first hatch and the total hatching period was much prolonged. At 60% R.H., for example, the first hatching occurred on the second day and continued through the eighth. At 30% R.H. the first hatch took place on the third day and, at 0% R.H., on the fourth.

DISCUSSION

The general pattern of occurrence and development of *S. seali* populations in south-east Louisiana has been reviewed in the Introduction to this report. To recapitulate briefly, exposed

habitats (*e.g.*, ditches and non-wooded basins) may support single-species populations of *S. seali* during any season of the year. Such populations are frequently of one age class, being derived from larvae hatched at the time of initial flooding of the basin. When populations of multiple age classes occur they may usually be correlated with successive stages of filling in which hatchings took place as additional peripheral areas of the basin were successively inundated. Diurnal water temperature fluctuations are great in these exposed habitats, especially during the winter season.

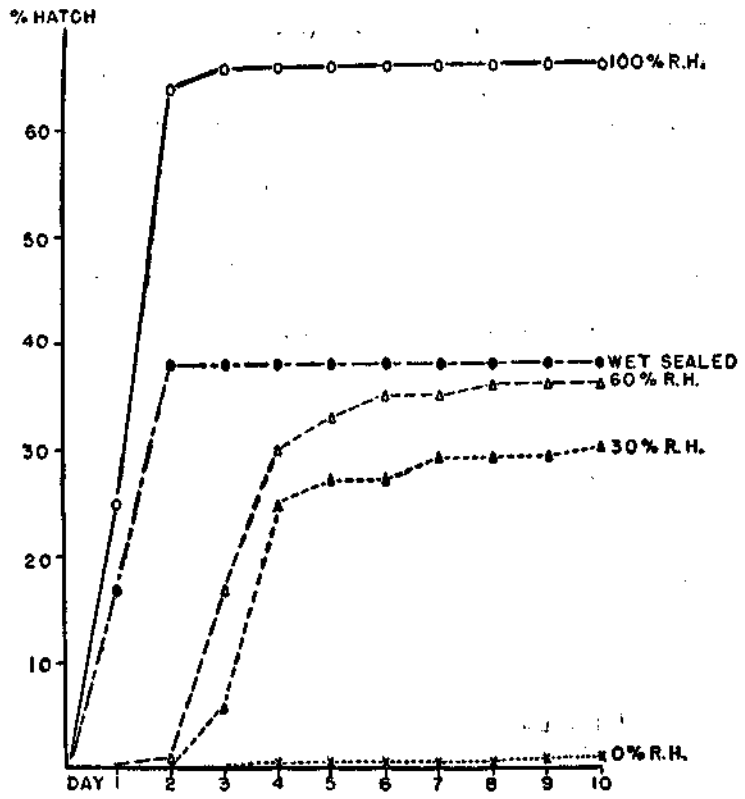


FIG. 1. The relationship between storage humidity and hatching time of eggs of *Streptocephalus seali*

A second type of habitat is represented by basins supporting dense stands of hard woods, especially swamp tupelo (*Nyssa sylvatica*) and water oak (*Quercus nigra*). Shelter and shading afforded by the trees leads to smaller diurnal water temperature fluctuations, with daily maxima consistently lower than in the exposed ponds. It is these basins which develop *S. seali* populations during periods of summer fill and (usually) single-species populations of *E. holmani* during the winter months. Occasional dual-species populations are found in winter when basin flooding took place during a warm period.

Among the complex of environmental factors which exercise a controlling influence over the development of these *Anostraca* populations, water temperatures undoubtedly are of great importance. Figure 2 summarizes as a graph data previously presented in Table I relating water temperatures to hatching of *S. seali* eggs. It has previously been pointed out that the test temperature extremes of 10° C. and 28° C. are both severely inhibitory. Further, if one considers an adjusted percentage hatch of less than 50 to be evidence of hatching inhibition, then any temperature below 17° C. and above 23½° C. must be limiting to some degree.

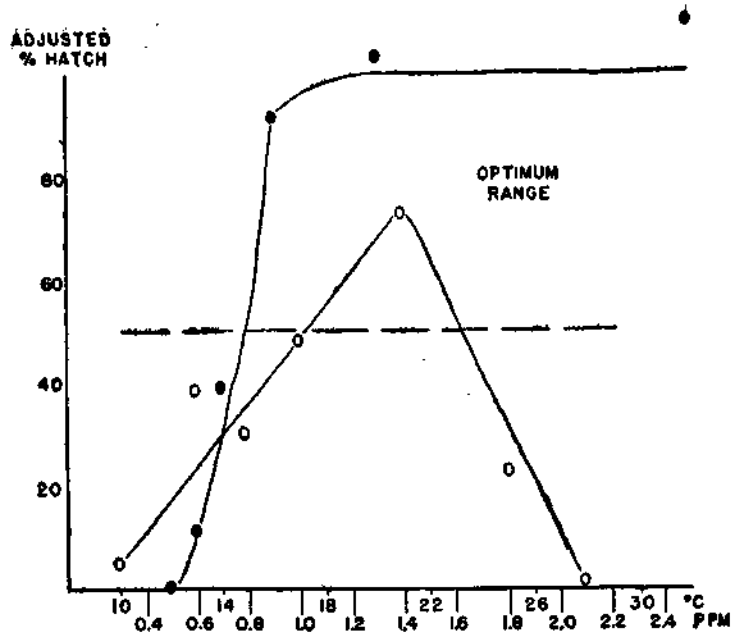
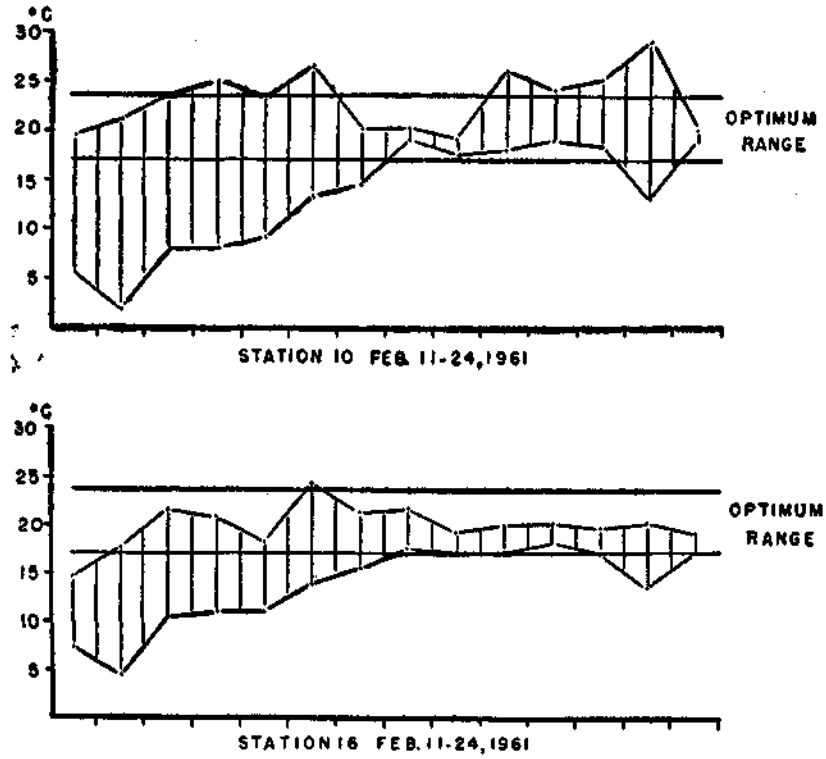


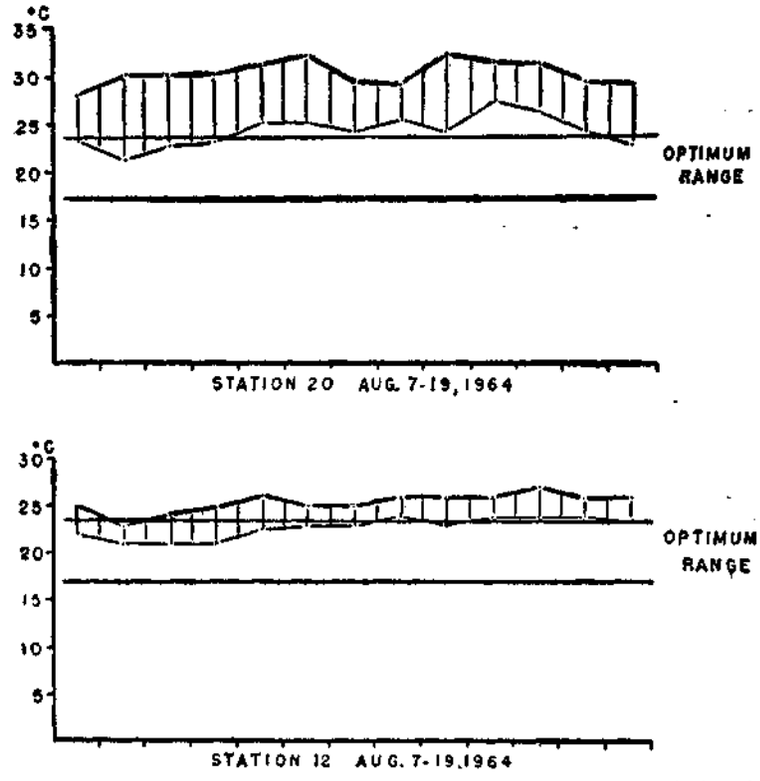
FIG. 2. The influence of constant temperatures (open circles) and dissolved oxygen content of the medium (closed circles) on the adjusted percentage hatch of eggs of *Streptocephalus seali*



FIGS. 3–4. Fig. 3 (Above). Daily water temperature ranges in an exposed habitat during the winter season. Fig. 4 (Below). Daily water temperature ranges in a sheltered habitat during the winter season

In an earlier paper (Moore, 1963, p. 133) I have graphed daily water temperature maxima in both a ditch pond and a forest pool during a representative two-week period in winter. Figures 3 and 4 include these previously published data to which have been added daily water temperature minima for the same period. Note that diurnal water temperature extremes fall outside the optimum hatching temperature range with great frequency; in fact, only on 2 days in the exposed habitat (Station 10) and on 6 days in the more equable sheltered habitat (Station 16) are water temperatures within the optimal range.

Similar graphs of daily water temperature maxima and minima are shown in Figs. 5 and 6 for 2 habitats, an exposed pool (Station 20) and a heavily shaded basin (Station 12) respectively, for a representative two-week period during summer flooding. Inhibitory hatching temperatures are even more common during this season. On no occasion did daily temperatures fall within the optimum range in the former habitat; moreover daily maxima invariably reached the almost completely inhibitory level of 28° C. More equable temperatures with lower maxima and higher minima were characteristic of the sheltered basin (Station 12), but even here there was only one day of temperatures within the optimum hatching range.



FIGS. 5–6. Fig. 5 (Above). Daily water temperature ranges in an exposed habitat during the summer season. Fig. 6 (Below). Daily water temperature ranges in a sheltered habitat during the summer season

This interpretation, based as it is on the influence of constant water temperatures, loses some pertinence when one considers the modifying effect of fluctuating temperatures (Table II). Temperatures cycled within the non-optimal range of 23–28° C., for example, resulted in an adjusted percentage hatch of 26·9, slightly though not significantly greater than the 22·5% hatch at a constant temperature of 25° C. but still an appreciable hatch. However, a daily temperature range encompassing minima of 10° C. continued to be drastically inhibitory, even when daily maxima were cycled as high as 25–27° C.

Temperature inhibition would thus appear to be a factor of major importance in the suppression of hatching of *S. seali* eggs. That it is not the only operative limiting factor is obvious since hatching fails to occur on those occasions when habitat temperatures fluctuate within favourable limits. I have suggested (Moore, 1963) that localized conditions of low oxygen concentration may develop at the mud-water interface of the pond bottom and exert an inhibitory influence after the initial hatch has occurred. This inhibition would presumably be most pronounced during the summer months when decomposition is accelerated, and in the shaded basins where leaf litter is abundant and the organic content of the substrate high. The present study has demonstrated that low oxygen is indeed inhibitory, the threshold of inhibition for *S. seali* hatching falling at about 0·9 ppm dissolved oxygen.

Whether such conditions prevail in the natural habitats and, if so, how general such conditions may be has not yet been ascertained. A few tests were conducted at 2 forest pool habitats during the summer of 1964. The method of Fremling and Evans (1963) was employed in which polyethylene sacks of water are placed in contact with the substrate and allowed to equilibrate over a period of several days with the oxygen concentration of the surrounding medium. In one of the ponds dissolved oxygen content was determined to be 0·57 ppm, a concentration which has been demonstrated to be inhibitory to hatching. In the second pond a value of 1·87 ppm was obtained, although a heavy rain just prior to the test had probably temporarily increased the dissolved oxygen content of the bottom stratum. In both cases the ponds were old (6–8 weeks since initial flooding of the basin) and the above observations reveal nothing of the conditions which characterized this stratum shortly after flooding. Further field tests must be deferred until the summer of 1965 when it is planned to carry out more extensive studies. Possibly the previously noted lethal effect of oxygen concentrations below 2·5 ppm on newly hatched nauplii may constitute an additional limiting factor.

A third factor influencing hatching is desiccation of the eggs. Both Hall (1961) and Nourisson (1964) have concluded that drying drastically slows or suspends embryonic development of *Chirocephalus diaphanus* and that rewetting allows development to proceed to the hatching point. My present studies show that the degree of desiccation to which *S. seali* eggs are subjected profoundly influences both rate of hatching and total percentage hatch following reimmersion, with virtually complete mortality of eggs occurring after 40–60 days storage in a moisture-free environment.

The soil moisture content of the upper substratum of the natural habitat varies widely. At one sheltered basin (Station 16) soil moisture was determined gravimetrically at weekly intervals during the course of a year. Soil moisture, expressed as % dry weight of the soil, was usually high (over 60%) but during one 2-month period (October–November, 1962) it fell as low as 10% on occasion and it never exceeded 40%. At an exposed dry basin (Station 24) during the summer of 1964 soil moisture never exceeded 42% and dropped to 9·5% in mid-June. These values are not necessarily representative of the basin substrate as a whole; since they were based on soil samples from the deepest part they probably are maximal. It is not possible, of course, to directly correlate soil moisture percentages with relative humidity, however the implication is clear that excessive drying of the basin soil will lead to prolongation of the hatching period and to a high mortality rate of the dried eggs if conditions are extreme.

The three factors discussed above do not exhaust the list of possible limiting influences to hatching of *S. seali* eggs. However, temperature, dissolved oxygen, and degree of desiccation are undoubtedly all operative factors, of varying importance depending upon the circumstances prevailing in a particular habitat at a given time.

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NOTES ON THE EGGS AND EARLY LARVAL STAGES OF *HIPPOLYSMATA ENSIROSTRIS* KEMP*

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ABSTRACT

Hippolysmata ensirostris which contributes to a minor extent to the crustacean fisheries of India is an ovoviviparous form. Berried females with eggs carried by the first four abdominal appendages are encountered in the shore-seine returns at Cannanore during the south-west monsoon months. The present paper gives an account of three different stages of the egg and three early larval stages reared in the laboratory.

The eggs are spherical with opaque yellow yolk and measure 0·406–0·449 mm. in the first stage. In the second stage they become transparent, more so in the periphery. Gastrulation, embryogenesis and most of the organogenesis are completed in the third stage (0·577–0·642 mm. long).

The newly hatched larva is a protozoea with a prominent rostral spine, well-developed carapace and sessile eyes. In the second larval stage which is designated as the first zoea the eyes have become stalked. The third larval stage which is the second zoea is marked by the formation of the uropods.

INTRODUCTION

OF the six species and varieties of the genus *Hippolysmata* Stimpson (family Hippolytidae, Macrura, Decapoda) known from India (Kemp, 1914), only *H. ensirostris* Kemp contributes, although to a minor extent, to the crustacean fisheries of our waters. The commercial importance of *H. ensirostris* was first reported by Shaikhmahmud and Tembe (1960) although Rai (1933), Chopra (1943) and Panikkar and Menon (1955) have dealt with various aspects of the prawn fisheries of the country.

H. ensirostris is not of common occurrence except around the waters off Bombay from April to September. At Sassoon Docks, an important prawn fishing centre in Bombay, Shaikhmahmud and Tembe (1960) have observed *H. punctata* and *H. dentata* along with *H. ensirostris*. Brief notes on the sex-ratio of *H. ensirostris* are given by these authors. Ramamurthy (1963), reporting on the prawn fishery of Kutch, mentions *Hippolysmata* sp. as occurring at Modhwa from September to January. From the scientific reports of the Central Marine Fisheries Research Institute, Mandapam Camp, South India, for the period 1960–1964, it can be seen that *H. ensirostris* accounts for a good proportion of the prawn fishery at Sassoon Docks. It occurs in good quantities along with other small-sized prawns like *Palaemon tenuipes, Parapenaeopsis stylifera, P. sculptilis, Metapenaeus affinis, Acetes indicus, Solenocera indicus*, etc. During certain months the species is reported to have formed as much as 18% of the prawn catches in this centre.

South of Bombay region, no information is available of the abundance of *H. ensirostris*. At Cannanore (north part of Kerala State), a few specimens can be observed occasionally in the boat-seine catches along with the common penaeid prawns, *Parapenaeopsis stylifera, Metapenaeus affinis,*

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** Present Address: Central Marine Fisheries Research Unit, Tuticorin.

‡ Present Address: Central Marine Fisheries Research Unit, Karwar.

M. dobsoni, etc. During the south-west monsoon (May–September) this species occurs in small numbers in the shore-seine units operated in the shallow inshore areas at a distance of about ¼ kilometer from the shore at a depth of 1–1½ fathoms. Most of the specimens observed during this period are egg-bearing females.

Apart from a post-larval stage described by Kemp (1916) from the Orissa coast nothing is known of the developmental history of *H. ensirostris*. The present paper reporting the early developmental stages of the species may therefore be of interest.

Material and Methods

For studying the structure of the egg, a few of them were removed from the general egg mass and observed under the microscope. In order to determine whether eggs of the different regions of the egg-mass were in different stages of development, eggs from a number of regions both from the periphery and the interior were examined. No significant difference in the embryonic development of the eggs from a single specimen was noticed. In the case of an allied species, *H. vittata*, Kuriyan (1951) has noted that more than one stage of development was present in individual specimens. In the present case three representative stages in the development of the egg have been collected from three specimens.

For rearing the berried females a large beaker with sea-water was brought to the fish-landing centre, and as the shore-seine units were being hauled up, the live berried female was picked up and transferred to the beaker.

In the laboratory, the berried female was fed with the flesh of the penaeid prawn, *Parapenaeopsis stylifera*, ground to a thin paste. The specimens took to this diet readily. Water in the aquarium was changed twice a day. The temperature of the sea-water varied between 24–28° C.

The larvae hatched from a berried female measuring 73 mm. long (measuring from the apex of the rostrum to the end of the telson), collected at 09·00 hours on 10–6–1964 are described in the present paper. Till the evening (17·30 hours) of the following day, 11–6–1964, the eggs were not ready for hatching. On the morning at 07·00 hours of 12–6–1964 all the eggs were found hatched out. Obviously the process of hatching took place during the preceding night. After the eggs hatched out the mother appeared pale and inactive.

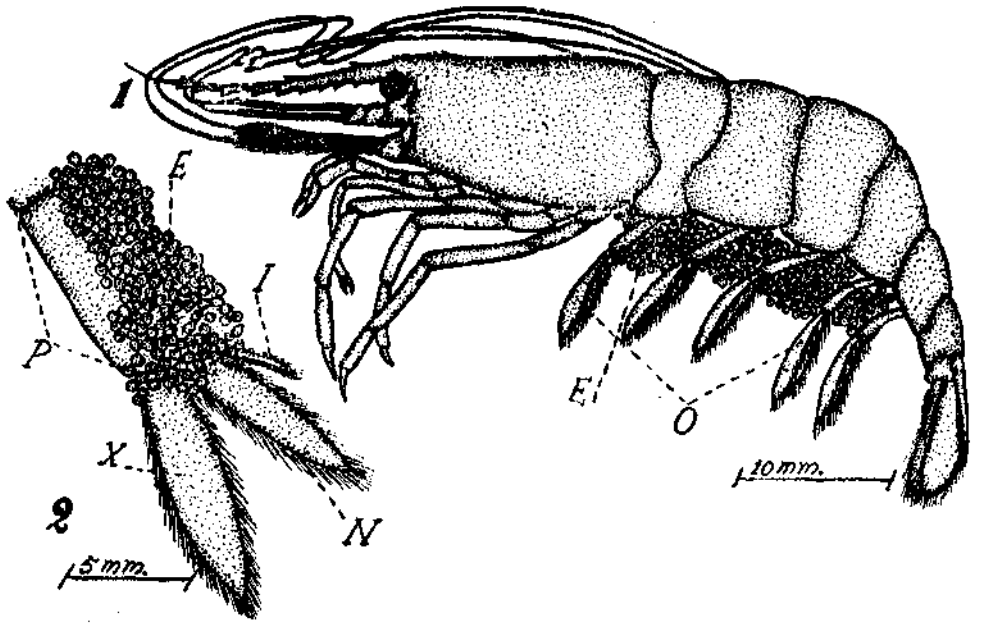
A few larvae were examined at each stage to observe the changes in the colour, pigmentation, etc. After this they were preserved for subsequent detailed studies. A close observation was also made of the locomotion as well as other habits of the larvae. They were fed with the well-ground thin paste of the flesh of *P. stylifera* and like the mother, the larvae also took to this diet readily. Sometimes a tiny food particle was found "attacked" by 3–5 larvae at the bottom of the aquarium. Everyday the larvae suffered large-scale mortality, chiefly owing to the attack of ciliates. Only a few larvae could be reared up to the second-zoea stage.

All the figures except 1 and 2 were drawn with the aid of a camera lucida on the material in formalin. In naming the various stages, the nomenclature used by Menon (1951) for the penaeid prawn, *Metapenaeus dobsoni* has been adapted.

Berried Female

Berried females of *H. ensirostris* (Fig. 1) lived in the aquarium for about five days. They were bright orange-red in colour and active and occasionally swam with the ventral side up. Generally they could be seen resting at the bottom of the aquarium. When disturbed they became restless,

If a support, such as a glass rod, was provided the specimens often climbed on to it with the aid of their pereiopods, ventral side upwards.



FIGS. 1 and 2. Fig. 1. A berried female specimen of *Hippolysmata ensirostris* measuring 72 mm. total length. Fig. 2. The third pleopod of a specimen of 70 mm. total length. E., Developing eggs; I, Epipodite; N, Endopodite; O, Ovigerous pleopods; P, Protopodite; X, Exopodite.

The egg-mass is attached to the median as well as to the posterio-median aspects of the protopodite (Fig. 2) of the first four pleopods. The eggs are clustered together by delicate, transparent membraneous processes (Fig. 3); and in the living condition were aerated by the vigorous movements of the pleopods.

EGG

Three typical stages in the development of the eggs of *H. ensirostris* have been collected and studied.

Stage I (Fig. 3)

Collected from a specimen measuring 70 mm. total length.

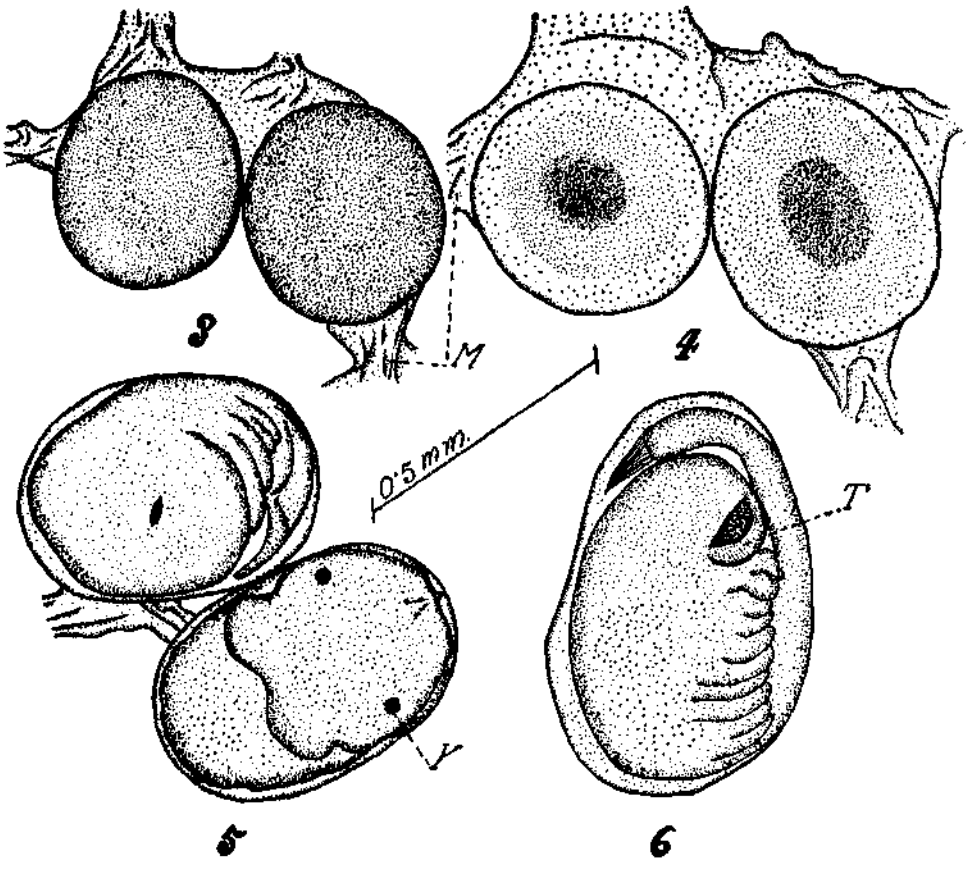
The eggs are roughly spherical with an average diameter of 0·427 mm. and ranging from 0·406–0·449 mm. They are opaque and the yolk fills the whole interior of the ovular cell and has a light yellow colour. Obviously, this stage is an early condition of the developing egg.

Stage II (Fig. 4)

Collected from a specimen 72 mm. in total length.

The eggs at this stage can be distinguished from the previous by the fact that they have become transparent in the region of the periphery. The yolk has assumed a granular structure and is chiefly

confined to the central region, thus assuming a centro-lecithal character, common to curstacea. The average diameter has also increased a little to 0·440 mm.



FIGS. 3–6. Developing egg stages of *H. ensirostris*. Fig. 3. Stage I. Fig. 4. Stage II. Fig. 5. Stage III A. Fig. 6. Stage III B. *M*, membraneous processes clustering the eggs with one another and with the pleopods. *T*, ommatidia of the eyes; *Y*, eye spot.

Stage III (Figs. 5 and 6)

The eggs have become elongated and pyriform. They measure an average diameter of 0·69 mm. and a range of 0·577–0·642 mm. along the longer axis. Most of the organogenesis has been completed at this stage. The eyes are indicated as black pigment spots, and about 4–6 appendages are recognisable.

The development of *H. ensirostris* unlike that of many panaeid prawns is devoid of a free-swimming nauplius stage. It is evident that the nauplius stage is suppressed and underwent in the embryonic period itself, as in stage III of the egg the embryo is apparently a protozoea. A free-swimming nauplius stage is also absent in an allied hippolytid prawn, *Saron marmoratus* (*see* Sankolli and Kewalramani, 1962).

Two different phases in the embryonic protozoea stage have been collected.

Stage III A (Fig. 5)

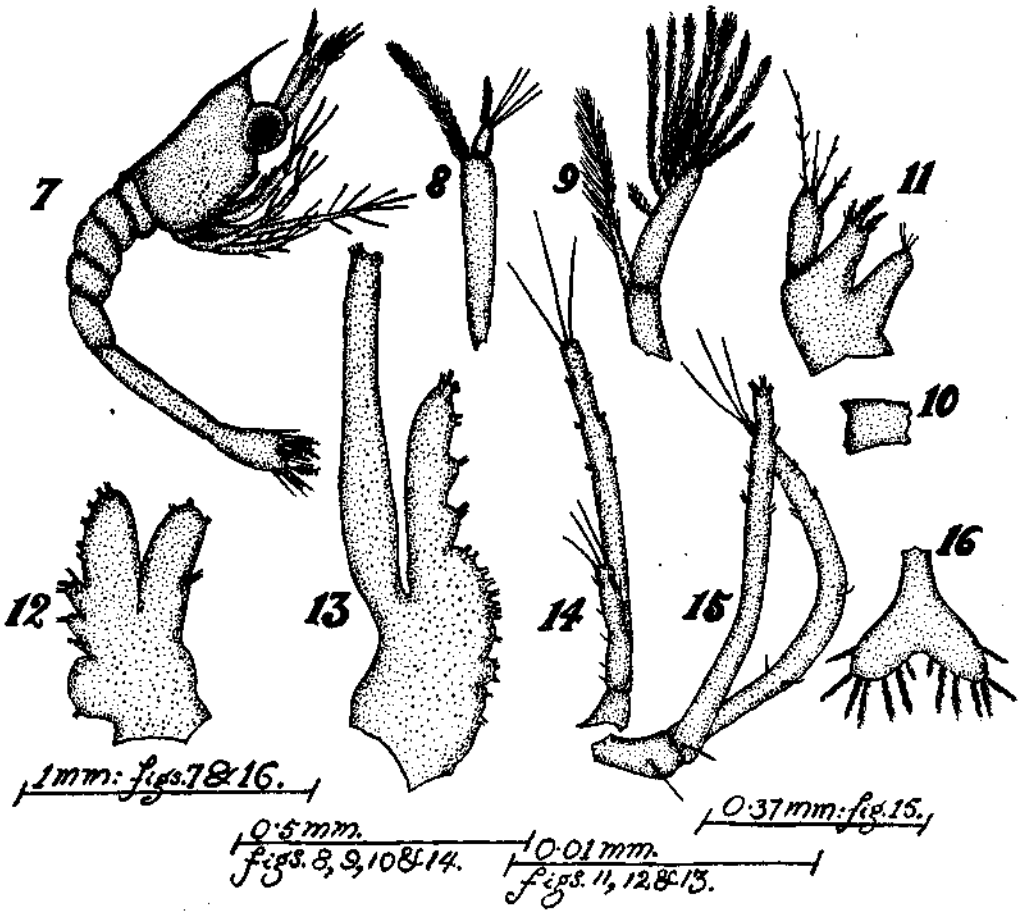
Collected from a specimen measuring 73 mm. total length.

Organogenesis is completed in the cephalothoracic region but the abdomen is not fully organised at this stage. In the eyes the region of the cornea is recognisable but the ommatidia are not yet developed.

Stage III B (Fig. 6)

Collected from a specimen measuring 72 mm. total length.

In this stage the abdomen is fully formed with well-developed telson; and the ommatidia of the eyes have developed.



FIGS. 7–16. Stage I larva (protozoea) of *H. ensirostris*. Fig. 7. Right side view of the entire larva. Fig. 8. First antenna. Fig. 9. Second antenna. Fig. 10. Mandible. Fig. 11. First maxilla. Fig. 12. Second maxilla. Fig. 13. First maxilliped. Fig. 14. Second maxilliped. Fig. 15. Third maxilliped. Fig. 16 Telson.

EARLY LARVAL STAGES

The larvae were reared successfully for six days from 12-6-1964 to 18-6-1964 and three typical stages in the early life-history were obtained.

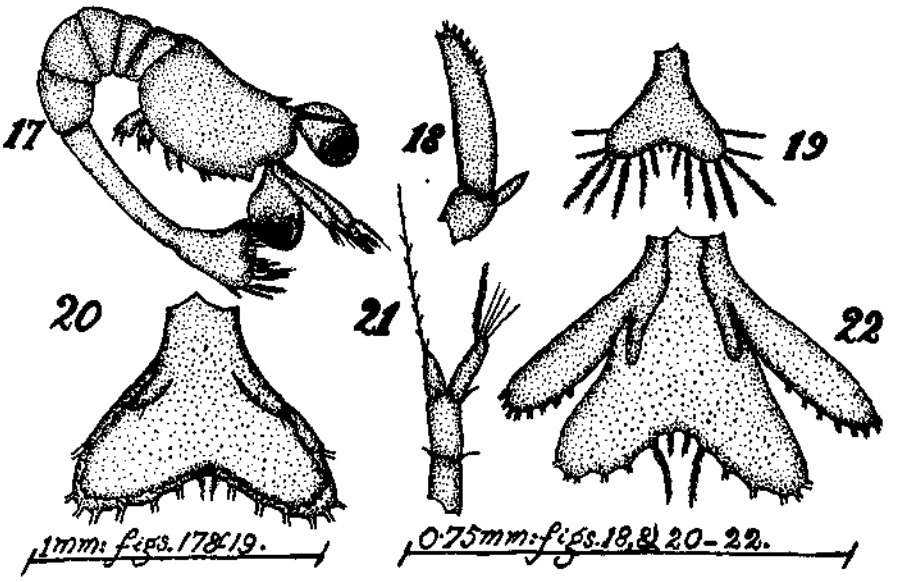
Stage I (Fig. 7)

As has already been mentioned, the process of hatching had taken place during the night of 11–6–1964, and this is the earliest stage observed at 07·00 hours on 12–6–1964. All the larvae were orange-red in colour in the thoracic region. At times the larvae became colourless and transparent. Such larvae when disturbed regained the orange-red colour after a few minutes. Colour changes in larval crustacea are of widespread occurrence and have been noted recently in the larvae of *Saron marmoratus* by Sankolli and Kewalramani (1962). The larvae of *H. ensirostris* were devoid of pigmentation.

The larvae were observed swimming by the active movements of the appendages. Sometimes they were moving with the head directed downwards, and when disturbed they moved with the head directed up. Very often the larvae could be seen browsing at the bottom of the aquarium. They are *positively phototropic* and gathered towards the side where the illumination due to sun-rays was maximum.

The larva at this stage is a protozoea. It has a total length of 2·15 mm., with a 0·22 mm. long rostrum. The cephalothoracic region is fairly stout but the abdomen is slender and long. The carapace has three minute marginal teeth along its antero-lateral aspects. The ventral margin of the carapace is smooth. The rostrum is long, slightly turned upwards and does not reach the distal end of the first and second antennae.* The eyes are sessile and large with well-developed ommatidia. The telson is broad with spines.

The first antenna (Fig. 8) is segmented distally. Its exopodite has four aesthetes and one medium-sized feathered seta on the inner side. The endopodite is represented by a single feathered seta.



FIGS. 17–22. Fig. 17. First zoea larva of *H. ensirostris*. Fig. 18. Second antenna. Fig. 19. Telson of the same. Fig. 20. Telson at 09·00 hours on 17–6–1964. Fig. 21. First antenna. Fig. 22. The uropods of the second zoea stage.

* The terms first antenna and second antenna are used in place of antennule and antenna respectively. Similarly first maxilla is used in place of maxillule.

The scale of the second antenna (Fig. 9) is feebly segmented distally and carries nine feathered setae. Its endopodite is represented by a single feathered seta which is long and has a stout basal region.

The mandible (Fig. 10) is represented only by the mastigatory portion. The molar process has several minute teeth.

The first maxilla (Fig. 11) has two endites, a proximal one with four setae and a distal one with three prominent serrated spines. The endopodite is unsegmented and carries four long setae. Two setose endites are present in the second maxilla (Fig. 12). Its *scaphognathite* also carries setae.

The first maxilliped (Fig. 13) is unsegmented and has two setose endites. Of the second and third maxillipeds the former (Fig. 14) has a three-segmented and the latter (Fig. 15) has a four-segmented endopodite. Both carry three terminal setae each. Segmentation of the exopodites is feeble.

The abdominal appendages are not indicated even as rudiments. There are six abdominal segments of which the last one is long, slender and is fused with the telson. The telson (Fig. 16) is broader than long and has a rather forked structure due to the presence of a shallow central notch in the hinder region. There are seven feathered spiny processes on each lobe of the telson; the first and the last spines being the shortest while the others are more or less of equal length.

The protozoea larvae remained in the same condition till 17·30 hours on 14–6–1964. The succeeding morning the larvae were observed to have passed on to the next stage.

Stage II (Fig. 17)

Reared larva at 09·00 hours on 15–6–1964.

It took nearly three days for protozoea to moult over to this stage which is designated as the first zoea. The presence of well-developed movable stalked eyes free from the carapace and formation of an additional spine on either side of the central notch in the telson are characteristic of this stage.

The larva has not increased in length. Behind the base of the rostrum a minute spiny process has developed on the carapace. The first antenna has become feebly segmented proximally. The second antennal peduncle has become well marked and carries a scale-like process ventrally (Fig. 18). The mandible, maxillae and maxillipeds do not show any appreciable change except that the segmentation of the exopodite of the third maxilliped has become marked. Abdominal appendages are not yet indicated. The telson (Fig. 19) has developed an eighth spine on either side of the notch. The larvae were devoid of pigmentation.

The first zoea larva did not show any appreciable change on 16–6–1964. On 17–6–1964 at 09·00 hours, the development of the uropods as lateral buds in the proximal region of the telson (Fig. 20) was observed. On 18–6–1964 at 09·00 hours the larva was in the first zoea stage only; but at 13·00 hours of the same day it was observed to have passed on to the next stage.

Stage III

Reared larva at 13·00 hours on 18–6–1964.

This is the second zoea larva and is characterised by the formation of the uropods. The segmentation in the proximal region of the first antenna is completed (Fig. 21); the mandible does not bear palp. The chief change noted is the formation of the uropods (Fig. 22). They are uniramous and bear eight setae. The biramous nature of the future uropods is however noticed in this stage by the presence of the rudiments of the inner rami. The telson has become narrower and its forked structure is marked in this stage. The number of spines of the telson has reverted to 7 + 7.

COMPARISON OF THE EARLY LARVAE WITH THOSE OF ALLIED PRAWNS

Kuriyan (1951) has described the first stage larva of an allied species, *H. vittata*. From the description given by Kuriyan (*l.c.*) the first stage larva described by him is obviously a protozoea. The protozoea of *H. ensirostris* differs from that of *H. vittata* in the longer size; the rostrum not reaching beyond the peduncle of the first antenna the six-segmented abdomen in contrast to the five-segmented condition in *H. vittata*; the absence of paired spines at the posterior margin of the fifth abdominal segment; the feebly-forked telson in contrast to the "triangular" condition in *H. vittata*; the presence of marginal teeth of the carapace in contrast to their absence in *H. vitatta* and in details of the structure of the appendages.

The early larval stages of *H. ensirostris* can be distinguished from those of an allied hippolytid prawn, *Saron marmoratus* described by Sankolli and Kewalramani (1962) in the absence of pigmentation; the smaller size; the simpler structure of the carapace; the shape of the telson; the structure of the appendages, etc.

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STUDIES ON LARVAL DEVELOPMENT IN ANOMURA (CRUSTACEA, DECAPODA)—I

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ABSTRACT

The knowledge of larval development of the Indian anomurans is limited to the work of Menon (1933, 1937 and 1940), which was based purely on planktonic material. His identification of the larvae, however, cannot be much relied upon as he could not get the earliest stages from the laboratory nor did he succeed in getting the sufficiently advanced stages of post-larvae that could be identified with certainty.

In this part, early larval stages, from pre-zoea to first zoea, of 5 porcellanids, *viz.*, (1) *Petrolisthes lamarckii* (Leach), (2) *Pachycheles natalensis* (Krauss), (3) *Porcellana ornata* Stimpson, (4) *Pisidia spinulifrons* (Miers) and (5) *Polyonyx hendersoni* Southwell and the first 3 stages of a thalassinid, *Thalassina anomala* (Herbst) and the entire life-history of a hippid, *Emertia holthuisi* Sankolli have been described in detail along with necessary illustrations.

Keys have been also prepared for the first zoeal stages of the known species of *Petrolisthes* and *Porcellana* and also of all the so far known species of porcellanids.

The present study reveals that Menon's (1937) *Petrolisthes* (sp. I and sp. II), as regards the telson characters of the first larval stage, is not really *Petrolisthes* but appears to be *Pisidia* rather than *Porcellana* as thought by Lebour (1943) and also Menon's (*op. cit.*). *Porcellanella* may be either *Petrolisthes* as felt by Lebour or even *Pachycheles* as per present studies.

As far as the first three stages of *Thalassina anomala* are concerned, the larvae agree well with those of the superfamily Paguroidea and the indication of a hair between the outer two telson spines on each side—a characteristic feature of the majority of anomuran larvae—and its distinct presence in the first zoea probably adds to the justification for the inclusion of the superfamily Thalassinoidea in Anomura.

The life-history of *Emerita holthuisi* Sankolli, as observed in the laboratory, consists of 6 distinct zoeal and one megalopa stages.

In the larvae of this species, the number of plumose setae on the exopodites of the first two maxillipeds is constant, *i.e.*, 4, 6, 8, 10, 11–12 and 13–14 corresponding to the 1st, 2nd, 3rd, 4th, 5th and 6th zoeal stages respectively. As far as these setae are concerned, the first 5 stages of *E. emeritus* as obtained by Menon (1933) correspond with the first 5 stages of *E. holthuisi*, but Menon's 3rd, 4th and 5th stage larvae possess advanced features such as thoracic limb buds and pleopods, etc.

This sort of differential development is possibly due to the differences in the environments of the larvae obtained from nature and those reared in the laboratory. Thus the zoeal moults are more in *E. holthuisi* when reared in the laboratory than in *E. emeritus* described by Menon from plankton.

The larval development of *E. holthuisi* should not be strictly considered as consisting of fixed number of stages, though the number of plumose setae on the exopodites of the first 2 maxillipeds may safely be taken as an indicator of the stage of the larva.

THE importance of larval studies in understanding the phylogenetic relations of decapod crustaceans, especially the Anomurans, has now been realised(Gurney, 1924 and 1942; Hart, 1937; Lebour, 1943; MacDonald *et al.*, 1957).

Considering that extensive studies have to be undertaken on the developmental aspect of the section Anomura, it is seen that comparatively more studies have been done by foreign authors than in India, where the present knowledge is solely due to Menon (1933, 1937 and 1940). Menon's identification of the larvae, it may be stated, is also not beyond doubt. Keeping this object in view, the present studies have been undertaken on the larval development in Anomura, dealt with in this

paper in 3 parts. Part I deals with the early larval stages of 5 porcellanids, the first 3 stages of a thalassinid and entire life-history of a hippid.

Superfamily GALATHEOIDEA

Family PORCELLANIDAE Dana

Menon (1937) dealt with the larvae of six species of porcellanids collected from the plankton at Madras. Of these, he got almost complete series of larval stages in three species and incomplete series in the remaining three. In 1940, the same author described a post-larva of a porcellanid. He could not fix up the specific identity of the larvae as he could neither succeed in getting the earliest stages from the eggs in the laboratory nor could he obtain the stages beyond the first post-larva. As such he could, in most of the cases, refer the larvae only upto the genera.

As regards the larval development of the foreign species of porcellanids, a considerable amount of work has been done by the following authors: Faxon (1879) dealt with some young stages in the development of *Porcellana* and described a larva which he attributed to *Polyonyx macrocheles*; Webb (1921) gave a brief review of the larvae belonging to two species, *viz.*, *Porcellana longicornis* and *P. platycheles*; Lebour (1943) described the complete life-histories of two species, *viz.*, *Porcellana longicornis* and *P. platycheles* and the first stage of *Petrolisthes armatus*; in all these cases, the first stage was obtained from the laboratory hatchings and the remaining stages from the larvae collected from plankton and made to moult in the laboratory and post-larva obtained from the last larva; Gurney (as cited by Lebour, 1943) dealt with only two larval stages in each of the two species, *Porcellana inaequalis* and *Petrolisthes*, which according to Lebour is *P. armatus* from the Red Sea; Gohar and Al-Kholy (1957) have followed the metamorphosis from pre-zoea to first post-larva in *Petrolisthes rufescens* from the Red Sea. They succeeded in rearing the larvae from egg to second zoea in the laboratory and from second zoea to megalopa they had to resort to plankton. Their illustrations of the first zoea, so far as the posterior spine of the carapace and telson are concerned, are incorrect since they do not tally with their own description of the larvae. As regrds the posterior spine, they describe it as having 6 long spinules at the base though their drawing indicates the presence of at least 15 spinules, not only at the base but also along the posterior spine; so also the telson seems to have been drawn inaccurately since the illustration does not depict the important character, namely the presence or absence of the central prominence of the posterior margin of the telson nor do they make any mention of it in their description. Lebour (*op. cit.*) has already shown the importance of the presence of the 7th telson process either on or outside the central prominence and Gurney (as cited by Lebour) has stressed the significance of the armature of the telson processes as a specific character. Gohar and Al-Kholy, however, do not seem to have noticed these points and as such their information regarding some of the important characters of the first zoea has not been of much use in the present study, specially regarding the key for the first zoeal stage of the known porcellanid larvae.

Complete life-histories of porcellanids is an exhaustive subject in itself and as such extensive work could not be undertaken in the present study. However, attempts were made to obtain the laboratory hatchings of the following species, *viz.*, (1) *Petrolisthes lamarckii*, (2) *Pachycheles natalensis*, (3) *Porcellana ornata*, (4) *Pisidia spinulifrons* and (5) *Polyonyx hendersoni*. It was not possible to rear the larvae beyond the first zoeal stage owing to the difficulties encountered in rearing the larvae under the laboratory conditions. Webb (*op. cit.*) puts this in a very convincing manner as "The much produced rostrum .... adds to the difficulty of rearing the larvae under the artificial conditions, as the long spines are easily caught in the surface film, so that the larva cannot free itself".

An attempt has also been made to formulate keys for the first zoeal stages of the known species of two genera, *viz.*, *Petrolisthes* and *Porcellana* and also of all the so far known species of Porcellanids.

Terminology

Lebour (*op. cit.*) used the terms setae, long setae or spines to describe the various processes such as spines, setae, plumose, long setae and reduced hairs, while describing the telson. Menon (*op. cit.*) and Gurney (1942) also used various terms to cover hairs, setae and spines. Pike and Williamson (1960), while working on the Pagurid larvae, introduced the term "telson processes" to include the spines, setae or hairs to avoid the confusion created by the usage of the various terms in describing the telson. In the present study also the term "telson process" is used and these telson processes are numbered from outside. Thus the 4th telson process in the present work corresponds to the 4th telson spine of Gurney (*op. cit.*), to 3rd telson spine of MacDonald *et al.* (1957) and 4th telson process of Pike *et al.* (1960).

Descriptions of Larval Stages

1. *Petrolisthes lamarckii* (Leach)

Pre-zoea

The larva hatched out from the egg was a pre-zoea which swam sluggishly for 3–4 hours before moulting into the first zoeal stage. The cuticle of the larva was so delicate that,whenever dissections of the appendages were attempted, it invariably got damaged, thus rendering the study of the characters of the pre-zoea difficult. Similar difficulty was experienced by Lebour (1943) while dealing with the larvae of *Petrolisthes armatus*.

First zoea (Fig. 1, *a*)

The rostrum is nearly six to eight times the length of the posterior spine and is more or less rounded in cross-section, with 6 longitudinal rows of minute spines around it. The posterior spine is armed with small stout spinules on either side, the ventral ones being much more prominent than the dorsal ones and these spinules become smaller towards the distal end so that the distal 1/5 of its entire length is more or less smooth.

Antennule (Fig. 1, *b*).—It is unsegmented with three long aesthetascs and three setae at its dip and is slightly larger than that of *P. boscii* (Shenoy and Sankolli, 1965—This Symposium).

Antenna (Fig. 1, *c*).—The basal portion is two segmented, the proximal segment having a papilla. The distal segment has two styliform processes—the inner one is smaller and stout bearing one small seta at its tip and the outer one has three setae and a minute tooth distally on the inner side.

Mandible (Fig. 1, *d*).—The anterior half of the cutting edge is armed with five stout and prominent teeth and the posterior with several small and sharp teeth.

First maxilla (Fig. 1, *e*).—The proximal endite bears six bristle-like setae and one single seta, whereas the distal one bears five bristle-like and three simple setae. The palp has four terminal setae.

Second maxilla (Fig. 1, *f*).—It consists of four endites, an unsegmented palp and a scaphognathite. The palp has six setae at its tip and a group of three along the inner margin. The scaphognathite bears seven marginal plumose setae and one long plumose seta posteriorly.

First maxilliped (Fig. 1, *g*).—The basipodite has six setae of which three are in a group. The first two segments of the four-segmented endopodite bear three setae each on the inner margin whereas the third segment carries six setae along its inner margin and one seta on the outer margin. The terminal segment bears only seven setae.

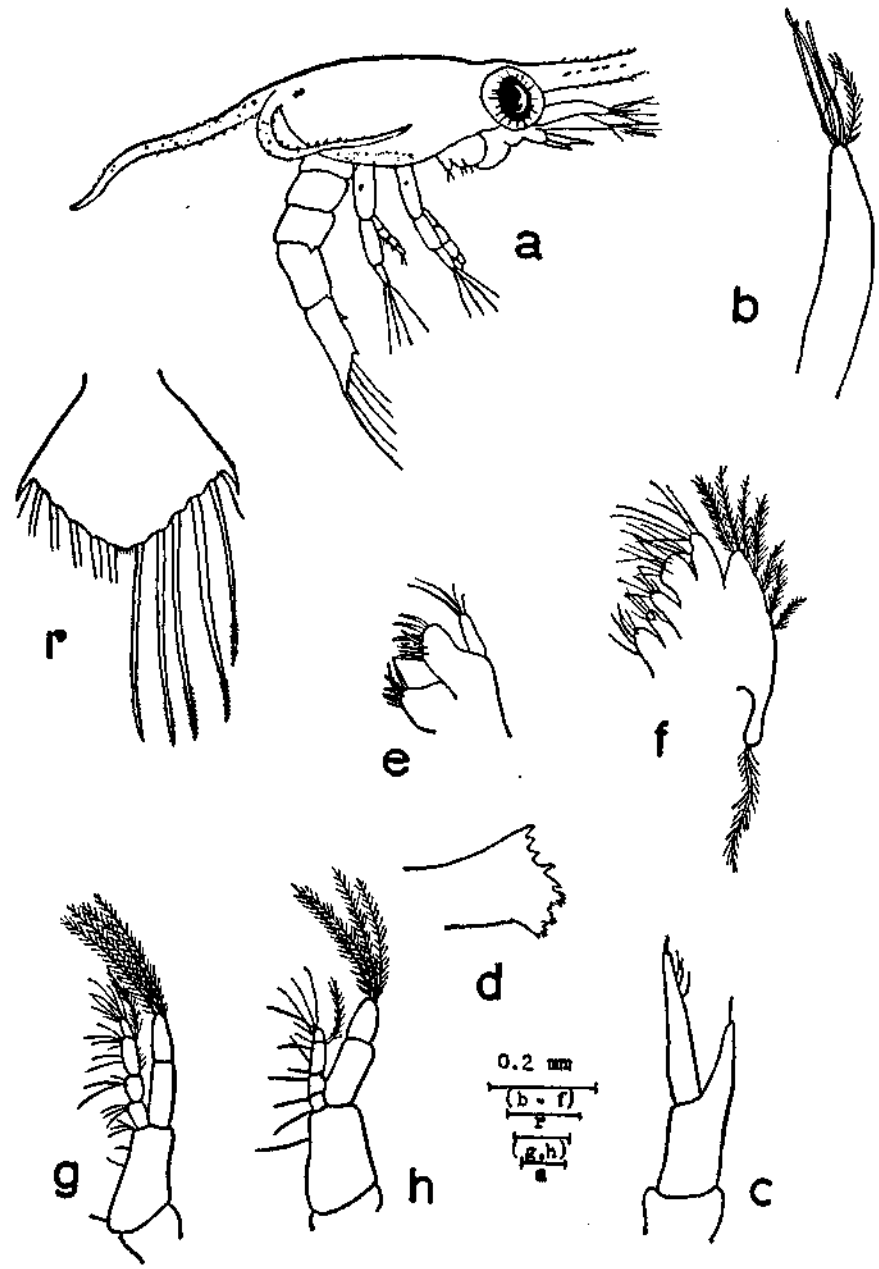

FIG. 1. *Petrolisthes lamarckii* (Leach), First zoea. (*a*) entire larva; (*b*) antennule; (*c*) antenna; (*d*) mandible; (*e*) first maxilla; (*f*) second maxilla; (*g*) first maxilliped; (*h*) second maxilliped; (*r*) telson.

Second maxilliped (Fig. 1, *h*).—The basipodite bears a single seta on the inner margin. The four segments of the endopodite bear one, two, four and five setae respectively from the first to the fourth. There is no other difference from the first maxilliped.

Other appendages.—The third maxilliped is biramous but rudimentary whereas the other thoracic appendages are present as small buds.

Abdomen.—It consists of five segments and a telson. The first segment is quite short, the second and third are broader than long and the remaining two are cylindrical. Each of the fourth and fifth segments bears at its postero-lateral angle, a sharp spine.

Telson (Fig. 1, *r*).—It is roughly "arrow-head"-shaped, wider in the middle, narrowing towards both ends. Telson formula is 7 + 7, the outer telson process is a fairly long spine, the second is a reduced hair, the third to seventh processes are long plumose setae. The distal ends of these plumose setae are armed with peculiar tooth-like spines, these being larger on the fifth telson process.

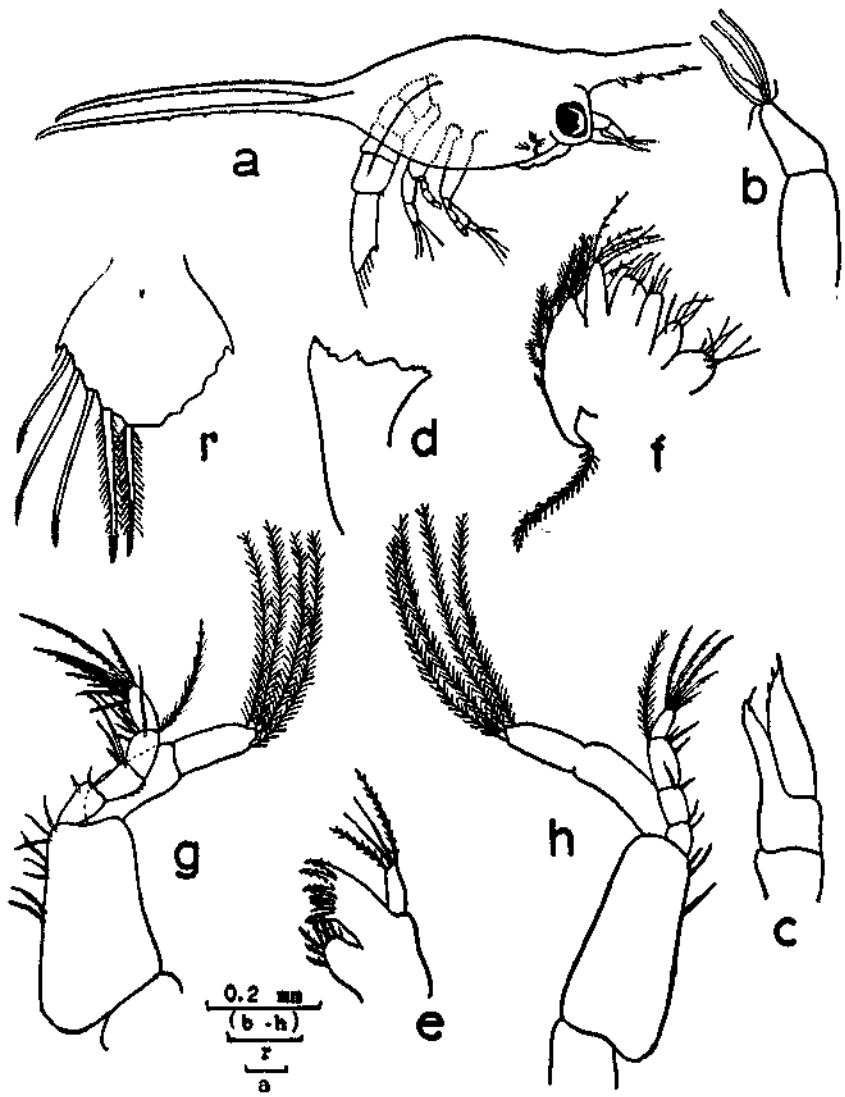

FIG. 2. *Pachycheles natalensis* (Krauss), first zoea. (*a*) entire larva; (*b*) antennule; (*c*) antenna; (*d*) mandible; (*e*) first maxilla; (*f*) second maxilla; (*g*) first maxilliped; (*h*) second maxilliped; (*r*) telson.

The seventh process (= 5th long telson seta of Lebour) is situated on the central prominence. The central prominence bears nearly eight minute delicate marginal hairs. The anal spine is present anteriorly on the ventral side.

Colour.—The rostral spine is bright yellow almost to the tip and the posterior spine is similarly coloured only in the ventral half. There is a pinkish-red chromatophore present on either side of the carapace just near the beginning of the posterior spines, and a similar one on each of the basipodite and protopodite of the maxillipeds. Except for these, the larva is almost transparent.

KEY TO THE FIRST ZOEA OF THE FOUR KNOWN SPECIES OF *Petrolisthes*

1. Central prominence of the telson absent.....*P. rufescens* (as per Gohar and Al-Kholy)
   Central prominence of the telson present.....2
2. Central prominence with microscopic hairs.....3
   Central prominence without microscopic hairs.....*P. armatus* (as per Lebour)
3. Central prominence with about 10 microscopic hairs....*P. boscii* (as per Shenoy and Sankolli)
   Central prominence with about 8 microscopic hairs.....*P. lamarckii*

2. *Pachycheles natalensis* (Krauss)

Pre-zoea

The pre-zoea is almost similar to that of *Polyonyx hendersoni* in all the morphological characters.

First zoea (Fig. 2, *a*).

The rostral spine is three times the length of the carapace and about thrice that of the posterior spine. The rostral spine has one to three rows of minute but long spinules along the ventral margin and no spinules are found on the rest of the portion of the spine. The posterior spine is almost smooth except for the presence of a few microscopic tubercles along the ventral margin.

Antennule (Fig. 2, *b*).—It is distinctly two-segmented, the distal segment being smaller than the proximal, and bearing three aesthetascs and three setae of unequal length.

Antenna (Fig. 2, *c*).—The basal portion is two-segmented; the proximal segment has a papilla on the inner side and the distal one bears two horn-like processes—endopodite and exopodite. The endopodite, which is a little stouter and longer than the exopodite, bears three spines distally along its inner edge. The exopodite has a minute seta near its tip.

Mandible (Fig. 2, *d*).—It has two large and two small teeth, in addition to two or three groups of minute teeth on the cutting edge. There is no palp.

First maxilla (Fig. 2, *e*).—The proximal endite has eight setae and the distal one has nine setae. The palp has two plumose and two simple setae.

Second maxilla (Fig. 2, *f*).—The endopodite has six setae at the tip and two or three along the inner margin. The scaphognathite has seven setae along the anterior margin and one prominent plumose seta at the posterior end. The usual four endites are also present.

First maxilliped (Fig. 2, *g*).—The basis of the protopodite is much longer and broader than the exopodite and bears ten setae in groups of three, three, two and two from the distal end downwards along the inner margin. The exopodite is two-segmented and bears four plumose setae. The endopodite is four-segmented bearing two, four, six and eight setae respectively.

Second maxilliped (Fig. 2, *h*).—The basipodite has two setae at its distal end and one seta along its inner margin. The four-segmented endopodite bears two, two, three and five setae respectively,

Other appendages.—Only the rudiments of the bilobed third maxillipeds could be seen distinctly through the carapace.

Abdomen.—It consists of five segments and a telson. Only the fifth segment has a pair of postero-lateral hook-like spines and no such spines are found on the fourth segment.

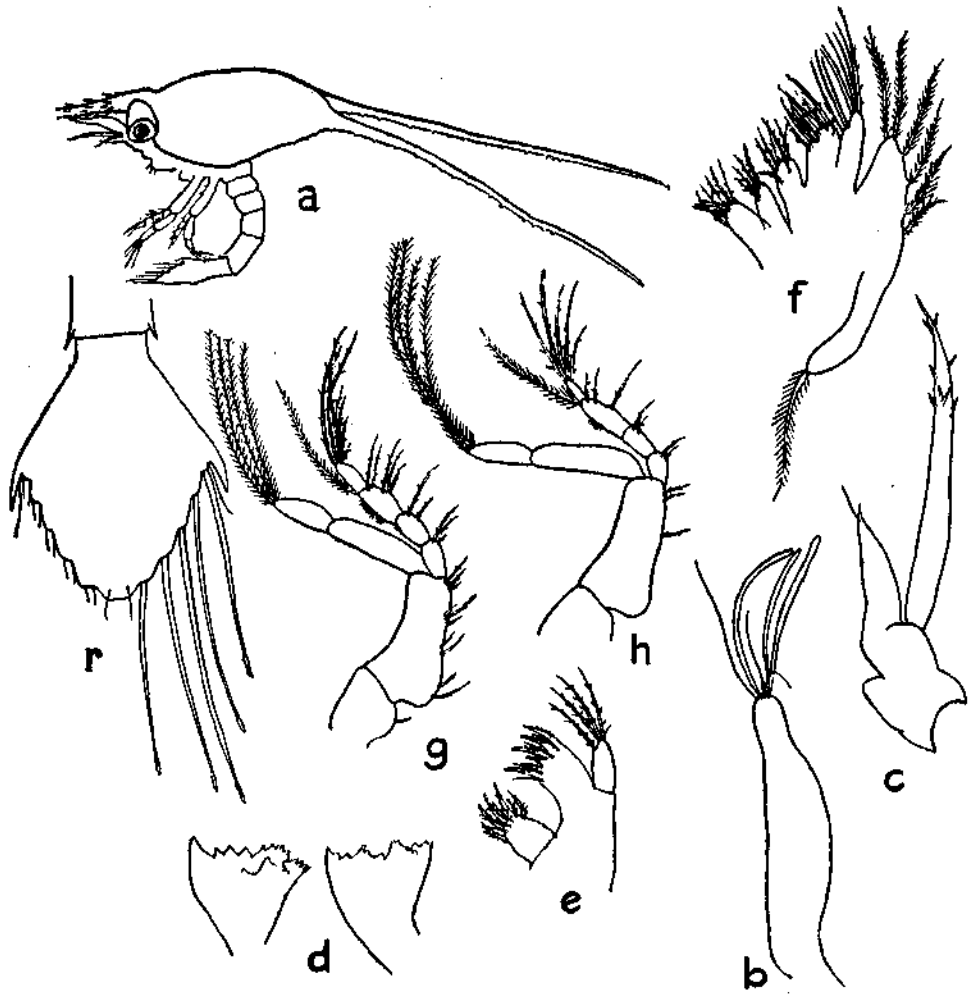

FIG. 3. *Porcellana ornata* Stimpson, first zoea. (*a*) entire larva; (*b*) antennule; (*c*) antenna; (*d*) mandible; (*e*) first maxilla; (*f*) second maxilla; (*g*) first maxilliped; (*h*) second maxilliped; (*r*) telson.

Telson (Fig. 2, r).—It is slightly broader than long; broadest near about its middle. The ventral anal spine is comparatively small. The telson formula is 7 + 7 and the seventh process is situated on the central prominence which is almost straight and devoid of any setae or delicate hairs. Each of the third to the seventh telson processes bears peculiar hook-like spines on the distal end; the first process is smooth and comparatively short.

Colour.—The body of the zoea is almost colourless except for the pinkish-red chromatophores in the proximity of the oral appendages as shown in figure; diffused pale yellow pigment on the

distal segment of the antennule and a faint streak of pinkish-red chromatophore running along the mid-line of the first to fifth abdominal segments.

3. *Porcellana ornata* Stimpson

Pre-zoea

As in other porcellanids, the larva hatches out as a pre-zoea from the egg and swims for 2 or 3 hours before moulting into the first zoeal stage.

Antennule.—It carries two long feathered setae on the endopodite and one feathered seta on the exopod.

Antenna.—There are five-feathered setae on the endopod and one seta on the exopod. The endopod, at some distance from its tip, bears two unequal spines, the larger one being on the inner side.

Telson.—The process formula is 6 + 6.

First zoea (Fig. 3, *a*)

The larva is fairly stout. The rostrum is about three times the length of the posterior spine and is armed with four to six rows of sharp spines extending upto the tip. The posterior spine bears two rows of blunt tubercles which are more prominent on the ventral side. The eyes are stalked and partially free from the carapace.

Antennule (Fig. 3, *b*).—The peduncle is unsegmented. It bears distally three aesthetascs and three unequal setae.

Antenna (Fig. 3, *c*).—The basal portion of the peduncle is one-segmented with a knob-like protuberance on the ventral side. The endopod is narrow, elongated and nearly twice the length of the exopod, bearing six to eight spine-like teeth in the distal half. The exopod is short, stout and ends in a tooth-like tip from the inner angle of which a delicate hair-like seta arises.

Mandible (Fig. 3, *d*).—The mandibles of either side are slightly asymmetrical. The upper cutting edge is armed with six long and several small teeth. The lower edge bears very small teeth. There is no palp.

First maxilla (Fig. 3, *e*).—The proximal endite is armed with nine setae, some of which are bristle-like; the distal endite with four big and two small bristles and four simple setae. The palp is unsegmented but with a distal, lateral notch bearing three terminal and one sub-terminal setae.

Second maxilla (Fig. 3, *f*).—The palp is unsegmented but is notched distally. It bears six setae at the tip and three on the inner margin. The scaphognathite is fringed with six plumose setae anteriorly and one prominent plumose seta posteriorly.

First maxilliped (Fig. 3, *g*).—The exopodite is two-segmented with four plumose setae at the tip. The endopodite is four-segmented and as long as the exopodite. The first and the second segments bear three and two setae respectively on the inner margin. The third segment has two setae distally and three situated somewhat in the middle on the inner margin. The last segment carries three long and four to five shorter setae distally and one long plumose seta proximally on the outer margin. The outer margin of the first three segments is fringed with fine hairs. The basipodite bears setae in four groups of three, three, two and two.

Second maxilliped (Fig. 3, *h*).—The exopodite is as in the first maxilliped. The four-segmented endopodite is shorter than the exopodite and bears two setae each on the first and the second segments. The third segment has two distal and one median seta on the inner margin, the outer margin being fringed with delicate hairs. The last segment is provided with five unequal setae terminally and one long, plumose seta on the outer margin. The basipod bears in all 3 setae.

Other appendages.—The third maxilliped is a rudimentary, biramous bud; only the first three pairs of legs are seen as buds beneath the carapace.

Abdomen.—It consists of five segments and a telson. Only the fifth segment, which is the longest, bears a pair of postero-lateral spines.

Telson (Fig. 3, *r*).—It is 'arrow-head'-shaped, longer than broad and with an anal spine. The telson process formula is 8 + 8, the 7th process being situated outside the central prominence. The first process is a simple spine, the second—the reduced anomuran hair. The third to seventh processes are plumose setae with minute hooks on their distal ends, those on the third being more prominent. The eighth process is present on the central prominence as a delicate hair.

Key to the First Zoea of the Known Species of *Porcellana*

1. Central prominence of telson with a pair of delicate hairs.....2
   Central prominence of telson without delicate hairs.....*P. platycheles* (as per Lebour)
2. Only 3rd telson process armed with distal hooks.....*P. longicornis* (as per Lebour)
   3rd to 7th telson processes armed with distal hooks, those on the 3rd being more prominent.....*P. ornata*

4. *Pisidia spinulifrons* (Miers)

Pre-zoea

The pre-zoea swims for a while before moulting into the first zoeal stage. As usual the rostral and posterior spines are held in folded condition.

Antennule.—It consists of two long feathered setae on the endopodite and no seta could be seen on the exopodite.

Antenna.—There are five feathered setae on the endopodite and one seta on the exopodite. The endopodite is elongated and pointed and bears two spinules, one on either margin; the exopodite terminates in a short tooth-like tip.

Telson.—The process formula is 6 + 6.

First zoea (Fig. 4, *a*)

The rostral spine is about six times the length of the posterior spine and has about six longitudinal rows of minute spinules, more or less symmetrically arranged all around upto the tip. The posterior spine is smooth, and so also the ventral margin of the carapace. The eyes are stalked but not fully free from the carapace.

Antennule (Fig. 4, *b*).—The peduncle is unjointed and much shorter than the antennal peduncle. Distally it bears three aesthetascs and three setae.

Antenna (Fig. 4, *c*).—The basal portion of the peduncle is one-segmented with a knob-like protuberance on the ventral side. The exopodite is almost one-third the length of the endopod and bears at its distal end one minute tooth from the inner angle of which a small delicate hair arises. The endopodite is elongated and narrow, gradually tapering distalwards. It bears five minute spines in the distal half along the outer margin, one distally along the inner margin and three in the middle.

Mandible (Fig. 4, *d*).—The upper half of the cutting edge is armed with four teeth arranged in two groups and the lower half bears a few irregularly arranged teeth. No palp.

First maxilla (Fig. 4, *e*).—The proximal endite is provided with about eight bristles and the distal endite with five strong bristles and four simple setae. The palp is single-jointed bearing at its tip two setae and one seta at a slight distance from the tip along the inner margin.

Second maxilla (Fig. 4, *f*).—The palp bears four setae at its tip and five setae in groups of two and three along the inner margin. The scaphognathite is fringed with five plumose setae anteriorly and one prominent plumose seta at its posterior end.

First maxilliped (Fig. 4, *g*).—The exopodite is partially two-segmented bearing four plumose setae at its tip. The endopodite is four-segmented, the first segment bearing one seta, the second two, the third one on the inner margin and one on the outer, and the fourth bears four seta. The basipodite is much larger than the exopodite and bears two setae distally along its inner margin.

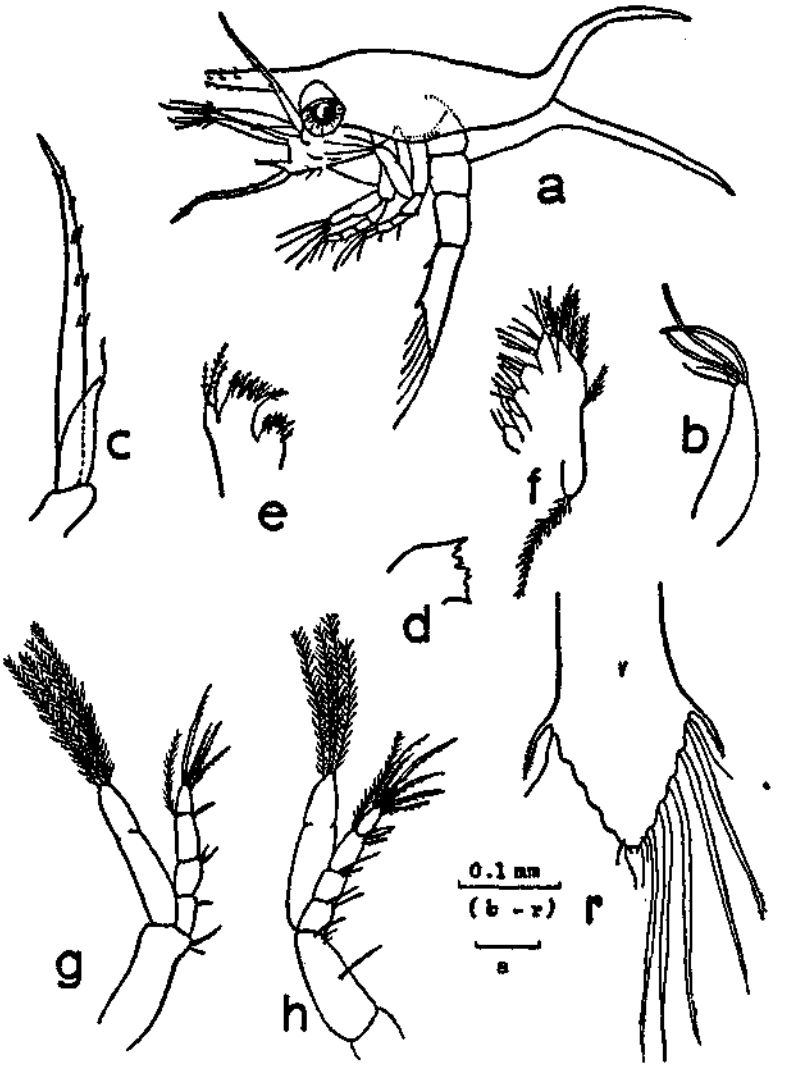

FIG. 4. *Pisidia spinulifrons* (Miers), first zoea. (*a*) entire larva; (*b*) antennule; (*c*) antenna; (*d*) mandible; (*e*) first maxilla; (*f*) second maxilla; (*g*) first maxilliped; (*h*) second maxilliped; (*r*) telson.

Second maxilliped (Fig. 4, *h*).—The basipodite bears four setae. The four segments of the endopod bear two, two, three and six setae respectively.

Other appendages.—The third maxilliped is bilobed but still a bud and the thoracic appendages are seen as rudimentary buds beneath the carapace.

Abdomen.—It consists of five segments and a telson. The fifth segment bears a distinct but small tooth at its postero-lateral angle but no tooth is present on the fourth segment.

Telson (Fig. 4, *r*).—It is much longer than broad, 'arrow-head'-shaped with a small anal spine. The process formula is 9 + 9 and the seventh process is borne outside the central prominence. The first process is a long spine and is armed with minute spinules on both the margins. The distal portion of the third process alone is provided with minute hooks which are more developed on the outer side than on the inner. Just on the inner side of the seventh process, the eighth process is present as a delicate hair. The central prominence bears, on either side, a minute spinule on the inner side of the eighth process, visible only under high magnification, and just on the outer side of this spinule, the 9th process is present as a delicate hair.

Colour.—The rostrum is light orange-red near about its middle and distal portions. A small patch of diffused yellow in front of the gastric region. In the mid-line of the buccal region, an orange-red patch extending from the base of the antennal peduncles to almost the base of the second maxilliped; on the mandible this patch takes the form of prominent, thin longitudinal streaks.

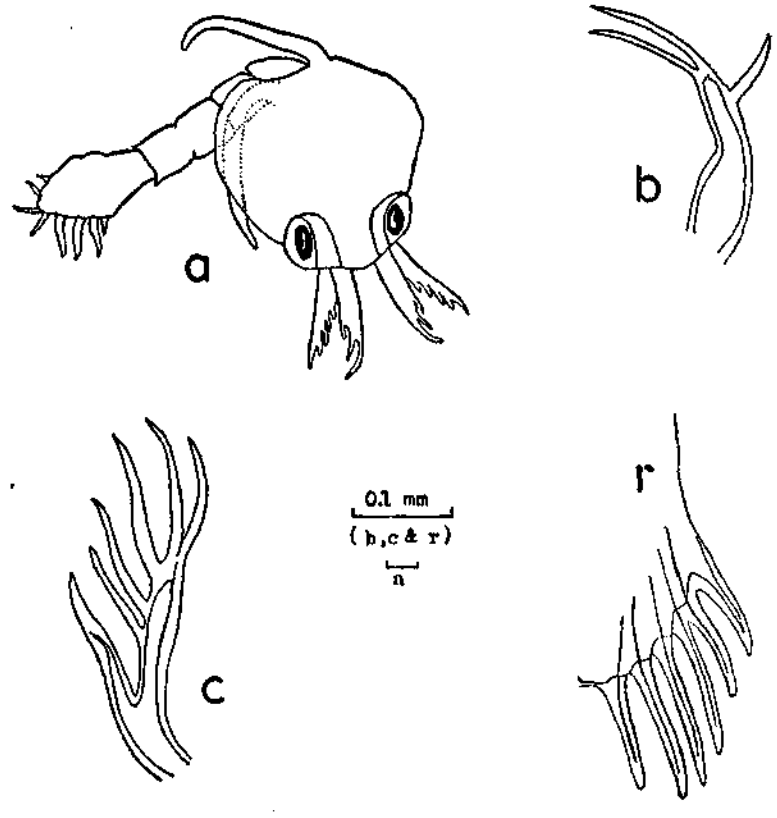

FIG. 5, *Polyonyx hendersoni* Southwell, pre-zoea. (*a*) entire larva; (*b*) antennule; (*c*) antenna; (*r*) telson.

5. *Polyonyx hendersoni* Southwell

Pre-zoea (Fig. 5, *a*)

The egg hatched into a pre-zoea which after swimming for a few hours moulted into the first zoeal stage.

Antennule (Fig. 5, *b*).—It carries two long feathered setae on the endopod and one feathered seta on the exopod.

Antenna (Fig. 5, *c*).—Its endopod is provided with five feathered setae and exopod with one feathered seta. Both have no lateral spines and terminate into spines.

Telson (Fig. 5, *r*).—The telson process formula is 6 + 6.

First zoea (Fig. 6, *a*)

The rostral spine is nearly twice the length of the posterior spine and has about eight longitudinal rows of minute spinules distributed all around, almost to the tip. The posterior spine is edged with small spinules on the sides, these being much larger and closely arranged near the proximal portion, especially on the ventral margin and decreasing in size towards the distal $\frac{3}{4}$ and the remaining $\frac{1}{4}$ being more or less smooth. The spinules on the posterior spine also continue on the carapace so that there are 3 or 4 such spinules present on the postero-lateral margin of the carapace. Though the eyes are stalked they are partially free in the anterior portion.

Antennule (Fig. 6, *b*).—The peduncle is unsegmented and longer than the antenna; it bears distally three aesthetascs and three unequal setae.

Antenna (Fig. 6, *c*).—The basal portion is one-segmented bearing two narrow hornlike styliform processes—exopod and endopod. The exopod is smaller than the endopod and bears near its distal end on the inner side one very minute tooth from the inner angle of which a small hair springs. The exopod tapers gradually towards the distal end, bearing near its tip a sharp minute tooth and slightly away three small setae.

Mandible (Fig. 6, *d*).—The cutting edge has five large teeth on the upper portion and is armed with comb-like arrangement of minute teeth on the ventral portion.

First maxilla (Fig. 6, *e*).—The proximal endite bears five bristles and five hairs whereas the distal endite carries five bristles and four hairs. The palp bears two terminal setae and one seta along the inner margin.

Second maxilla (Fig. 6, *f*).—It has four endites, a palp and a scaphognathite. The palp bears four setae at its tip, and four setae in groups of two along the inner margin. The scaphognathite is anteriorly fringed with six plumose setae and one prominent seta at its posterior end.

First maxilliped (Fig. 6, *g*).—The exopodite is two-segmented and bears four long apical plumose setae. The endopodite is four-segmented, the first segment bears two setae, the second four, the third about five on the inner side and one seta on the outer side, and the fourth segment bears six setae. The basipodite is larger than the exopodite bearing six setae along its inner margin.

Second maxilliped (Fig. 6, *h*).—The basipodite bears three setae. The four-segmented endopodite bears three setae on each of the first, second and third segments but the third segment has one additional seta on the outer margin and the last segment has seven setae.

Other appendages.—The five pairs of thoracic appendages are still rudimentary buds seen beneath the carapace and the third maxilliped is bilobed.

Abdomen.—It consists of five segments and the telson. Each of the fourth and fifth segments bears a tooth on the postero-lateral angle, but the tooth on the fifth segment is longer than that on the fourth.

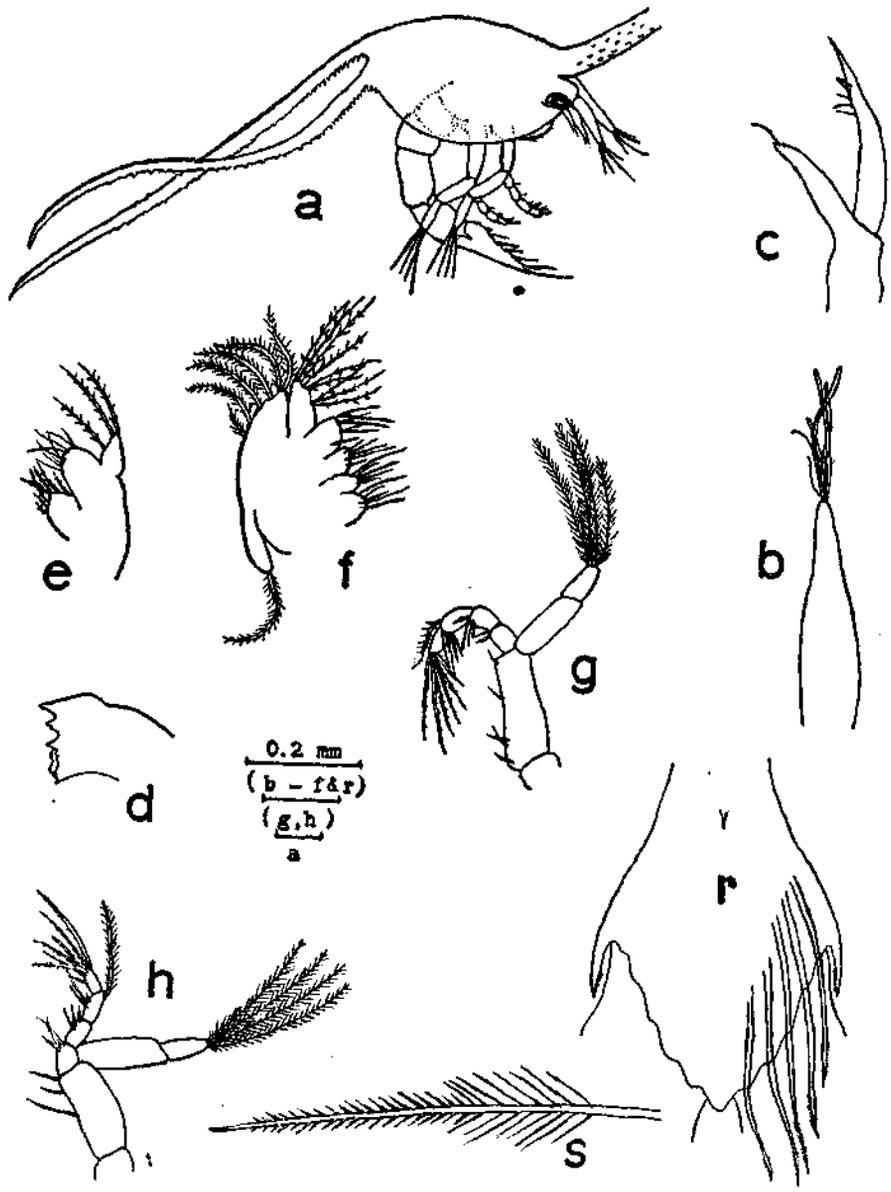

FIG. 6. *Polyonyx hendersoni* Southwell, first zoea. (*a*) entire larva; (*b*) antennule; (*c*) antenna; (*d*) mandible; (*e*) first maxilla; (*g*) first maxilliped; (*h*) second maxilliped; (*r*) telson; (*s*) telson process (magnified).

Telson (Fig. 6, *r*).—It is longer than broad and is 'arrow-head'-shaped with an anal spine. The seventh telson process is situated outside the central prominence. The process formula of the telson

is 8 + 8, the third to the seventh processes being long plumose setae provided with hook-like minute spines in the distal portion and the eighth process being represented by a reduced hair; the hook-like spines are more conspicuous on the third process (Fig. 6, *s*). The first process is armed on its inner margin with seven to nine minute but sharp spinules near its distal portion. The central prominence is bluntly acute.

Remarks.—It is interesting to note that, though all the appendages of this stage were free from the embryonic membrane, the telson processes were only partially free in the portions which were projecting outside the posterior margin of the telson, and the portion inside the telson could be still seen covered with the embryonic membrane. Repeated attempts were made to obtain the larvae with the telson processes completely projecting from the telson and free from the membrane, but the zoeae invariably died in the laboratory before the telson processes were completely free from the embryonic sac.

Discussion

Lebour (1943) observed *Petrolisthes* sp. I and II of Menon (1937) actually belong to *Porcellana* because of the presence of the 5th long seta (= 7th telson process in the present studies) on the telson outside the central prominence. At the time when Lebour put forth her opinion, the knowledge of the Porcellanid larvae was confined to that of only two genera, *viz.*, *Petrolisthes* and *Porcellana*. The present study has showed the possibility that *Petrolisthes* of Menon, considering the characters of the telson of the first larval stage, appears to belong to the corresponding stage of *Pisidia* rather than to *Porcellana* as thought by Lebour. But, at this stage, it is premature to say anything definite about the identity of Menon's larvae since our knowledge of the Porcellanid larvae, of either the Indian or the foreign species, is very limited.

Menon's *Porcellanella* can well be *Petrolisthes* as felt by Lebour (*op. cit.*) on the basis of the telson characters of the first zoeal stage. The present study reveals that Menon's *Porcellanella* may be either *Petrolisthes* or even *Pachycheles*. Menon (1940) described what he believed to be the first post-larva of *Porcellana serratifrons*, his observations being based on the study of a single first post-larva.

Key to First Zoeal Stage of the Known Porcellanid Larvae

1. 7th telson process (= 5th long seta as per Lebour) on central prominence.....2
   7th process outside central prominence.....5
2. Central prominence with microscopic hairs.....3
   Central prominence without microscopic hairs.....4
3. Central prominence with about 10 microscopic hairs.....
   .....*Petrolisthes boscii* (Shenoy and Sankolli)
   Central prominence with at least 4 pairs of microscopic hairs....*Petrolisthes lamarckii*
4. Telson formula 8 + 8.....*Petrolisthes armatus* (Lebour)
   Telson formula 7 + 7.....*Pachycheles natalensis*
5. Central prominence without delicate hair.....*Porcellana platycheles* (Lebour)
   Central prominence with a pair of delicate hairs.....6
6. Central prominence with a pair of minute spinules also.....*Pisidia spinulifrons*
   Central prominence without any spinules.....7
7. 1st process with fine spinules near its distal portion on inner margin only.....
   ..... *Polyonyx hendersoni*
   1st process simple without any spinules on either margin.....8
8. Only 3rd process with distal hooks.....*Porcellana longicornis* (Lebour)
   3rd to 7th processes with distal hooks, those on 3rd being more prominent.....
   .....*Porcellana ornata*

Superfamily THALASSINOIDEA

Family THALASSINIDAE Dana

This family is monotypic and no information is available on the larvae of this family.

Thalassina anomala (Herbst)

(Figs. 7–9)

This animal causes damage to the bunds, backyard of houses, paddy fields and structures situated in the proximity of creeks by its burrowing activities. It is extremely euryhaline and can protect itself from desiccation (Sankolli, 1963). It is these characteristics and the taxonomic importance of this animal which prompted the study on its life-history. Only the first three larval stages could be obtained during the present study.

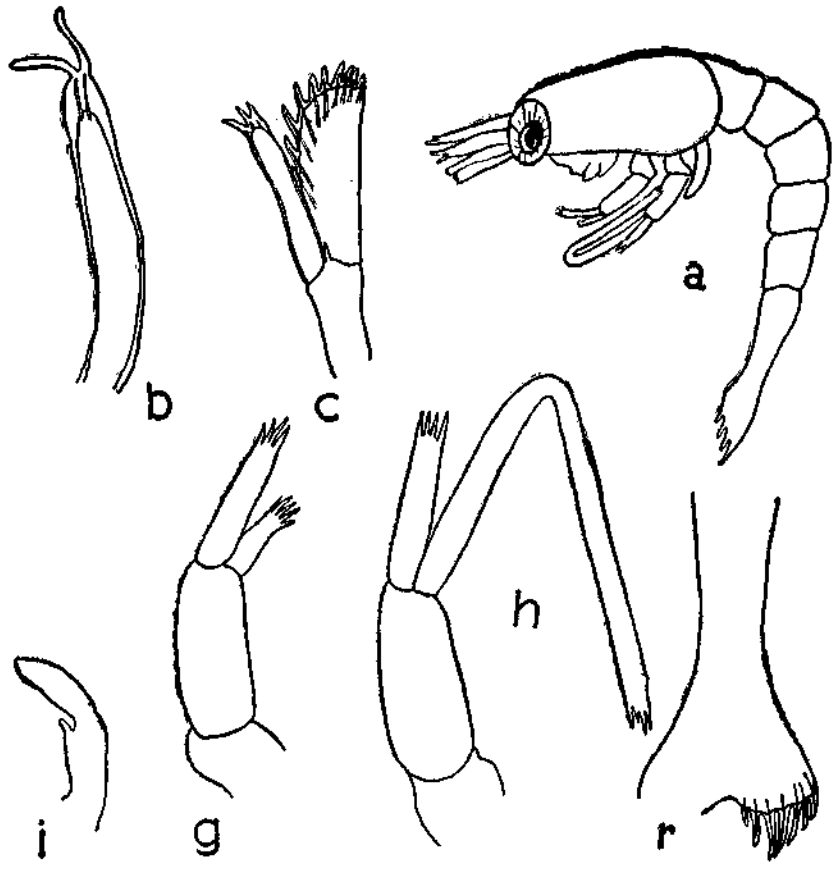

FIG. 7. *Thalassina anomala* (Herbst.), pre-zoea. (*a*) entire larva; (*b*) antennule; (*c*) antenna; (*g*) first maxilliped; (*h*) second maxilliped; (*i*) third maxilliped; (*r*) telson

MATERIAL AND METHODS

As the breeding period of this species is confined to the month of October, egg-bearing females were hard to get. In all, only three berried specimens could be collected during 1961–63. Probably

because of injuries sustained during collecting, one died and the other discarded the eggs. Only one specimen could be kept alive in the aquarium tank.

The larvae were reared in 10 finger-bowls of uniform size, with 20 larvae in each bowl and were fed with live microplankton and freshly hatched *Artemia* nauplii. The water in the bowls was renewed once a day.

Compared to the larvae of *Emerita* or Porcellanids the larvae of *Thalassina* were hardy.

Description of Larval Stages

Pre-zoea (Fig. 7, *a*)

The egg hatches out into a pre-zoea. The pre-zoea swims for about 12–16 hours after which it moults into the first zoeal stage.

The rostrum is kept folded and the appendages are covered by the embryonic sheath. The eyes are sessile.

Antennule (Fig. 7, *b*).—It is unsegmented, elongated with two apical processes. Within the embryonic sheath are seen two clusters of developing setae.

Antenna (Fig. 7, *c*).—The antennal scale is provided with 10 setae on the inner margin; no setae are present on the outer margin. The endopodite bears three apical setae. Ventrally there is a small spine, just near the scale, on the distal margin of the basal segment of the peduncle.

Maxillipeds (Fig. 7, *g, h, i*).—The third maxilliped is much less developed than the remaining two and in all the three pairs, the protopodite is fairly long, *i.e.*, longer than the exopodite. In the first maxilliped the protopodite is nearly two times as long as the exopodite, the latter bears five short setae. The endopodite is nearly one and a one-half times the length of the exopodite, bearing four terminal setae. The second maxilliped is characteristic since its endopodite is very long, slightly less than four times the length of its exopodite, and bears four setae at its distal end. The third maxilliped is a rudimentary bilobed bud.

Telson (Fig. 7, *r*).—The telson is bilobed, with seven pairs of cuticular processes. The second process from the outside is a delicate hair-like process which later becomes the reduced hair of the first zoea. Underneath the cuticular sheath, the future setae of the telson can be seen; three hook-like minute spines can also be seen on the inner margin of the first telson process and four such hooks on the outer margin of the seventh process. The central cleft, dividing the posterior margin of the telson into two lobes, is very shallow and is broader than deep.

First Zoea (Fig. 8, *a*)

The rostrum is narrow, slightly bent, extending upto the tip of the antennular peduncle. The carapace has no teeth or serrations on its ventral margin. The eyes are stalked and free from the carapace. The abdomen consists of five segments as in the pre-zoea and each of the last three segments carries a pair of postero-lateral spines, the spines on the last segment are more prominent than the rest.

Antennule (Fig. 8, *b*).—Terminally it bears one small and two long setae and two aesthetascs. It also bears a sub-apical plumose seta on the inner side.

Antenna (Fig. 8, *c*).—The antennal scale has ten setae along the inner margin and the endopod has three terminal setae, the basal segment has a ventral spine.

Mandible (Fig. 8, *d*).—It is sickle-shaped, the cutting edge is provided with seven minute teeth. There is no palp.

First maxilla (Fig. 8, *e*).—The exopodite is absent and the endopodite is unsegmented bearing three setae at its tip. The coxopodite has three minute stumpy setae and the basipodite has five setae.

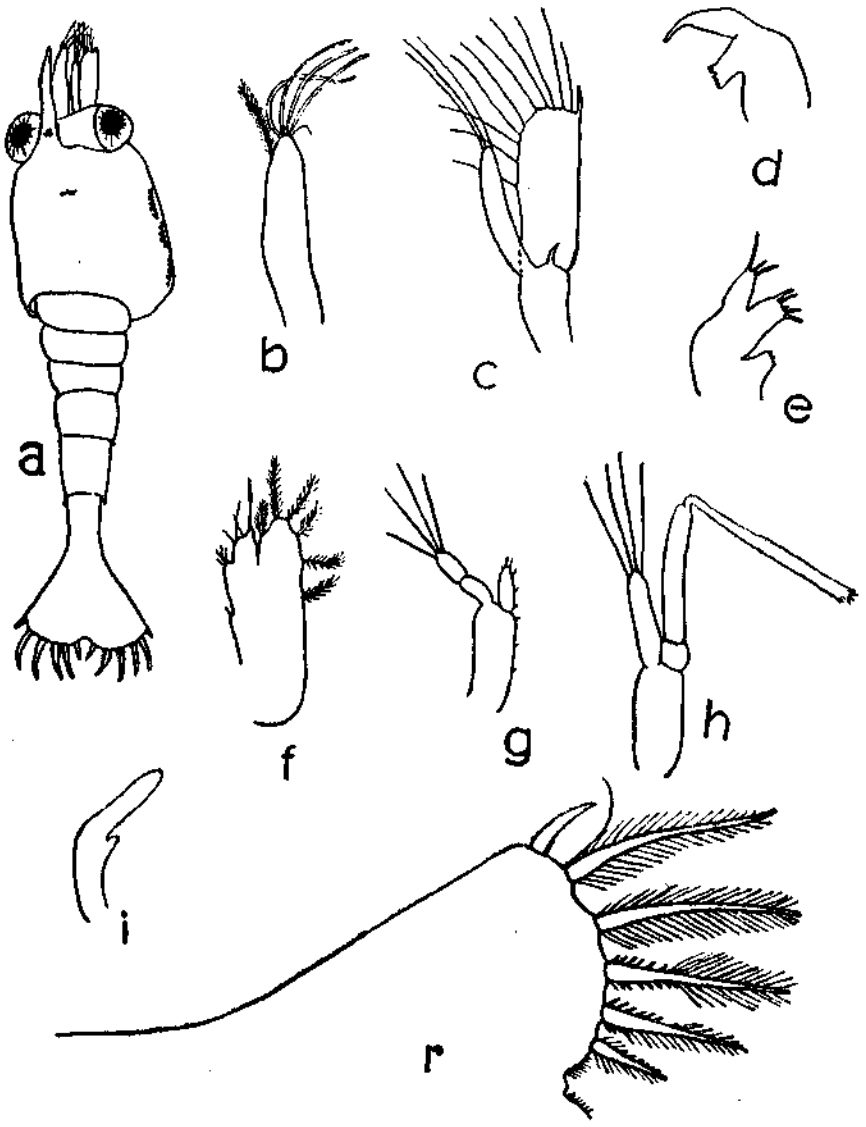

FIG. 8. *Thalassina anomala* (Herbst.), first zoea. (*a*) entire larva; (*b*) antennule; (*c*) antenna; (*d*) mandible; (*e*) first maxilla; (*f*) second maxilla; (*g*) first maxilliped; (*h*) second maxilliped; (*i*) third maxilliped; (*r*) telson.

Second maxilla (Fig. 8, *f*).—Its four endites are poorly developed and are provided with few setae. The scaphognathite bears six plumose setae on the distal part, the proximal part is naked.

First maxilliped (Fig. 8, *g*).—The endopodite is short with about five spiniform short setae at its distal portion and with two short setae on the inner margin. The exopodite is two-segmented,

nearly one and a half times the endopodite in length and bears four plumose setae at the tip. Three short setae are present on the inner margin of the protopodite.

Second maxilliped (Fig. 8, *h*).—The endopodite, which is about four times the length of the exopodite, is three-segmented, the last segment bearing six short slender distal spines.

Third maxilliped (Fig. 8, *i*).—This appendage is still in a rudimentary condition.

Telson (Fig. 8, *r*).—The process formula is 7 + 7, with a convex knob in the middle of the central cleft of the posterior margin. The first process bears six minute spine-like hooks in the proximal part along the inner margin; the fifth process is armed with about six such hooks on the outer and eight on the inner margins in the proximal part; the sixth one with seven hooks along the outer margin and three hooks on the inner margin; the last process with about six hooks in the distal portion along the outer margin only. The posterior margin between the central knob, and the last telson process on either side, is fringed with about seven short delicate hairs, which can be seen only under the microscope.

Colour.—The larva is almost colourless except for the presence of a slightly branched, orange-red chromatophore on the proximal part of the rostrum; three similar but elongated chromatophores are present along either ventral margin of the carapace. On the ventral side, one small chromatophore is present in between the two antennal peduncles, and one between the mandibles and the first maxillae.

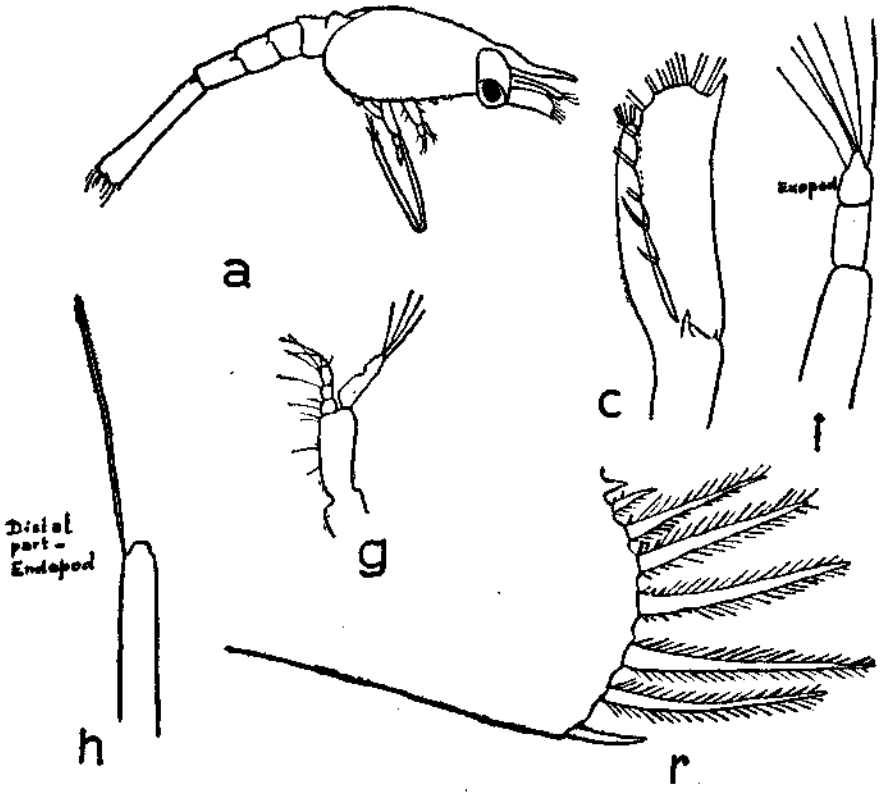

FIG. 9. *Thalassina anomala* (Herbst.), second zoea. (*a*) entire larva; (*c*) antenna; (*g*) first maxilliped; (*h*) second maxilliped; (*r*) telson

Second Zoea (Fig. 9, *a*)

The second zoea shows very few changes from the first.

Antenna (Fig. 9, *c*).—The scale is armed distally with a distinct spine on the outer margin, and there are now 12 setae instead of ten as in the first zoea, along the inner margin. Ventrally there is an addition of a small spine near the outer side of the basal segment of the peduncle and the larger spine has very minute microscopic hooks on its inner margin.

First maxilliped (Fig. 9, *g*).—The endopodite is four-segmented and its segments bear two, two, one and two setae respectively beginning distally. The protopodite bears five setae in three groups of two, two and one.

Second maxilliped (Fig. 9, *h*).—The six terminal setae of the endopodite are armed with peculiar microscopic hooks which extend slightly farther from the middle of the setae to its distal end; the hooks, in the middle portion, are somewhat spine-like, directed backwards with their tips curving slightly outwards.

Third maxilliped (Fig. 9, *i*).—The exopodite is two-segmented.

Telson (Fig. 9, *r*).—Though the telson formula remains the same as in the first zoea, *i.e.*, 7 + 7, the reduced hair, *i.e.*, the second process, is absent in this stage and there is an addition of one small process on either side of the central cleft. The central knob, which was convex in the first zoea, now becomes elongated and pointed. The delicate hairs on either side of the cleft have disappeared. The fourth process has five spines on the outer margin and four on the inner margin; the fifth process has three spines on either margin; in the sixth process there are about eight proximal spines and four in the distal portion, along the outer margin, and only one spine, that too in the proximal portion on the inner margin.

Discussion

The superfamily Thalassinoidea, to which *Thalassina anomala* (Hebrst) belongs, has been included in Macrura by several authors. Calman (1909), Balss (1927 and 1957) and Barnard (1950) are of opinion that it must belong to Anomura. As far as the larval characteristics of *T. anomala* are concerned, they agree well with those of the superfamily Paguroidea, considering the list of characters drawn by MacDonald *et al.* (1957) for Paguroidea. The indication of a hair between the outer two telson spines on each side—a characteristic feature of a majority of the Anomuran zoeae —and its distinct presence in the first zoea of *T. anomala*, probably justifies the inclusion of the Thalassinoidea in Anomura.

Superfamily **HIPPOIDEA**

Family HIPPIDAE Latreille

***Emerita holthuisi* Sankolli**

(Figs. 10–13)

The present knowledge of the larval development of the Indian species of Hippidae is limited to the pioneering work of Menon (1933) who described five larval and one post-larval stages of *Emerita emeritus* (L.) = *E. asiatica* H. Milne-Edwards, the only species recorded from the east coast of India. He collected the larvae from the Madras plankton. As he found it difficult to get the eggs hatched in the laboratory he could not describe the first larva.

A study of the literature on the subject shows that larval development of only two genera, *Emerita* and *Hippa*, of the family Hippidae, has been studied. Al-Kholy (1959) described the first

zoeal stage of *Hippa adactyla*, hatched in the laboratory. Smith (1877), Faxon (1879 *a*), and Rees (1959) studied the larvae of *E. talpoida* and Johnson and Lewis (1942) studied those of *E. analoga*. Smith described an incomplete series of larval stages obtained from the plankton of Vineyard Sound, Mass. Faxon was able to obtain the first zoeal stage in the laboratory, whereas Rees worked out the complete life-history of *E. talpoida* from larvae hatched in the laboratory. Johnson and Lewis described five zoeal stages for *E. analoga*, the first stage being obtained in the laboratory and the remaining stages from the plankton.

Larval development of *E. holthuisi* comprises six zoeal and a megalopa stages, as observed in the laboratory.

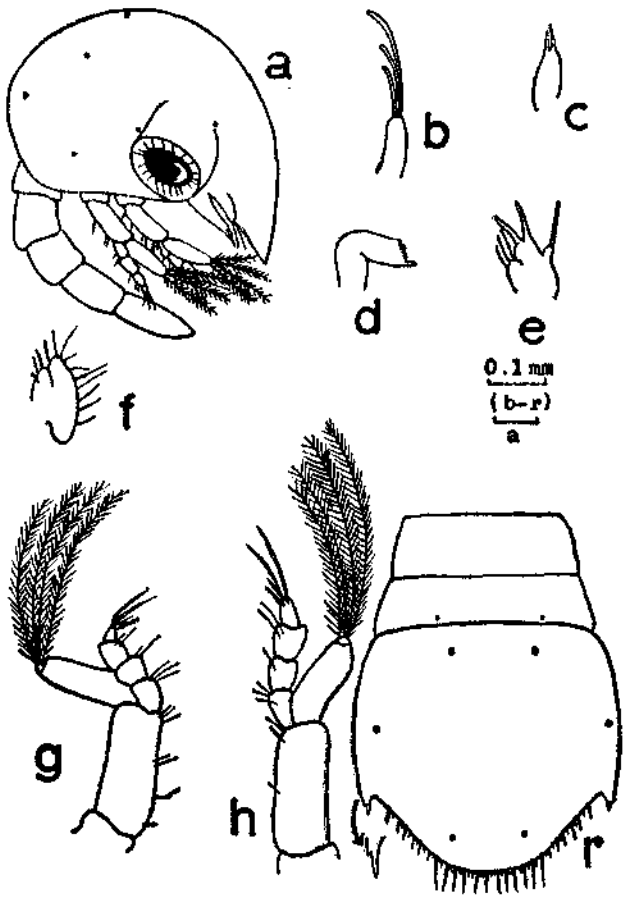

FIG. 10. *Emerita holthuisi* Sankolli, first zoea. (*a*) entire larva; (*b*) antennule; (*c*) antenna; (*d*) mandible; (*e*) first maxilla; (*f*) second maxilla; (*g*) first maxilliped; (*h*) second maxilliped; (*r*) telson.

MATERIAL AND METHODS

Berried females of *E. holthuisi* were collected from the beach at Ratnagiri (Mirya), and kept in sea-water aquaria until the eggs hatched out into the first zoeal stage. Method for rearing larvae was more or less the same as suggested by Rees (1959), *i.e.*, using sea-water which had been filtered through glass wool and inoculated with 2,00,000 units of penicillin per litre. Rees used *Nitschia* sp.

and freshly hatched *Artemia* nauplii for feeding the larvae, but, in the present case, only *Artemia* nauplii could be used. The larvae were observed to feed readily upon this food.

During the course of the development, the temperature of the water varied from 26° to 29° C.

Results

The average time required by each of the six zoeal stages to develop into the megalopa stage is given in Table I. All the individuals entered the megalopa stage after passing through six distinct zoeal stages; there was no seventh stage, as in *E. talpoida*.

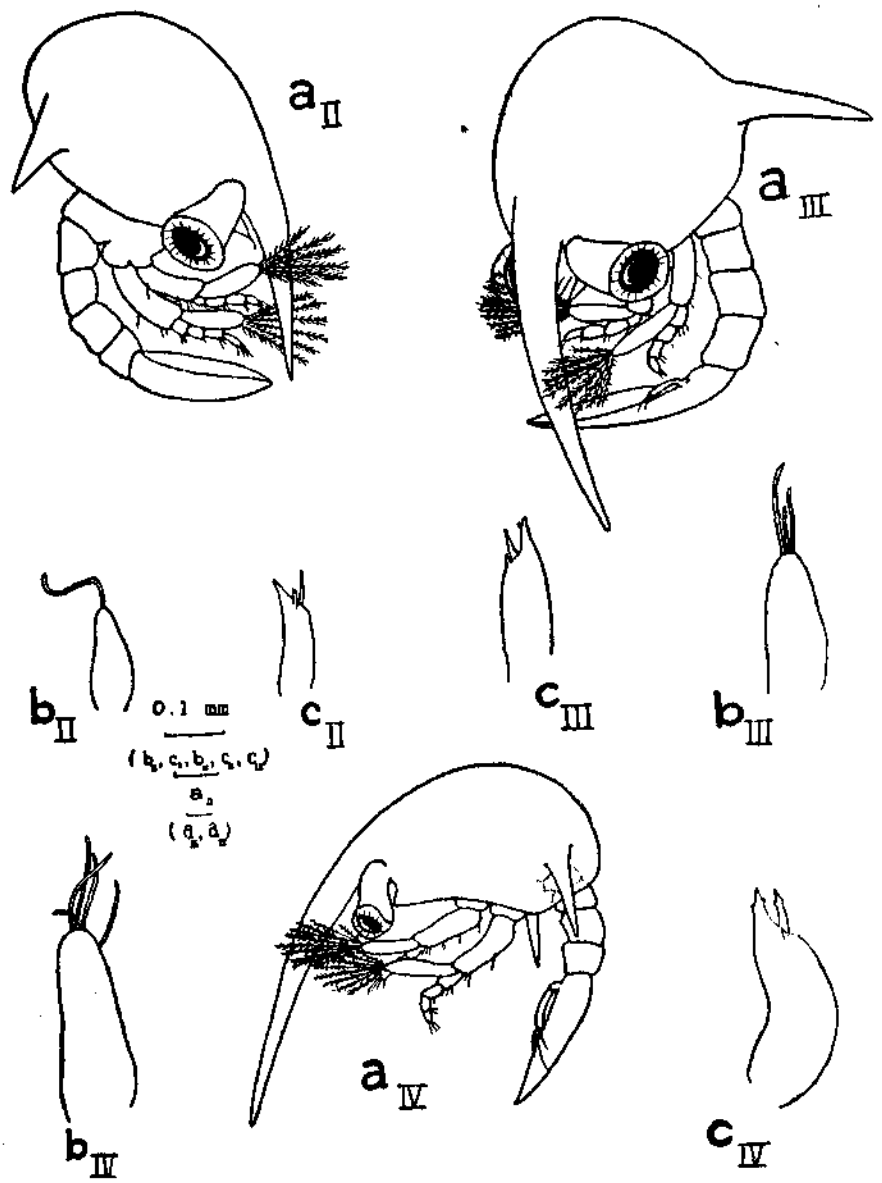

Fig. 11. *Emerita holthuisi* Sankolli, second to fourth zoea. (*a*) entire larva; (*b*) antennule; (*c*) antenna; (Roman suffixes indicate the corresponding larval stages).

Although the percentage of larval mortality was not high, it was observed that mortality occurred mainly during the inter-moult period, the reason for which has already been suggested by Rees (1959). It was also observed that those larvae which died at the time of moulting were struggling hard to get free from the old exuviae which were still adhering to the body on the regions of the maxillipeds and the rostral tip. This is in agreement with the observations made by Rees.

TABLE I

Average duration of each zoeal stage in the development of E. holthuisi

Stage	I	II	III	IV	V	VI	Megalopa
Average No. of days spent in each stage ..	4	3	4	4	4	8	

DESCRIPTION OF LARVAL STAGES

First Zoea (Fig. 10, *a*)

In general appearance, the first zoeal stage is quite similar to the corresponding stage of *Emerita emeritus*, *E. analoga* and *E. talpoida*. The characteristic feature of this stage is the absence of lateral spines on the carapace. The carapace is smooth and rounded, translucent and almost colourless and is produced anteriorly to form a short broad but conical rostrum. The eyestalks are stumpy and are not free from the carapace, lying more or less obliquely. The abdomen, when the larva is not swimming, is flexed ventralwards in such a manner that the telson is held almost parallel to and beneath the carapace. The exopodites of the maxillipeds bear four plumose setae.

Antennule (Fig. 10, *b*).—It is unsegmented, short and thick bearing three unequal terminal setae.

Antenna (Fig. 10, *c*).—It is also unsegmented and has two spine-like processes and a much smaller spine at the tip.

Mandible (Fig. 10, *d*).—It has a right angular bend about its middle and its cutting edge is armed with a stout tooth, which is followed by two small triangular teeth, then six to seven slender long setiform processes and finally a small triangular tooth.

First maxilla (Fig. 10, *e*).—The endopodite is much smaller than the exopodite and bears three setae. The exopodite is distally divided into two horn-like setae and near about the middle of its outer margin there is a small palp, bearing a long seta.

Second maxilla (Fig. 10, *f*).—The protopodite bears three setae at its distal end and a small one on the inner side slightly beyond the middle. The scaphognathite bears about nine plumose setae on the outer margin.

First maxilliped (Fig. 10, *g*).—The coxopodite is short and the basipodite is long. On the inner margin of the basipodite, are four groups of setae. In the first group of three setae (starting from the distal end of the basis), one is short and stout and is armed with minute spines. This is followed by a group of two setae; then after a short distance a single seta near its articulation with the coxopodite. The endopodite is four-segmented; first segment bears three setae of which the shorter and stouter one is armed with minute spines; second segment has two unequal setae, the stouter one being provided with minute spines; third segment has two setae; last segment bears at its tip four setae, two long and two small. Except for one of the small setae, all the other three bear small spines along their inner margins. The proximal segment of the two-segmented exopodite is nearly as long as the endopodite and its distal segment, which is very short, bears four long plumose setae.

Second maxilliped (Fig. 10, *h*).—The endopodite, which is a little longer than the exopodite, bears on its second segment a single seta. The basipodite bears two setae near its distal end and a single seta about its middle on the inner margin. Except for these features, it does not differ from the first maxilliped.

Abdomen.—It consists of five segments; the sixth segment is fused with the telson.

Telson (Fig. 10, *r*).—It is broader than long as in *E. talpoida.* The posterior margin is prominently convex and is armed with a row of 25-26 spines, with minute denticles in between. Of these, the eighth from each side is the longest, and nine to ten spines in between, being of intermediate length. The lateral margins end in a prominent tooth with a minute notch on the outer side.

Colour.—The larva is almost colourless except for the presence of a few minute bright orange-yellow and dark brown chromatophores. The distribution of the orange-yellow chromatophores is as follows: one each at the middle of the lateral side and one on either side of the posterior portion of the carapace, one in the cardiac region and on either side of it, at the middle of the fourth segment, on either side of the fifth segment of the abdomen, and at the middle of either side of the telson. Of the dark brown chromatophores, two are present in the anterior region of the carapace, very near to the eyestalks, and a pair on the telson just near its union with the abdominal segment.

Second Zoea (Fig. 11, a_{II})

The lateral spines develop on the carapace and the rostrum becomes considerably longer. These two features develop progressively in the subsequent zoeal stages. The two lateral spines are directed downwards and backwards. The eyestalks are longer and free from the carapace and the eyes are directed forwards than in the first stage. The number of plumose setae on the exopodite of the maxillipeds is now increased to six.

Antennule (Fig. 11, b_{II}).—Instead of three setae present in the first zoea the antennule has only a single long stout seta.

Antenna (Fig. 11, c_{II}).—As in the first zoea.

Mandible.—As in the first zoea.

First maxilla.—Except for the exopodite which now bears three long teeth, there is no difference from the corresponding appendage of the first zoea.

Third Zoea (Fig. 11, a_{III})

The carapace is pear-shaped when viewed laterally. The rostrum is slightly less than twice the length of that of the second zoea, and the eyestalks have enlarged. Uropods make their appearance and the number of setae on the exopodites of the maxillipeds increases to eight.

Antennule (Fig. 11, b_{III}).—The peduncle bears three setae as in the first zoea.

Antenna (Fig. 11, c_{III}).—The outer dentiform process has one small spine near its tip on the inner side.

Mandible.—No change.

First maxilla.—Practically there is no difference from the previous stage.

Second maxilla.—The scaphognathite is provided with ten plumose setae.

Maxillipeds.—There are now eight plumose setae on the exopodite. No additional thoracic appendages are seen through the carapace.

Uropods.—It is uniramous and composed of a stout unjointed basal segment carrying a slender lobe which later becomes the exopodite. The lobe bears two unequal setae at its tip. The uropods are hidden entirely beneath the telson.

Fourth zoea (Fig. 11, a_{IV})

In this stage, the larva has ten plumose setae on the exopodites of the maxillipeds and four on those of the uropods. The rostrum exceeds the length of the carapace.

Antennule (Fig. 11, b_{IV}).—It bears one small seta in addition to the three setae at the tip and one long seta on the inner side near its distal end.

Antenna (Fig. 11, c_{IV}).—The outer dentiform process has two small spines and the inner one has one small spine.

Mandible.—No change.

First maxilla.—No change.

Second maxilla.—The scaphognathite has 16–18 plumose setae on its outer margin extending almost to its posterior end. The anterior end of the scale projects beyond the protopodite.

Maxillipeds.—The exopodites bear ten plumose setae at their tips. The third maxilliped is represented by a small rudiment.

Abdomen.—Each of the four free abdominal segments bears a pair of small rudimentary buds, the future pleopods.

Uropods.—The exopodite bears four unequal setae and there is general increase in size. There are no rudiments of endopodite.

Fifth Zoea (Fig. 12, a_V)

This stage is characterized by (i) the presence of 11 or 12 setae on the exopodites of the maxillipeds, (ii) the appearance of the endopodite of the uropods and (iii) the presence of the rudiments of the five thoracic appendages which are now seen through the carapace.

Antennule (Fig. 12, b_V).—There are seven setae, arranged at the tip and on the inner margin.

Antenna (Fig. 12, c_V).—A knob-like rudiment of the future flagellum has developed and the outer dentiform process has four spines.

Mandible.—As in previous stage.

First maxilla.—There is no change.

Second maxilla.—The scaphognathite has 27–31 plumose setae.

Maxillipeds.—The exopodites have 11 or 12 plumose setae. Twelve appears to be the more common number, though some of the specimens had eleven setae on one or more maxillipeds. In none of the individuals, the number was found to be less than eleven or more than twelve.

Abdomen.—As in the fourth zoea.

Uropods.—The endopods now appear as small buds below the exopods. The exopod has increased in length and bears five setae at the tip.

Sixth Zoea (Fig. 12, a_{VI})

In this stage, the pleopods are uniramous and the number of plumose setae on the first and second maxillipeds is 13–14.

Antennule (Fig. 12, b_{VI}).—There are twelve setae in four groups of four, four, two and two counting from the tip.

Antenna (Fig. 12, c_{VI}).—The flagellum has very much increased in size reaching well beyond the antennule.

Mandible (Fig. 12, d_{VI}).—There is no change except for the slenderness of the apophysis.

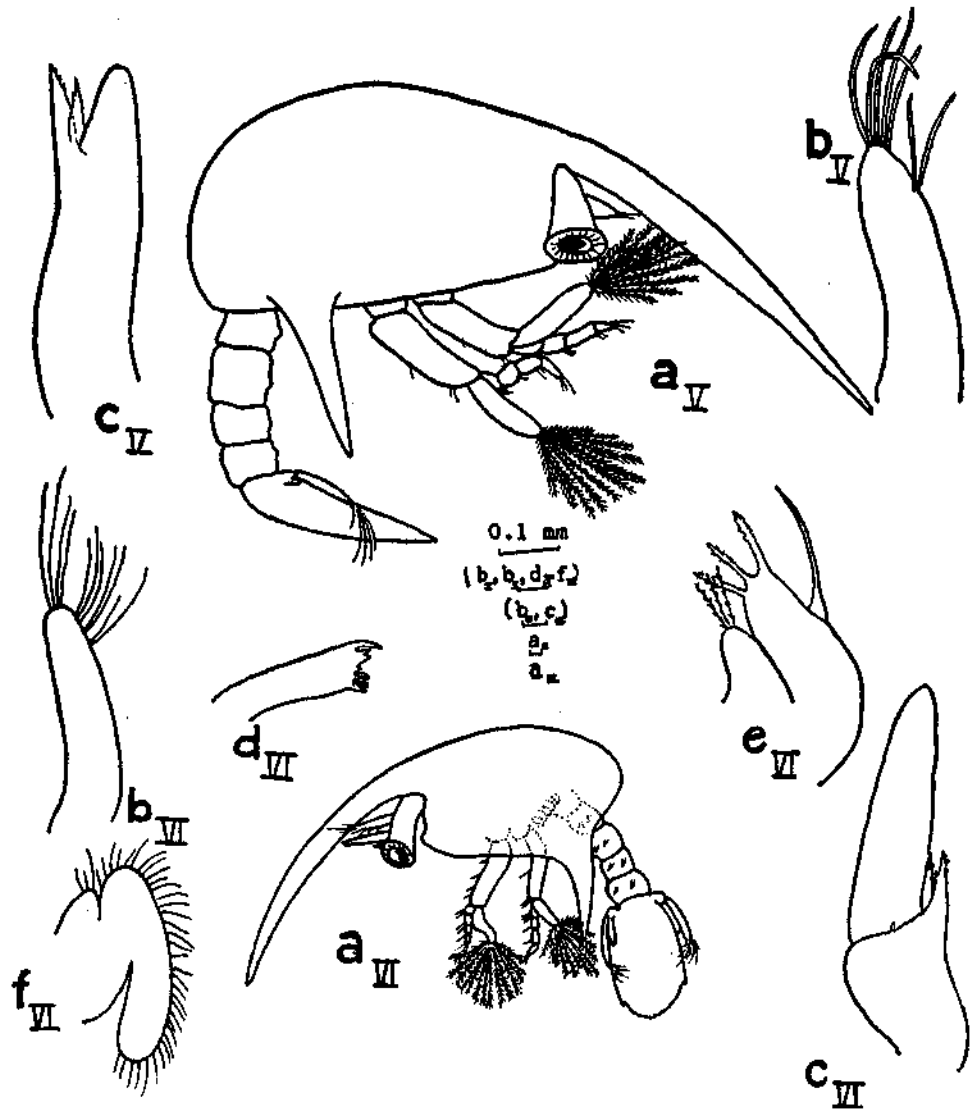

FIG. 12. *Emerita holthuisi* Sankolli, fifth to sixth zoea. (*a*) entire larva; (*b*) antennule; (*c*) antenna; (*d*) mandible; (*e*) first maxilla; (*f*) second maxilla (Roman suffixes indicate the corresponding larval stages).

First maxilla (Fig. 12, e_{VI}).—There is no much change from the previous stage except for the appearance of minute spines on the three teeth-like processes of the previous stage.

Second maxilla (Fig. 12, f_{VI}).—The outer margin of the scaphognathite is fringed with 35-37 plumose setae.

Maxillipeds.—There are 13-14 plumose setae on the exopodite. The third maxilliped becomes appreciably longer than in the previous stage.

Abdomen.—There is a pair of uniramous, unsegmented pleopods present on each of the abdominal segments, from second to fifth.

Uropods.—The exopodite bears six or seven unequal setae at its distal end. The endopodite increases considerably in length and is now about two-thirds the length of the exopodite.

Megalopa (Fig. 13, *a*)

During the course of this study, all the individuals of the sixth zoea directly entered into the megalopa stage, without undergoing any additional zoeal stage, as observed by Rees (1959).

Except for its relatively large eyes, stout eye stalks and the presence of four pairs of pleopods which are unlike those of the adults, the magalopa resembles the adult very closely. Unlike the adult, the megalopa can swim both forwards and backwards, the abdomen being flexed forwards beneath the cephalothorax. This movement in both directions lasted for only 24 hours, after which it was observed to move or swim only backwards; the abdomen was rarely observed to be extended. It never moved forwards even when disturbed from behind.

Antennule (Fig. 13, *b*).—The peduncle is composed of three basal segments and two flagella as in *E. emeritus*. The dorsal flagellum consists of eight segments; the first segment was naked, whereas the remaining seven segments showed the following setation 3, 2, 3 , 4, 3, 3 and 5 on the ventral side. The ventral flagellum is represented by a small rudiment bearing two apical setae.

Antenna (Fig. 13, *c*).—It consists of a scale-like exopodite, three-segmented endopodite with a long flagellum. The distal part of the exopodite is more broadly rounded than that of *E. talpoida*. The flagellum is stout tapering gradually to its distal end and is composed of 20 segments. Each segment bears four setae of which the two outer ones are long and plumose and the inner two are short and naked.

Mandible (Fig. 13, *d*).—It very much resembles the mandible of the adult, except for the presence of setae. It consists of two parts, a broad lamellar lobe with three stout setae on its lateral margin and an inner palp fringed with setae along its anterior and median margins.

First maxilla (Fig. 13, *e*).—It differs from that of *E. talpoida* in not having a long seta at the tip of the palp, and from that of *E. emeritus*, in not having a minute tooth at about the middle of the outer margin of the palp. The endopodite is broad and is provided with setae of unequal length along its distal and inner margins. The exopodite is long and is armed with short setae at its distal end and along the inner margin. There is a long plumose seta at the beginning of the outer margin. Palp is a sac-like lateral projection.

Second maxilla (Fig. 13, *f*).—It is composed of three endites, a small triangular endopodite and a scaphognathite. The inner endite is bordered with setae a little down on the inner margin, and the outer endite is fringed with setae from the tip along the inner margin. In between these two is a small slender endite bearing a single seta.

First maxilliped (Fig. 13, *g*).—The protopodite is elongated, and flat with setae along its inner margin and postero-internal portion. The endopodite is a long lobe, bearing two thin setae at the tip. The exopodite is two-segmented, the proximal segment bearing a few short setae on the outer margin near its articulation with the distal segment, which is knob-like and bears plumose hairs all along the margin.

Second maxilliped (Fig. 13, *h*).—It differs very little from the corresponding appendage of the adult. The third segment of the five-segmented endopodite is nearly straight and does not make the right-angled bend as in the adult. The exopodite is two-segmented, the basal segment, unlike

as in the adult, tapers gradually; the oval terminal segment is smaller in the megalopa than in the adult. The setae of this appendage are shorter and fewer than in the adult.

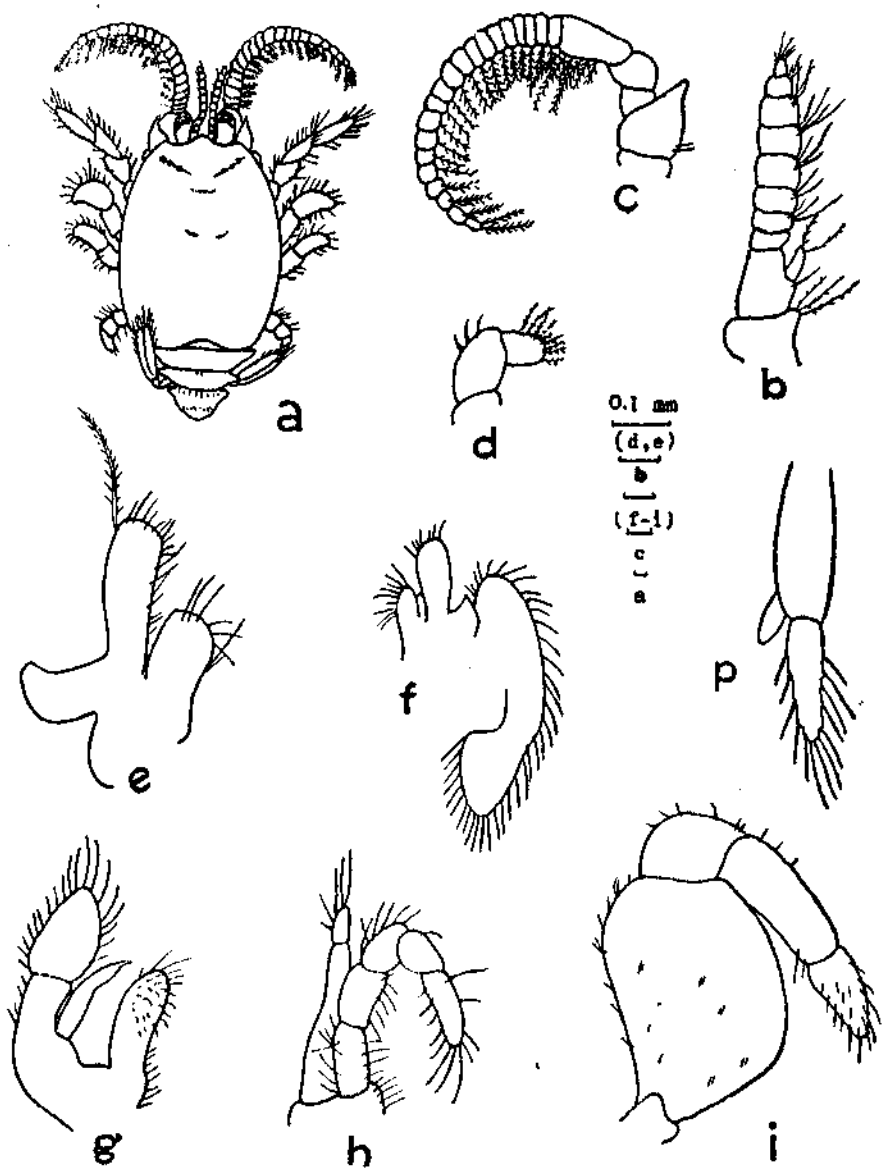

FIG. 13. *Emerita holthuisi* Sankolli, megalopa. (*a*) entire larva; (*b*) antennule; (*c*) antenna; (*e*) first maxilla; (*f*) second maxilla; (*g*) first maxilliped; (*h*) second maxilliped; (*i*) third maxilliped.

Third maxilliped (Fig. 13, *i*).—It is a broad operculiform appendage with a three-segmented palp at its distal end, The palp is stout and its last segment is much shorter than in the adult.

Pereiopods.—The pereiopods are very much like those of the adult. The first four pairs are adapted for burrowing, but the fourth pair projects backwards. The fifth pair is very slender, chelate and held within the branchial chamber.

Abdomen.—The abdomen now consists of six segments, and a triangular telson. The first segment is small and in the posterior margin of the carapace. The second segment is the largest with a broad lamellar expansion on each side and is about five times as wide as long. The third, fourth and fifth segments are rounded on the outer margins and successively decrease in size posteriorly. The sixth segment is wider than the fifth and is the longest segment of the abdomen.

Pleopods (Fig. 13, *p*).—Four pairs of pleopods are borne on the second to the fifth abdominal segments. The pleopods are biramous and consist of a long basal stalk, a lobe-like exopodite and a knob-like endopodite. The exopodites of the four pleopods bear 11, 12–14, 13 and 14–15 plumose setae respectively. The endopodites are provided with a series of minute hooks at their distal portions and they gradually increase in size from the first to the fourth pleopod.

Uropods.—These appendages differ slightly from those of the adult. Each uropod is composed of three parts, a two-segmented protopodite, an exopodite and an endopodite. The distal segment of the protopod is much longer, stouter and more flattened than the proximal segment which is short and round. Both the exopodite and the endopodite are more or less alike in shape; oval and broadly rounded at the tip and fringed with long setae which decrease in length along the sides.

Colour.—The colouration is very much similar to that of the megalopa (first post-larva) of *E. emeritus* as described by Menon (1933). On the dorsal side of the carapace a little away from the frontal lobes, there is on each side an oblique band of finely branched red chromatophores. The bands do not meet as in *E. emeritus* but thin out towards the median line of the carapace. On either side of the posterior end of the sixth abdominal segment, there is a light red branching chromatophore, from which a branch runs into the antero-lateral portion of the telson and continue to the protopodite of the uropods, unlike as in *E. emeritus*.

Discussion

From the foregoing account, it can be seen that *E. holthuisi* passes through six distinct zoeal stages before it moults into the megalopa. One of the chief characteristics of the six zoeal stages was the number of plumose setae on the first two maxillipeds, which was 4, 6, 8, 10, 11–12 and 13–14 corresponding to the first, second, third, fourth, fifth and sixth zoeal stages respectively. Menon (1933), describing the larval development of the *E. emeritus*, observed that there are only five zoeal stages, the sixth being the megalopa. So far as the number of plumose setae on the maxillipeds is concerned these five stages correspond to the first five stages of *E. holthuisi*, described above. However, the sixth zoeal stage with 13 or 14 plumose setae was not obtained by Menon in his planktonic material. He stated that the fifth zoea obtained from plankton moulted directly into the megalopa stage in the laboratory. Besides the number of setae on the maxillipeds, the third, fourth and fifth zoeal stages described by Menon are in a more advanced stage of development and correspond to the fourth, fifth and sixth stages of *E. holthuisi*, considering such characters as thoracic limb buds, pleopods, etc. This sort of difference in the development may be due to the larvae found in nature and those reared in the laboratory.

A similar case of differential development found in nature and that reared in the laboratory has been described by Rees (1959) in the case of *E. talpoida*. Smith (1877) described three stages in the development of *E. talpoida* from the plankton before the larvae pass into megalopa. Later Faxon (1879 *a*), who got only the first zoeal stage from the laboratory hatching, suggested that one or more stages remain to be discovered between the first and the earliest described by Smith. However, Rees (1959), who succeeded in rearing *E. talpoida* in the laboratory from the first zoea to the megalopa, got six zoeal stages and in a few instances obtained a seventh zoeal stage before the megalopa. His experience was that each zoeal moult resulted in an increase in the number of setae borne

Table showing the salient features of the Isi

Characters	*Petrolisthes boscii* (Shenoy and Sankolli)	*P. lamarckii*	*P. armatus* (Lebour)	*P. rufescens* (Gohar *et al.*)	*Pachycheles natalensis*
Rostrum	4 times posterior spine, with 10 longitudinal rows of spinules	6-8 times posterior spine; with 6 longitudinal rows of spinules	Nearly 4 times posterior spine; with small spinules and protuberances	2 times the posterior spine, with numerous spinules on ventral margin only	3 times posterior spine with 1 to 3 longitudinal rows of minute but long spinules only on ventral margin
Posterior spine of carapace	With minute blunt tubercle-like spinules	With small stout spinules	With small spinules	With 6 long spinules at base on ventral margin only. (In Fig. 15 spinules are shown from base to all along the posterior spine)	Almost plain but for a few blunt tubercles on ventral margin only
Ventral margin of carapace	Plain	Plain	Posterior part with spinules of posterior spines	Plain	Plain
Antennule	3 aesthetascs + 3 setae	3 aesthetascs + 3 setae	3 aesthetascs + 3 setae (as per fig.)	Without aesthetascs but with 7 simple setae	3 aesthetascs + 3 setae
Antenna	Endopod slightly longer than exopod and with 3 short setae and 1 minute tooth	Endopod nearly 2 times exopod with 3 short setae and 1 minute tooth	..	Endopod about 3/5 the exopod and without any hair or setae or spines	Endopod slightly longer than exopod with 3 spine-like teeth
Telson	Broader than long; process formula 7+7, 7th seta on central prominence, all the 5 long setae with coarse hooks, most conspicuous on 3rd seta. Central prominence with about 10 very small delicate hair	Broader than long; process formula 7+7, 7th seta on central prominence, all 5 long setae with coarse hooks, most conspicuous on 3rd seta. Central prominence with comparatively lesser number of very small delicate hair	As broad as long; process formula 8+8, 7th seta on central prominence, all 5 long setae with coarse spines at tip, on 3rd seta these spines are more numerous and longer. Central prominence without any delicate hair	Nearly as broad as long; process formula 6+6 (nothing can be said about the presence of 7th process on or outside central prominence). All 5 setae are long and plumose and the 1st process is smooth and short	Slightly broader than long; process formula 7+7, 7th seta on central prominence, all the 5 long setae with minute spinule-like hooks near distal end. Central prominence without any delicate hair

zoeal stage of so far known Porcellanid larvae

Porcellana ornata	*P. longicornis* (Lebour)	*P. platycheles* (Lebour)	*Pisidia spinulifrons*	*Polyonyx hendersoni*
Nearly 3 times posterior spine with 4 to 6 rows of spinules	3 times posterior spine and never twice	2 times posterior spine and never less	6 times posterior spine with 6 longitudinal rows of spinules, symmetrically placed all around	2 times posterior spine with 8 longitudinal rows of spinules
2 rows of tubercles	With small spines but the 2 nearer the origin being more conspicuous than the rest	With a few short spines	Plain	Small spinules on ventral margin
Plain	With a few rounded protuberances in the posterior part only (as per fig.)	..	Plain	Spinules of posterior spine continue on ventral margin
3 aesthetascs + 3 setae	3 aesthetascs + 3setae (as per fig.)	..	3 aesthetascs + 3 setae	3 aesthetascs + 3 setae
Endopod twice exopod and with 6–8 spinules	..	..	Endopod 3 times exoped and with about 8 spinules	Endopod slightly longer than exopod and with 1 spinule and 1 delicate hair
Longer than broad; process formula 8+8, 7th seta outside central prominence, 3rd to 7th setae with simple hooks near distal end, 1st telson process simple. Central prominence with a pair of hair	Process formula 8+8, 7th seta outside central prominence, only 3rd seta with plumose hook-like spines at tip, 1st telson process simple, Central prominance with a pair of hair	Process formula 8+8; 7th seta outside central prominence, 3rd seta with long fine spines at tip, coarser, however, than on main part, 1st telson process simple. Central prominence without any hair	Longer than broad; process formula 9+9, 7th seta outside central prominence, only the 3rd seta with simple hooks, 1st telson process with minute hooks on both sides. Central prominence with a pair of minute spinules and two pairs of hair	Longer than broad; process formula 8+8 7th seta outside central prominence, all 5 long setae with spine-like hooks being most conspicuous on the 3rd seta, 1st telson process with 7–9 minute long and sharp spinules on its inner side near its distal portion only. Central prominence with a pair of hair

on the exopods of the first and second maxillipeds. He further stated: "In the laboratory their number never increased by more than two setae at any moult." He also found that Smith's three stages obtained from the plankton corresponded to the third, fourth and fifth zoeal stages reared by him in the laboratory and that the larvae from nature possessed such advanced features of development as the appearance of thoracic limb buds, pleopods, etc. As discussed above, *E. holthuisi* also has more zoeal stages when reared in the laboratory than *E. emeritus* described by Menon from plankton. Attempts to collect the various zoeal stages of *E. holthuisi* from plankton were not successful.

Gurney (1942) suggests that the abnormal stages are met with in the laboratory rearings where the conditions are not as normal as to be expected in the natural environment. Even then, owing to certain changes in the natural environments such extra stages are also met with in nature as observed by Gurney (1942), Faxon (1879 *b*), Lebour (1940), Gurney and Lebour (1941) and Broad (1957 *a*). It thus appears that the environmental factors such as temperature, salinity, food, etc., may have some influence on the developmental stages. Influence of environmental conditions on the development has not been much studied, except that Broad (1957 *b*) has shown a direct relationship between the diet of the larvae and the rate of development and frequency of moulting. Rees (1959) has also shown that all the larvae fed on only *Nitzschia* sp. died while still in the first zoeal stage. He, however, succeeded in rearing the larvae only when newly hatched *Artemia* nauplii were added to *Nitzschia*. Besides the importance of food, no other factor seems to have been dealt with by any one. *E. emeritus* is known to breed at least for eight months during the year (Menon, 1933). Berried specimens of *E. holthuisi* were collected from the end of September till the beginning of June and it is likely that *E. holthuisi* breeds almost throughout the year except for the rainy season when observations could not be made. It is likely that temperature may have some influence on development because of the differential temperature found in nature during winter (25° C.) and summer (30° C.).

Rees (1957) summarises that the larval development of *E. talpoida* should not be regarded as consisting of a fixed number of stages determined by a fixed number of larval inter-moults. A more or less similar conclusion can be drawn if the developmental stages of *E. holthuisi* and *E. emeritus* both from the Indian waters are compared. Such a comparison between the larvae reared in the laboratory and those obtained from the plankton of *E. holthuisi* could not be made for the reasons already stated above.

The present study has shown that the observation of Rees that the number of setae on the exopodite of the maxillipeds gives a clue to the identification of the zoeal stages, is valid for the genus *Emerita*.

Acknowledgements

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DISCUSSION

Dr. N. B. Nair: Whether there is any relation between temperature and larval development?

Mr. K. N. Sankolli: Yes. But in this study, the larvae were reared at room temperature ranging between 26–29° C.

Dr. V. Hansen stressed the importance of the studies on larval development in Decapod crustacea, especially by laboratory rearings, and he said that they should be published in form of monographs so that they will be useful for checking and confirming the identification of the planktonic material.

Dr. A. L. Rice: Suggested that as said by Mr. Sankolli, this kind of studies will throw a good deal of light on solving the adult-taxonomic problems.

STUDIES ON LARVAL DEVELOPMENT IN ANOMURA (CRUSTACEA, DECAPODA)—II*

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ABSTRACT

No work has been done on the life-history of the Indian species of genus *Pagurus*.

Life-history of *Pagurus kulkarnii* Sankolli, worked out in the laboratory, consists of three zoeal stages as against four zoeal stages observed in the British species of *Pagurus* by MacDonald *et al.* (1957) who studied the life-histories based on the planktonic material.

The presence of 4 pairs of pleopod buds in the third stage indicates an advancement over corresponding stage of the British species wherein it is found in the fourth stage. Environmental differences between the larvae reared in the laboratory and those from plankton may probably be the cause for this kind of differential development.

Characteristics of the zoeal stages of *P. kulkarnii*:

1. Eyes sessile; telson process formula 7 + 7; exopodites of first two maxillipeds each with 4 setae.

2. Eyes stalked; telson formula 8 + 8; exopodite of maxillipeds each with 7, 7 and 6 setae respectively.

3. 6th abdominal segment distinctly articulated to the telson; exopodites of maxillipeds bear 7 setae each; unsegmented uropods and four pairs of pleopod buds present.

The life-history of *Upogebia* (*Upogebia*) *kempi* n. sp. comprises four zoeal and two post-larval stages. Morphological features of all these larvae correspond to those belonging to the sub-family Upogebiinae as listed by Gurney (1924).

Division of each larval stage into two classes as described by Webb (1919), was not observed from first larvae to first post-larvae. This was only seen in the second post-larvae, comprising fringed and non-fringed forms.

Following are the characteristics of the stages:

1. Eyes sessile; telson process formula 8 + 8, 2nd and 8th pairs being delicate hairs; no central spine on posterior margin of telson.

2. Eyes stalked; telson process formula 8 + 1 + 8, only the 8th pair becomes spine-like and the central spine present; pleopod buds present; biramous uropod buds seen inside the telson.

3. Telson process formula 8 + 1 + 8, the 2nd pair being replaced by spines, first 4 pairs and the median spine fused with the telson; unsegmented biramous uropods with functional exopodites.

4. Telson process formula as in Stage III; uropods distinctly segmented with both the rami functional.

Post-larva I—Telson process formula 4 + 1 + 4; all spines very small; antennal flagellum with 19 segments; antennular endopodite unsegmented; mandible with unjointed palp; pleopods with 4–5 and 26–27 setae on endopodites and exopodites respectively.

Post-larva II—Antennal flagellum with 24 segments; antennular endopodite and mandibular palp three-segmented; 14–16 and 27–31 setae on endopodites and exopodites respectively of the pleopods.

* Part I of this series is by K. N. Sankolli appearing in this publication.

THIS part deals with the complete life-history of a pagurid, *Pagurus kulkarnii* Sankolli and an upogebiid, *Upogebia* (*Upogebia*) *kempi* n.sp.**

Super-family PAGUROIDEA

Family PAGURIDAE Latreille

Pagurus kulkarnii Sankolli

Since the work of Menon (1937) on the larvae of *Spiropagurus*, *Diogenes* and *Clibanarius*, there has been no further work on the larval development of the Indian pagurids.

MacDonald *et al.* (1957) have described the prezoeal and first zoeal stages of six British species from laboratory hatchings and the subsequent stages were collected from plankton to complete the life-history in each case.

Pagurus kulkarnii is the only species described from Bombay waters (Sankolli, 1961) and its life-history consists of 4 stages, 3 zoeal and a glaucothoe, all the stages having been obtained in the laboratory.

MATERIAL AND METHODS

The specimens were collected from Bombay (Chawpaty and Cuff-parade). To ascertain the berried condition of the crab in the shell, a hole was made carefully by breaking the apex of the shell with a mechanical device. The crab inside was then irritated with a piece of plastic wire which forced it to come out. This way females, which had eggs in an advanced state of embryonic development, were selected and empty shells of similar species and nearly similar size were provided in the aquarium tanks for their re-occupation. When left in the broken shell, they were found to shed their eggs. The female crabs were then separated, one in each aquarium tank, suitably aerated until the larvae hatched out.

The method of rearing the larvae was more or less similar to that followed by Rees (1959) while studying the development of the sand crab, *Emerita talpoida* (Say), using sea-water filtered through glass-wool and inoculated with 2,00,000 units of Penicillin per litre. The larvae were then reared in a series of small finger bowls, each of 250 c.c. capacity, containing freshly inoculated sea-water, renewed daily. The presence of moults or exuviae was carefully examined in each bowl before renewing the water.

Freshly hatched *Artemia* nauplii were used for feeding. Feeding with microplankton was found undesirable since it stuck on to the setae on the body and the appendages and interfered with the free movement of the larvae.

Killing and preservation of the larvae were done as suggested by Thakur (1960) so as to avoid flexure of the abdomen. Dissection of the appendages was made with the help of entomological needles under a binocular microscope in glycerine and drawings were made with the aid of a drawing prism.

OBSERVATIONS

Table I indicates the average time required by each zoea to moult to the next stage. Percentage mortality was high upto the II zoeal stage and thereafter there was hardly any mortality.

** Sankolli, K. N. (in press).

The glaucothoe stage was obtained after three distinct zoeal stages and there was no fourth zoeal stage as in most of the British species of *Pagurus*.

Several attempts were made to get the glaucothoe moulted further by providing natural as well as artificial shells, but they failed to moult in spite of the fact that they survived for about 15 days.

TABLE I

Average duration of each zoeal stage

Stages	I	II	III	Glaucothoe
Average No. of days spent in each stage ..	6	4	4	Lived only for about 15 days

DESCRIPTION OF LARVAL STAGES

First zoea (Fig. 1 *a*)

The larva is long and slender. The rostrum reaches well beyond the antennule and antenna. The carapace has a small, slightly curved spine at its postero-lateral angle. The eyes are sessile, measuring slightly more than one-half the length of the rostrum. There are paired spines on the posterior margin of abdominal segments one to four, a dorsal, two dorso-lateral and one ventro-lateral pair of spines on each segment. The fifth abdominal segment has one dorsal and one ventro-lateral pairs of spines. The spines on this segment are larger than those on the first four segments, and the ventro-lateral spines are very large.

Antennule (Fig. 1 *b*).—The inner ramus is minute and represented by a single plumose seta. The outer ramus ends in two aesthetases and three setae, one of which is very small.

Antenna (Fig. 1 *c*).—The endopodite is unsegmented and broad at its base and bears two terminal setae. Scale is narrow, much longer than the endopodite with a terminal spine about half the length of the setae. The scale bears nine long, marginal setae and one very small, hair-like delicate seta near the terminal spine. The basal segment bears ventrally a minutely serrated spine which is nearly half the length of the endopodite.

Mandible (Fig. 1 *d*).—Distally the incisor process is slightly produced and the edge is provided with five to six teeth. There is no palp. The mandibles are asymmetrical.

First maxilla (Fig. 1 *e*).—Consists of two endites and a palp. The proximal endite bears six setae and the distal terminates in two long serrated teeth. The palp is three-segmented bearing two long and one small setae on the terminal segment and a single long seta on the penultimate segment.

Second maxilla (Fig. 1 *f*).—Consists of two bilobed setose endites, an unsegmented palp and the scaphognathite. The proximal endite bears on the first lobe four simple and four plumose setae, and four setae on the second lobe; the distal endite bears four and five setae on the outer and inner lobes respectively. The palp bears two long and a short setae on its inner margin and three long setae on the outer margin. The scaphognathite bears five marginal setae.

First maxilliped (Fig. 1 *g*).—The basal segment has six well-spaced setae on the inner margin and a group of two long and a short setae distally. The endopodite is five-segmented. Segments one to four bear on their inner margins, two long and one short, one long and one short, a single, long, and one long and one short setae respectively. On the outer margin of the first and second segments are tufts of fine, delicate hairs, distally. The last segment terminates in four setae of

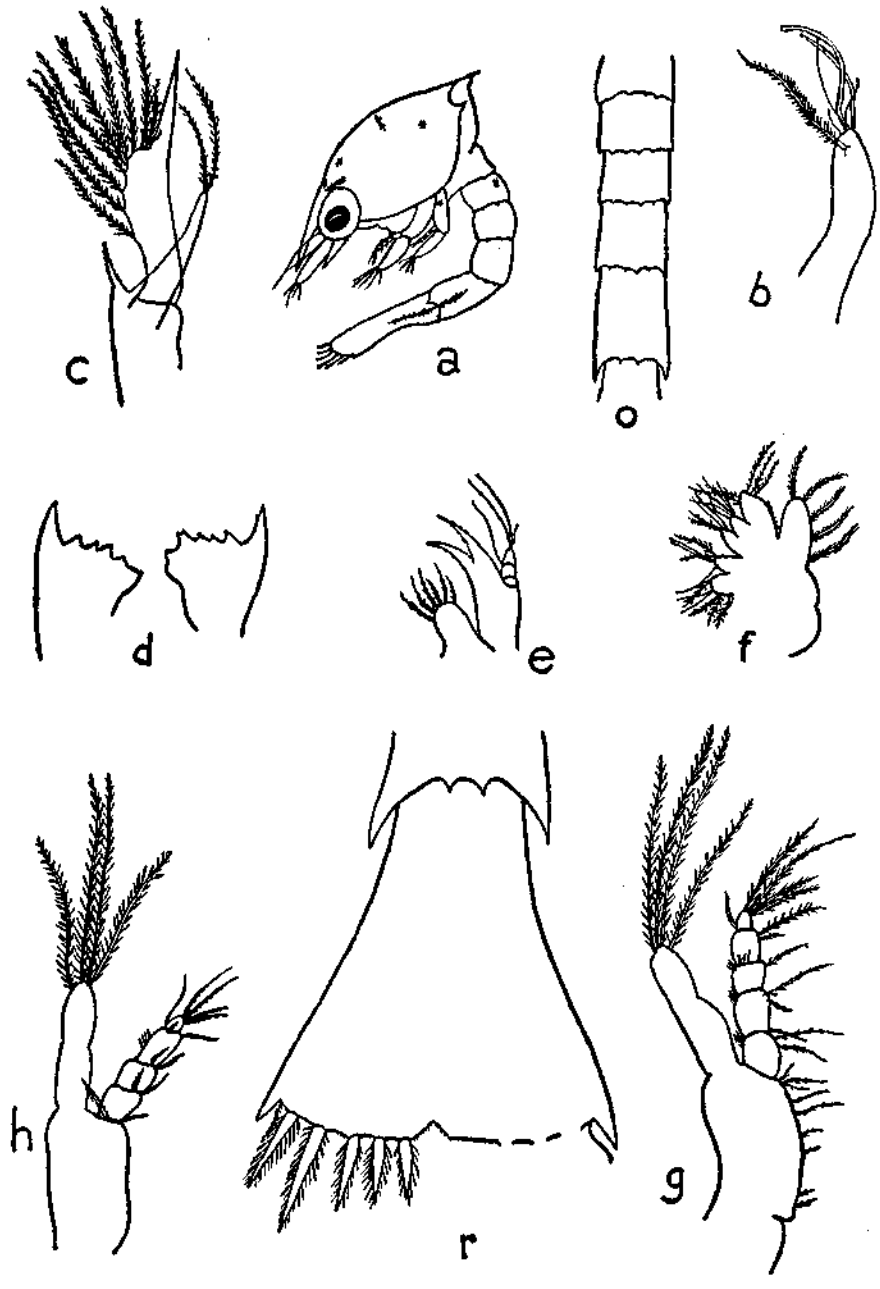

FIG. 1. *Pagurus kulkarnii* Sankolli, First zoea. (*a*) entire larva; (*b*) antennule; (*c*) antenna; (*d*) mandible; (*e*) first maxilla; (*f*) second maxilla; (*g*) first maxilliped; (*h*) second maxilliped; (*o*) abdomen; (*r*) telson.

which two are long, thin and bristle-like and the other two are simple, there is also a simple proximal seta.

The exopodite is indistinctly two-segmented bearing four terminal, plumose setae.

Second maxilliped (Fig. 1 *h*).—Basal segment is devoid of setae. The endopodite is four-segmented. First, second and third segments each bears a pair of setae distally, one of which is bristle-like and the other simple. At the base of the first segment a similar pair of setae is present. The last segment bears four terminal and one proximal setae.

The exopodite is indistinctly two-segmented with four long, terminal, plumose setae.

Third maxilliped.—It is a rudimentary bud.

Pereiopods.—Rudiments of the first three pairs of legs are present in this stage.

Telson (Fig. 1 *r*).—Telson process formula is 7 + 7. The second process is represented by a hair, *i.e.*, anomuran hair. The fourth process is the longest, 5th to 7th processes are minutely spinulose on both margins. The posterior margin between the third and fourth, and fourth and fifth processes is armed with minute spinules. The central cleft is shallow with minute spinules on either sides.

Colour (Fig. 1 *a*).—The basal portion of the rostrum shows on the dorsal side a deeply embedded bluish tinge. The chromatophores are mainly branched, dark crimson red with orange-yellow as component and their distribution is as follows: a ventral pair at the base of the rostrum and between the eyes, these often appear to be united anteriorly; a single in the mandibular region and on the protopodite of the second maxillipeds; one finely branched chromatophore near the posterior margin of the carapace and so also one on the second abdominal segment. There is one horizontal, unbranched strip of dark crimson red about the middle of the carapace.

The last abdominal segment and telson have each a longitudinal branched crimson red chromatophore and these are united for greater part, giving an appearance of a single chromatophore.

Second zoea (Fig. 2)

It took nearly six days for the Ist zoea to moult into the II stage. In this stage, the eyes become stalked, telson process formula becomes 8 + 8, the number of setae on the exopodite of the first two maxillipeds increases to seven and the third maxilliped becomes functional with six setae on the exopodite.

Antennule (Fig. 2 *b*).—The inner ramus is represented by a small papilla with a terminal plumose seta. The outer ramus ends in three aesthetascs of which one is very prominent, and two setae, one of which is minute.

Antenna (Fig. 2 *c*).—Except for the increase in the length of the endopodite, there is no other appreciable change.

Mandible (Fig. 2 *d*).—As in stage I, mandibular palp is not yet developed.

First maxilla (Fig. 2 *e*).—Of the two endites, the distal endite now bears four, instead of two serrated teeth as in the Ist stage.

Second maxilla (Fig. 2 *f*).—The proximal endite bears six setae on the outer lobe and four on the inner and the distal endite bears four setae on each lobe. The scaphognathite bears six marginal setae.

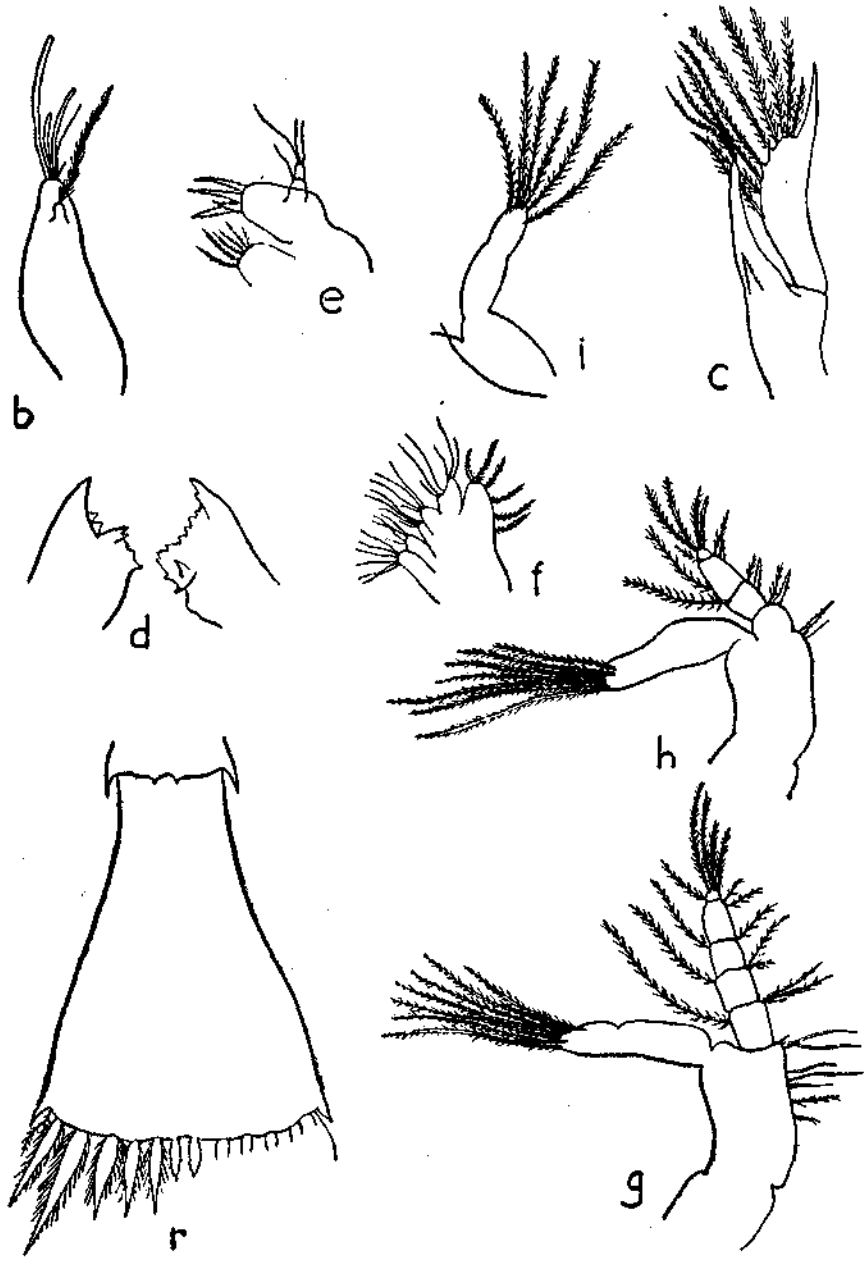

FIG. 2. *Pagurus kulkarnii* Sankolli, Second zoea. (*b*) antennule; (*c*) antenna; (*d*) mandible; (*e*) first maxilla; (*f*) second maxilla; (*g*) first maxilliped; (*h*) second maxilliped; (*i*) third maxilliped; (*r*) telson.

First maxilliped (Fig. 2 *g*).—The distribution of the setae on the segments of the endopodite is as follows: a pair of long and a short setae on the inner and a long plumose seta on the outer margins of the first and a pair of unequal and a long plumose on the inner and outer margin respectively of second; one on inner margin and a longer plumose seta on the outer margin of the third; a pair on the fourth; four apical and one proximal setae on the last segment.

The exopodite bears seven long, plumose terminal setae and the basipodite has eight marginal setae.

Second maxilliped (Fig. 2 *h*).—In the endopodite, the first segment bears one smooth and one bristle-like setae on the inner margin. Second segment, in addition to the above two setae, bears a long plumose seta on the outer margin. Third segment is similar to the second, but with two finely plumose setae on the outer margin. The last segment terminates in four plumose setae.

The exopodite bears seven long terminal plumose setae and the basipodite bears a thin, hair-like and a spinulose setae on the inner margin.

Third maxilliped (Fig. 2 *i*).—The exopodite is indistinctly two-segmented with six terminal plumose setae.

The endopodite is rudimentary, small and bud-like, with two terminal hair-like processes.

Pereiopods.—No change from that of the 1st stage.

Telson (Fig. 2 *r*).—Telson process formula is now 8 + 8. The 1st and 2nd processes are as in stage I, 3rd and 4th processes are plumose with minute spinules at their basal portion; 5th, 6th and 7th are with minute spinules on either side except at the tip which is naked. Telson processes except the median are plumose, the latter is minutely spinulose. The posterior margin of the telson is provided with minute spinules in between the processes. The central notch is now very indistinct.

Colour.—The only change in the chromatophore pattern is that there are two minute crimson red spots, one on either ocular peduncles.

Third zoea (Fig. 3)

The IInd zoea moulted into the IIIrd after 4 days.

The 6th abdominal segment becomes distinctly articulated to the telson; exopodites of the maxillipeds bear seven setae each; unsegmented uropods and four pairs of pleopod buds are present.

Antennule (Fig. 3 *b*).—The inner ramus is longer than in the previous stage and shows partial segmentation. In addition to its terminal seta, there is now a small seta at its base. The outer ramus is also indistinctly segmented.

Antenna (Fig. 3 *c*).—The endopodite is still unsegmented but becomes longer and narrower and the setae of stage II disappear. The number of marginal setae is reduced to seven.

Mandible (Fig. 3 *d*).—No marked change.

First maxilla (Fig. 3 *e*).—On the distal endite, in addition to the four serrated teeth, two thin hair-like setae have developed.

Second maxilla (Fig. 3 *f*).—On the palp, instead of three setae each on outer and inner margins, there are now two on the outer and three on the inner margins. The scaphognathite bears eight marginal, plumose setae.

First maxilliped (Fig. 3 *g*).—There is no change in the first and second segments of the endopodite, but the third has a single, finely plumose seta on the inner side; fourth has one long and a short setae distally on inner side and fifth has four terminal setae,

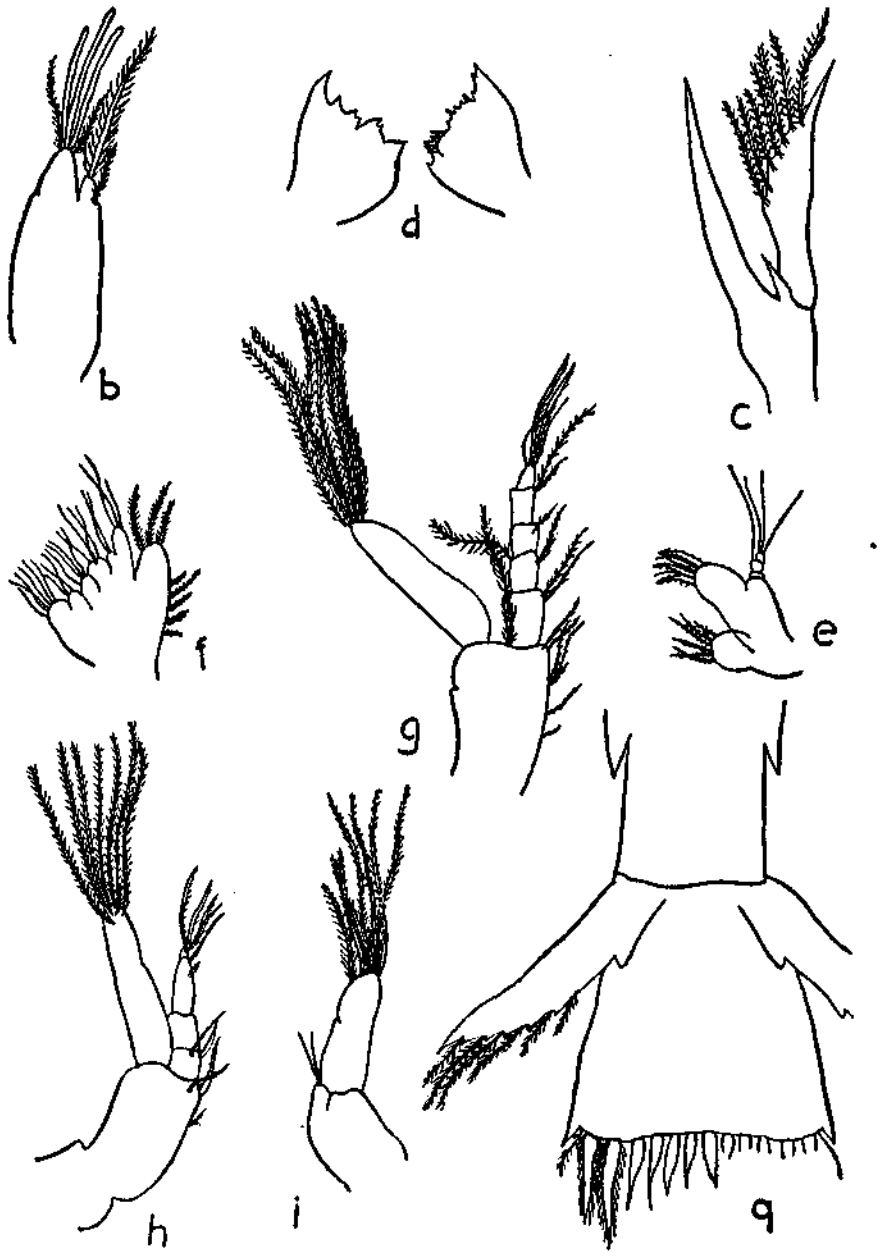

FIG. 3. *Pagurus kulkarnii* Sankolli, Third zoea. (*b*) antennule; (*c*) antenna; (*d*) mandible; (*e*) first maxilla; (*f*) second maxilla; (*g*) first maxilliped; (*h*) second maxilliped; (*i*) third maxilliped; (*q*) uropod with telson.

No change in the exopodite. Basipodite bears distally 2 groups of 2 and 3 setae respectively and 2 setae singly on inner margin.

Second maxilliped (Fig. 3 *h*).—The second segment of the endopodite has only a single long seta on the outer margin, the third has lost its long seta on the outer margin and the last segment has four terminal setae of which three have long spinules on the inner side.

No change in the exopodite.

Third maxilliped (Fig. 3 *i*).—The exopodite has now seven terminal setae.

The endopodite shows no segmentation but bears two sparsely plumose terminal setae.

Pereiopods.—Present as rudimentary buds.

Abdomen.—6th abdominal segment becomes articulated to the telson. Four pairs of rudimentary pleopods are developed, on abdominal segments 2–5.

Telson (Fig. 3 *q*).—Telson process formula is 8 + 8. The 3rd and 4th processes are plumose. The inner margin of the 5th, 6th and 7th processes is spinulose and only the basal portion of the outer margin is plumose. The central pair of processes is spinulose from tip to base on both margins. Spinules are also present in between the 3rd to the 8th processes. The 2nd process (Anomuran hair) is also plumose. Uropods are developed.

Uropods (Fig. 3 *q*).—Uropods are nearly as long as the telson. The endopodite is small and rudimentary. The exopodite bears six setae, each of which arises from the inner angle of a minute spine-like tooth, on the inner margin and tapers to a terminal spine. The marginal spine-like teeth are absent in the British species of *Pagurus*.

Colour.—The chromatophores of this stage are similar to those of II stage except for the following changes. The branched chromatophore of the mandibular area gets shifted a bit backwards and the chromatophore near the posterior margin of the carapace becomes large and much prominent.

Glaucothoe (Figs. 4 and 5).

The carapace is shorter than the abdomen (Fig. 4 *a*). The rostrum is short and blunt.

Eye-stalks are fairly stout, and slightly longer than broad. The cornea is slightly narrower than the stalk. Ophthalmic scales were not observed.

Antennule (Fig. 4 *b*).—The antennular peduncle is three-jointed, the distal segment with two thin setae on either margin. The inner ramus is two-segmented bearing two and four setae on first and second segments respectively. The outer ramus is four-segmented and slightly longer than the inner. It bears four terminal setae of which three are short, eleven aesthetascs in three groups of three, five and three each on the inner margin and one to two setae on the outer margin. The antennule reaches well beyond the eyes.

Antenna (Fig. 4 *c*).—Antennal peduncle is five-jointed. The scale arises from the second segment, extending beyond the base of the fifth segment. It bears a few short spine-like setae. The flagellum is composed of six to seven segments and reaches well beyond the right chela. The arrangement of the setae on the flagellum is as in the figure.

Mandible (Fig. 4 *d*).—The palp is well developed showing traces of three segments, no setae on the palp. The cutting edge is provided with a few minute teeth as in the adult.

First maxilla (Fig. 4 *e*).—The proximal endite bears one stout and three delicate setae. The distal endite now bears several short bristles and setae. The palp is unsegmented and without setae.

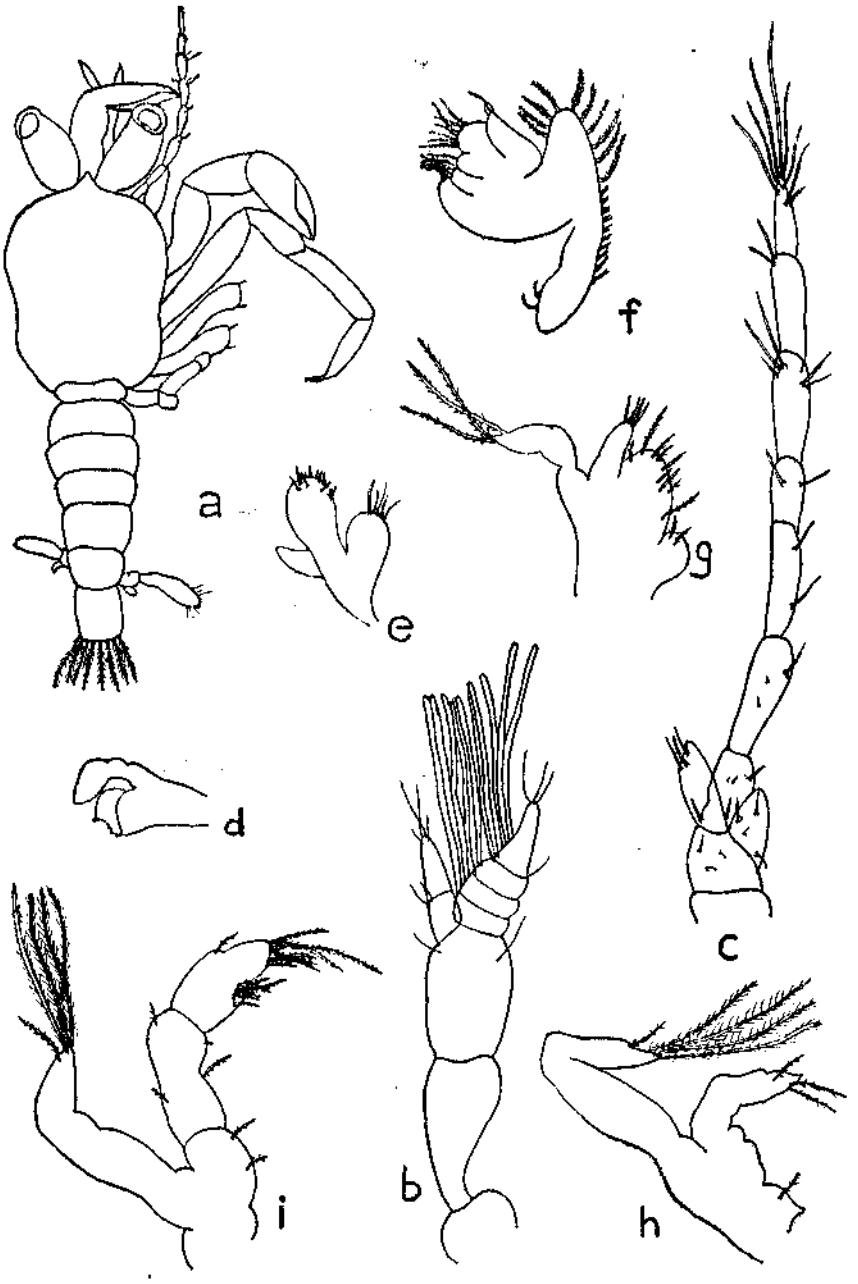

FIG. 4. *Pagurus kulkarnii* Sankolli, Glaucothoe. (*a*) Entire larva; (*b*) antennule; (*c*) antenna; (*d*) mandible; (*e*) first maxilla; (*f*) second maxilla; (*g*) first maxilliped; (*h*) second maxilliped; (*i*) third maxilliped,

Second maxilla (Fig. 4 *f*).—The proximal and distal endites are setose bearing five and thirteen setae respectively on the outer margin. The terminal portion of the palp is somewhat papilla-like with a single seta. The scaphognathite has now developed a rather rounded proximal lobe and bears twenty-six marginal setae.

First maxilliped (Fig. 4 *g*).—This appendage undergoes considerable change. The endopodite is very much reduced, partially two-segmented with four small terminal setae. The exopodite is also reduced, indistinctly two-segmented with three terminal plumose setae. The protopodite is produced into two lobes, the small proximal lobe bearing two setae and the large distal one with eleven setae on their inner margin.

Second maxilliped (Fig. 4 *h*).—The endopodite is four-segmented, though not well marked. The terminal segment bears three setae and one small hair-like process at its tip. No change in the exopodite except for one short seta. There is a single seta on the basipodite.

Third maxilliped (Fig. 4 *i*).—The endopodite is distinctly five-segmented, segments one to three with a pair of small setae, fourth segment with eight inner and one outer setae, last segment with seven unequal setae. The exopodite now bears four terminal, plumose setae and a short proximal seta.

Pereiopods.—Five pairs of pereiopods are well developed. First pair of pereiopods or chelipeds (Fig. 5 *j*) is strongly chelate, with the right being larger than the left. There are no spines or protuberances on any segments though in the right cheliped, there appears to be a faint indication of inner lateral lobes on merus and carpus. There are no spines on propodus and dactylus except two or three tubercles on inner margins and a few setae.

Second and third pereiopods (Fig. 5 *k* and *l*).—These are quite similar. Propodus has a distal spinule on its posterior margin and dactylus has three minute spines, increasing in size distally on the posterior margin.

Fourth pereiopods (Fig. 5 *m*).—Fourth pereiopods are similar and weakly sub-chelate.

Fifth pereiopods (Fig. 5 *n*).—It is weakly chelate, dactylus bearing a few short setae and a long plumose seta.

Abdomen (Fig. 4 *a*).—The length of the abdomen is nearly 1½ times that of the carapace. Abdominal segments 2–5 bear pleopods.

Pleopods.—There are four pairs of symmetrical pleopods decreasing in size posteriorly on the 2nd to 5th abdominal segments. Each pleopod consists of a large peduncle, flattened outer ramus, and a small inner ramus. The first three (Fig. 5 p_1–p_3) bear nine long plumose natatory setae, whereas the fourth (Fig. 5 p_4) carries eight setae. The endopodite of all the pleopods is small ending in two minute hooked spines discernible only under the high power of the microscope.

Telson (Fig. 4 *a*).—It is longer than broad, the posterior margin is slightly convex, with eight setae.

Uropods (Fig. 4 *a*).—The left uropod is slightly larger than the right. Each consists of a short peduncle, a small inner ramus with a single small seta, and a large flattened outer ramus with twelve to thirteen setae and a few short hairs on the border.

Discussion

Pagurus kulkarnii passes through three distinct zoeal stages before moulting into the glaucothoe whereas the British species of *Pagurus* as described by MacDonald *et al.* (1957) have four zoeal stages prior to the glaucothoe. The first two stages of *P. kulkarnii* correspond with the

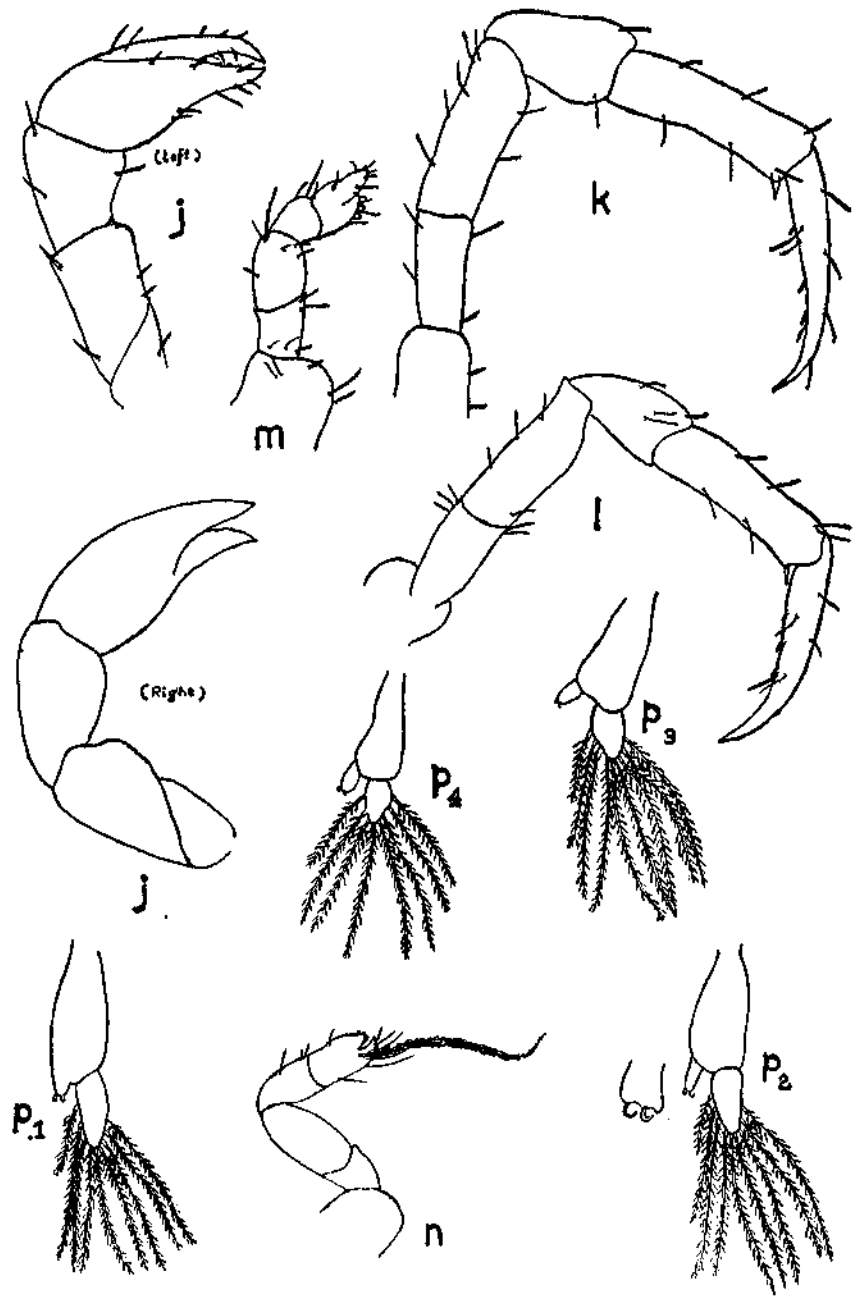

FIG. 5. *Pagurus kulkarnii* Sankolli; Glaucothoe. (*j*) first leg; (*k*) second leg; (*l*) third leg; (*m*) fourth leg; (*n*) fifth leg; (p_1) first pleopod; (p_2) second pleopod; (p_3) third pleopod; (p_4) fourth pleopod.

respective stages of the British species. However, the III stage although compares well with the corresponding stage of the British species, shows the presence of pleopod buds indicating slight advancement in development. This feature is evident only in the IV stage of the British species. It is interesting to note, therefore, that *P. kulkarnii* reared in the laboratory, skips over one stage. This discrepancy is obviously due to the fact that the development of the British species was studied from plankton collections, while that of *P. kulkarnii* was from laboratory hatchings.

Similar difference in development has been observed by Gurney (1927 and 1942), Lebour (1940) and Rees (1959). The development of *Diogenes pugilator* (Roux) is an outstanding example. Gurney (1927) and Menon (1937) described only four stages from Suez Canal and Madras material respectively, whereas MacDonald *et al.* (1957) described five zoeal stages in the British specimens and suggested that, probably in warmer waters, the species has only four stages. Similar observations have been made by Sankolli and Kewalramani (1962) in the development of a prawn, *Saron marmoratus* (Olivier).

Based on development studies MacDonald *et al.* (*op. cit.*) divided *Pagurus* species into two groups A and B. *P. kulkarnii* in its developmental characters shows greater affinity to group B than A but at the same time shows features not seen in latter. It may therefore represent a third group.

Super-family **THALASSINOIDEA**

Family CALLIANASSIDAE

Sub-family UPOGEBIINAE

***Upogebia* (*Upogebia*) *kempi* n. sp.**

The only account of the larval development of the members of the sub-family Upogebiinae from the Indian waters is that by Menon (1933 and 1940). Working on planktonic collections he described five larval stages and the post-larva of a Upogebiid, the last larva and the first post-larva of *Upogebia* sp. and the third and fourth larvae and the first post-larva of *Calliadne* (*Gebiopsis*) sp. Because of the incompleteness of the stages, specific identification was not possible.

Webb (1919) described the larvae of *U. stellata* (Mont.) and *U. deltura* Leach, based on the material collected from the Plymouth plankton. Gurney (1924) described the entire metamorphosis of *U. danai* Miers. In 1937, he showed that the larval life of *U. savigny* is highly reduced. Gurney (1938) described the larvae of apparently four species of the sub-family Upogebiinae, while working on the Thalassinid larvae collected from the Barrier Reef Expedition (Discovery collection) and also plankton material from Samoa and drew a list of the characters for larvae of the sub-family Upogebiinae.

The life-history of *Upogebia* (*Upogebia*) *kempi* n.sp. consists of four zoeal and two post-larval stages, in the laboratory.

MATERIAL AND METHODS

Because of their burrowing habit it is rather difficult to collect the adults. However, a few berried females were collected from Bombay (Chawpaty and Cuff-parade) during September to December, 1963. Attempts to keep them alive under laboratory conditions met with little success as the specimens died invariably within a few hours after introducing them into the tank. But they survived when each of them was provided with a rubber or plastic tubing of suitable size, and a sufficient quantity of fine sand was spread along with small stones. In this manner, each berried female was kept separately in the tanks until the larvae hatched out.

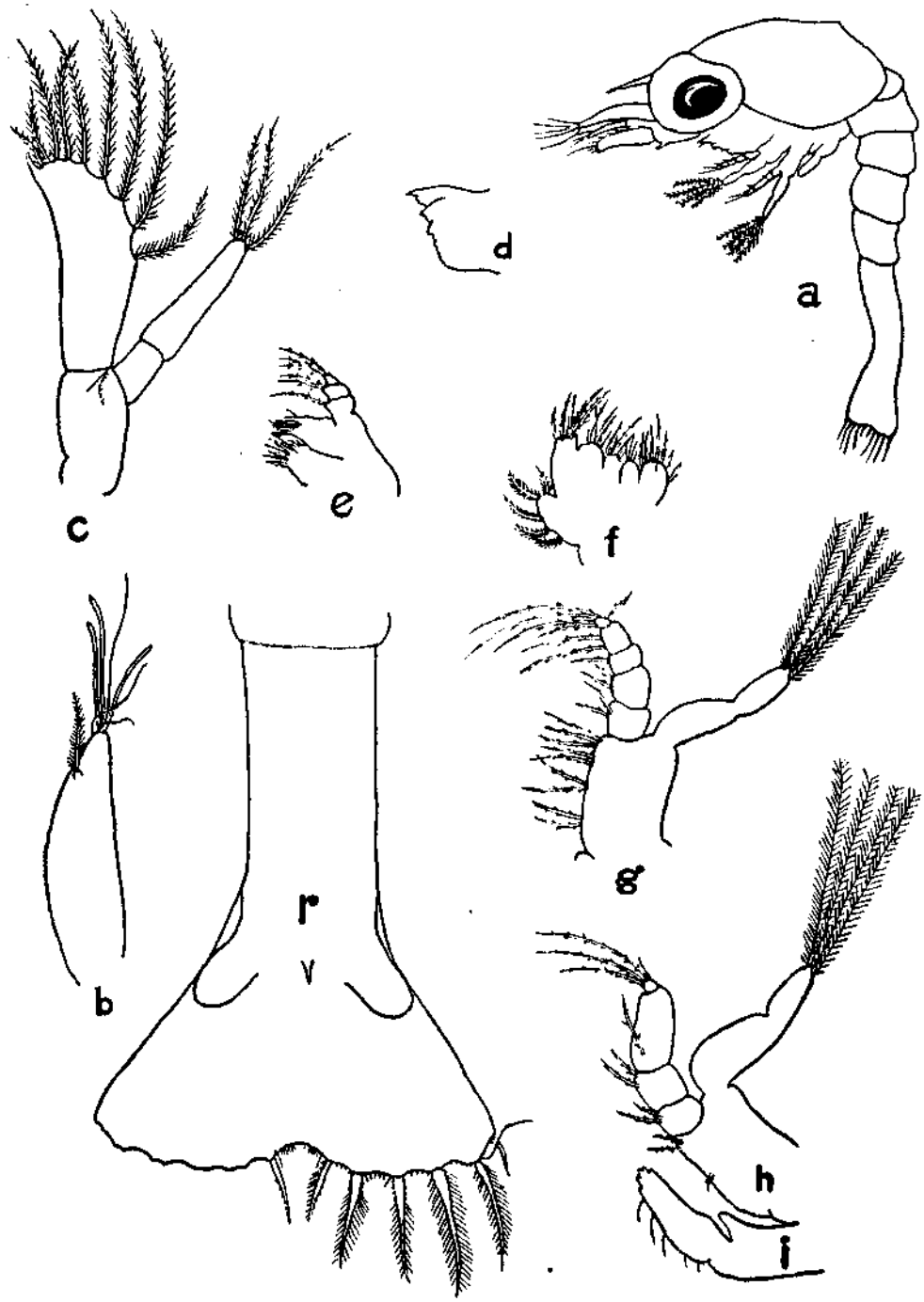

FIG. 6. *Upogebia* (*Upogebia*) *kempi* n. sp., first zoea. (*a*) entire larva; (*b*) antennule; (*c*) antenna; (*d*) mandible; (*e*) first maxilla; (*f*) second maxilla; (*g*) first maxilliped; (*h*) second maxilliped; (*i*) third maxilliped; (*r*) telson.

Method of rearing the larvae was the same as used by Rees (1959) in his studies on the development of the mole crab, *Emerita talpoida* (Say).

OBSERVATIONS

The life-history of *U.* (*U.*) *kempi* n.sp., as worked out in the laboratory, includes four zoeal and two post-larval stages.

Table II shows the duration of each stage.

TABLE II

Average duration of each stage

Stage	I	II	III	IV	1st post-larva	2nd post-larva
Average number of days spent in each stage	4	6	6	6	5	Lived for about 10 days

Attempts were also made to rear the 2nd post-larvae by keeping them in shallow glass-dishes filled with sea-water, and provided with sand at the bottom, collected from the original habitat. Water was renewed everyday. However, the larvae did not live long to moult into the next stage despite the fact that they could burrow themselves into the sand.

Description of the Larval Stages

First zoea (Fig. 6 *a*)

The rostrum is narrow, pointed, extending beyond the middle of the antennule. The carapace is postero-laterally rounded. The eyes are sessile, large, nearly twice as long as the rostrum.

Antennule (Fig. 6 *b*).—The inner ramus is minute bearing one small plumose seta, whereas the outer one bears three aesthetascs and three setae, of which one is long.

Antenna (Fig. 6 *c*).—Its endopodite is two-segmented and bears two plumose terminal setae and one long plumose seta on the inner margin near the distal end. The scale is as long as the endopodite and carries a terminal spine and nine marginal setae, of which the one near the terminal spine is the smallest. The basal segment has a ventral spine which is minutely spinulose on the inner margin.

Mandible (Fig. 6 *d*).—It is fairly well developed, the cutting edge is provided with three to four teeth and several minute teeth. There is no palp.

First maxilla (Fig. 6 *e*).—It bears two endites—proximal and distal, with eight and six setae respectively on their inner margin. The palp is three-jointed, with the segments carrying one, two and three setae respectively.

Second maxilla (Fig. 6*f*).—It has two bilobed setose endites, an unsegmented palp and the scaphognathite. The proximal endite bears eight and four setae respectively on each of its lobes and the distal endite has five and six setae respectively. The palp bears setae in three groups of three, two and one. The scaphognathite has five marginal setae.

First maxilliped (Fig. 6 *g*)—The endopodite is five-segmented, with the following setation, two, two, one, two and five on the inner margin. The exopodite is incompletely two-segmented

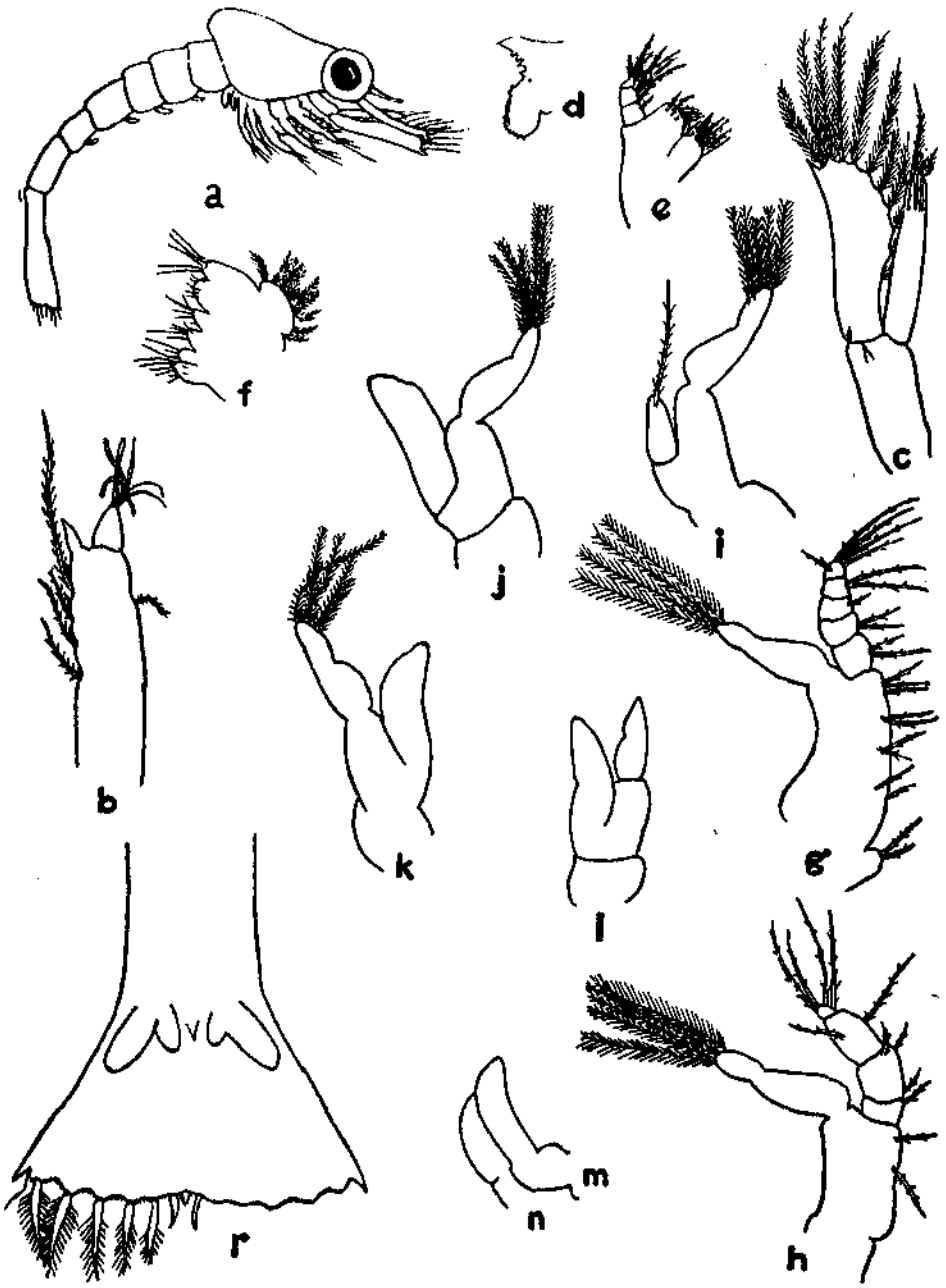

FIG. 7. *Upogebia* (*Upogebia*) *kempi* n. sp., second zoea. (*a*) entire larva; (*b*) antennule; (*c*) antenna; (*d*) mandible; (*e*) first maxilla; (*f*) second maxilla; (*g*) first maxilliped; (*h*) second maxilliped; (*i*) third maxilliped; (*j*) first leg; (*k*) second leg; (*l*) third leg; (*m*) fourth leg; (*n*) fifth leg; (*r*) telson.

with four terminal, plumose setae. The basipodite has on its inner margin four groups of setae as follows: two, two, two and three.

Second maxilliped (Fig. 6 *h*).—The endopodite is four-segmented with its first two segments bearing two setae each, the third with one and the fourth with four. The basipodite bears two setae distally and one seta near the middle of its inner margin. Except for these, there is no other change from the first maxilliped.

Third maxilliped (Fig. 6 *i*).—It is biramous, rudimentary with its exopodite indistinctly two-segmented bearing a few setae on the inner margin.

Pereiopods.—Only the first three pairs are present as rudimentary bilobed buds.

Telson (Fig. 6 *r*).—Telson process formula is 7 + 7. The posterior margin is divided into two roughly convex lobes by a central shallow cleft. The 1st process is a spine which is serrated on its distal inner margin, the 2nd is a delicate hair and the remaining 5 processes are plumose. The 5th and 6th processes bear distally about three minute teeth-like spinules on either margins and the 7th process also bears such spinules but on the outer margin only. In between the 5th and the 6th processes, there is a short, delicate hair. There is also a delicate slightly longer hair, on either side of the central notch which is fringed with several delicate hairs. The posterior margin is armed with minute spinules which vary in size, as shown in the figure.

The anal spine is present. In the several larvae examined, the future uropod-buds could also be seen.

Second zoea (Fig. 7 *a*)

The characteristics of this stage are:

The eyes are stalked and movable; five pairs of pereiopods are developed, of which the third to the fifth are rudimentary; the 6th abdominal somite becomes distinctly articulated to the telson; four pairs of pleopod buds are developed; the telson process formula becomes 8 + 1 + 8.

Antennule (Fig. 7 *b*).—There is an addition of one seta on the outer ramus which now becomes distinctly separated from the peduncle by a partition. So also the inner ramus is now well formed but loses the plumose seta found in the 1st stage. It, however, ends in a minute, pointed tip. The peduncle bears four plumose setae on its inner margin, the anteriormost being the longest; on the outer margin there is a short, distal seta. The inner margin now shows faint segmentation.

Antenna (Fig. 7 *c*).—The endopodite is unsegmented and carries three terminal plumose setae of which two were seen to be still partially projecting. The scale is longer than the endopodite with a terminal spine and eleven marginal setae. In addition to the ventral spine, the peduncle bears another spine near the base of the scale which is minutely spinulose on both the margins.

Mandible (Fig. 7 *d*).—There is slight increase in the number of teeth on the cutting edge.

First maxilla (Fig. 7 *e*).—No marked change other than the increase in the number of setae.

Second maxilla (Fig 7 *f*).—There is no change except for the increase in the number of setae on the proximal and distal endites which bear sixteen and fifteen setae respectively. The number of setae on the scaphognathite is now increased from five to nine.

First maxilliped (Fig. 7 *g*).—There is no change.

Second maxilliped (Fig. 7 *h*).—The exopodite bears five to six plumose setae and the third segment of the endopodite has an additional seta on its outer margin.

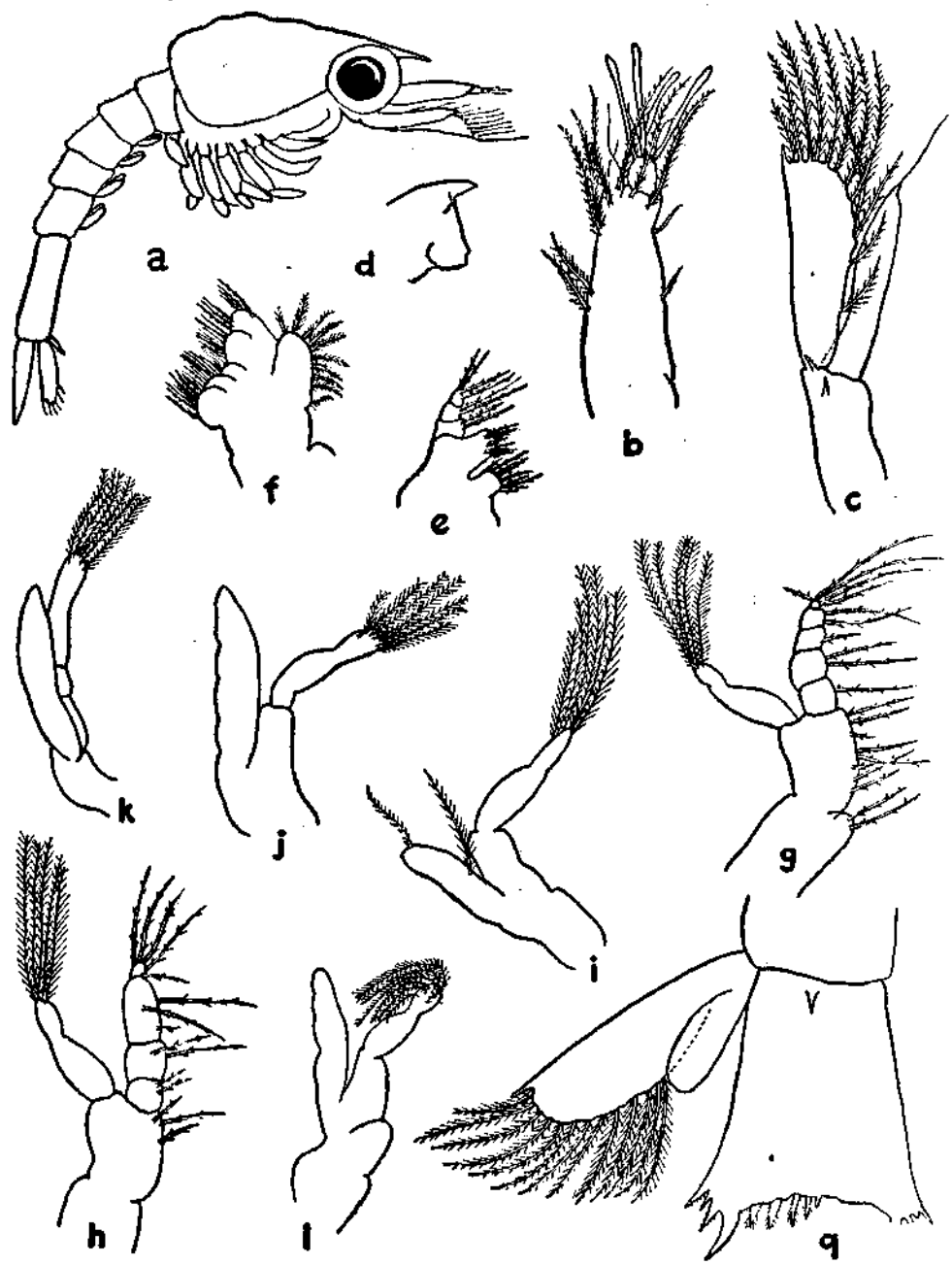

FIG. 8. *Upogebia* (*Upogebia*) *kempi* n. sp., Third zoea. (*a*) entire larva; (*b*) antennule; (*c*) antenna; (*d*) mandible; (*e*) first maxilla; (*f*) second maxilla; (*g*) first maxilliped; (*h*) second maxilliped; (*i*) third maxilliped; (*j*) first leg; (*k*) second leg; (*l*) third leg; (*q*) uropod with telson.

Third maxilliped (Fig. 7 *i*).—The exopodite bears five terminal plumose setae and the endopodite is ussegmented bearing a small, terminal plumose seta.

Pereiopods.—The first two pairs of pereiopods (Fig. 7 *j, k*) are better developed than in the 1st stage and bear on their exopodites six and five setae respectively. The endopodites are bud-like. The fourth and fifth pairs (Fig. 7 *m, n*) are uniramous buds.

Abdomen (Fig. 7 *a*).—It is now 6-segmented, the 6th segment being the longest and clearly separated from the telson by a partition. The pleopod buds are developed on abdominal segments 2–5.

Telson (Fig. 7 *r*).—Telson process formula is 8 + 1 + 8. At the middle of the central cleft there is a short and stumpy spine, on either side of which is a small, delicate process serrated on both the margins. The 3rd to the 8th processes are plumose. The posterior margin bears fine spinules, which are visible only under the high power of the microscope, between the 3rd to the 8th processes.

The uropod buds, still seen within the telson, are now biramous.

Third zoea (Fig. 8 *a*)

The presence of biramous uropods with functional exopodites and a general increase in the size of the larva mark the advancement over the II zoea.

Antennule (Fig. 8 *b*).—The outer ramus bears four aesthetascs and two delicate setae. The inner ramus now bears two hair-like terminal setae. On the peduncle, there are, in all, eight setae of which three are situated at the distal end and five on the inner margin. There are also two delicate setae on its outer margin.

Antenna (Fig. 8 *c*).—The number of setae on the scale is increased to twelve whereas on the endopodite, it is reduced to a single, hair-like seta arising from a minute distal papilla.

Mandible (Fig. 8 *d*).—No noticeable change.

First maxilla (Fig. 8 *e*).—The number of setae is increased to nine on both the endites.

Second maxilla (Fig. 8 *f*).—The number of setae on the proximal and distal endites is increased to eighteen and nineteen respectively. The scaphognathite bears ten setae and there is no change in the palp.

First maxilliped (Fig. 8 *g*).—The exopodite bears five terminal setae instead of four in the previous stage. There is no other appreciable change.

Second maxilliped (Fig. 8 *h*).—There is no change.

Third maxilliped (Fig. 8 *i*).—The unsegmented endopodite, in addition to the terminal seta, bears one more seta in the basal part. The exopodite now bears six terminal setae.

Pereiopods.—The first, second and third legs (Fig. 8 *j–l*) bear seven, six and six setae respectively on their exopodites. The fourth and fifth legs are now elongated but uniramous (Fig. 8 *m, n*).

Abdomen.—The pleopod buds show increase in size but still they are not functional.

Uropods (Fig. 8 *q*).—Though the uropods are biramous and well developed they are still without a distinct protopodite. The exopodite is functional bearing thirteen plumose setae on the inner margin and terminates posteriorly in a spine. The endopodite is much smaller and non-setose.

FIG. 9. *Upogebia* (*Upogebia*) *kempi* n. sp., fourth zoea. (*a*) entire larva; (*b*) antennule; (*c*) antenna; (*d*) mandible; (*e*) first maxilla; (*f*) second maxilla; (*g*) second maxilliped; (*h*) second maxilliped; (*i*) third maxilliped; (*j*) first leg; (*k*) second leg; (*l*) third leg; (*q*) uropod with telson.

Telson (Fig. 8 *q*).—Telson process formula remains the same, *i.e.*, 8 + 1 + 8, but the 2nd process which was hair-like in the previous stages, now becomes a spine. The 4th process is the longest. The first four and the central processes are now fused to the telson, whereas the remaining processes are articulated with the telson, as in the previous stages. The central spine is distally serrated on both margins. The posterior margin, as a whole, is slightly convex. Fine spinules are present between the 4th to the 8th processes. The anal spine persists.

Fourth zoea (Fig. 9 *a*).

In this stage, the uropods become distinctly segmented, with both the exopodite and endopodite becoming functional.

Antennule (Fig. 9 *b*).—There is no change in the inner ramus, but the outer ramus bears one more small seta. The number of setae on the peduncle is increased to ten.

Antenna (Fig. 9 *c*).—The scale now bears fourteen setae.

Mandible (Fig. 9 *d*).—There is no advancement over that of the III stage.

First maxilla (Fig. 9 *e*).—It is increased in size and each endite bears ten setae. The palp is unchanged.

Second maxilla (Fig. 9 *f*).—The proximal and distal endites bear twelve and thirteen setae respectively. The number of setae on the palp is reduced to four. The scaphognathite has sixteen setae.

First maxilliped (Fig. 9 *g*).—The first segment of the endopodite bears three setae; there is no other change in the endopodite. The exopodite continues to bear five terminal setae. The protopodite has in all twelve setae on its inner margin.

Second maxilliped (Fig. 9 *h*).—The endopodite is five-segmented. The first four segments carry 3, 3, 1 and 2 setae respectively. The second segment has one seta on the outer margin. The fifth segment bears five terminal and one outer setae.

The exopodite bears six terminal setae.

Third maxilliped (Fig. 9 *i*).—There is no change except for the loss of the terminal seta in the endopodite.

Pereiopods.—The endopodites of the first three pairs of legs (Fig. 9 *j*, *k*, *l*) increase in size and there is no other change.

Abdomen.—The pleopods still remain non-functional, though there is appreciable increase in their size.

Uropods (Fig. 9 *q*).—These are now distinctly articulated to the 6th abdominal segment by a small basal segment.

The exopodite bears fourteen plumose setae and is about $\frac{1}{4}$ times longer than the endopodite which bears thirteen setae on the inner margin.

Telson (Fig. 9 *q*).—Telson process formula remains the same as in the III stage. The only change is that the telson becomes narrower and longer.

First Post-larva (Figs. 10 and 11)

The post-larva (Fig. 10 *a*) differs from the last zoea, both in structure and habits. It resembles the adult in having more or less a straight abdomen, in the presence of functional pleopods with long setae, in the telson and uropods forming a complete tail-fan and in the

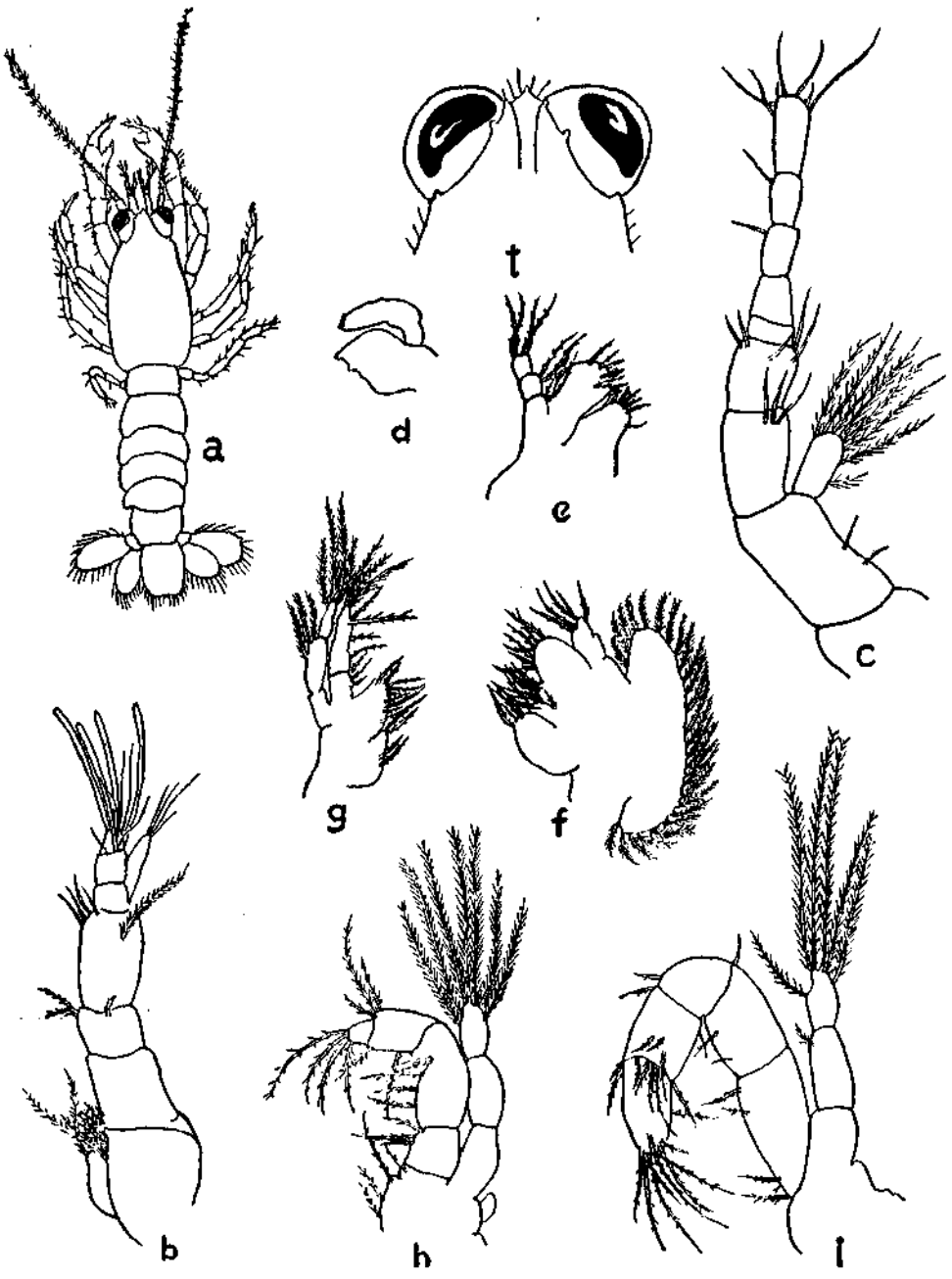

FIG. 10. *Upogebia* (*Upogebia*) *kempi* n. sp., first post-larva. (*a*) entire larva; (*b*) antennule; (*c*) antenna; (*d*) mandible; (*e*) first maxilla; (*f*) second maxilla; (*g*) first maxilliped; (*h*) second maxilliped; (*i*) third maxilliped; (*t*) frontal part (magnified).

reduction of the fifth leg. Abandoning its free swimming life the post-larva shows a tendency to settle down.

The carapace is laterally compressed. The front is triangular (Fig. 10 *t*) with a median and two lateral bead-like tubercles and also with fine delicate setae. It over-reaches the eyes. Compared with those of the zoeal stages the eyes are small. The antennal flagellum is longer than the carapace, and antennules reach almost to the middle of the propodus of the chelipeds. The first legs are distinctly chelate and robust; the first two pairs still retain the exopodites.

Antennule (Fig. 10 *b*).—The peduncle is four-segmented, the basal segment being more or less globular with a bunch of setae on the outer margin. The second segment has one short seta and the third has two setae on the outer margin. The fourth segment bears a long plumose seta on the inner margin and a few setae on the outer distal margin.

The inner ramus is unsegmented, with four terminal delicate setae. The outer ramus is three-segmented, its last segment bears four aesthetascs and five setae.

Antenna (Fig. 10 *c*).—The peduncle is four-segmented and its second segment bears the antennal scale. The scale is leaf-like, almost rounded and reaches nearly $\frac{3}{4}$ of the length of the third segment and carries eight plumose setae, of which the last one is the smallest. The third segment bears three setae and the fourth bears a number of them. The flagellum is composed of nineteen segments, most of which have a circlet of setae at the distal ends.

Mandible (Fg. 10 *d*).—The cutting edge is provided with three to four small teeth. The palp is developed but unsegmented, bearing minute spine-like processes terminally.

First maxilla (Fig. 10 *e*).—The proximal endite bears eight bristles of which five are setiform. The distal endite has four bristles, four small teeth and five setae. The palp shows no change.

Second maxilla (Fig. 10 *f*).—The proximal and distal endites bear fourteen and fifteen setae respectively. The palp shows traces of segmentation and carries five setae in three groups of two, two and one. The scaphognathite bears twenty-seven to twenty-eight setae.

First maxilliped (Fig. 10 *g*).—The protopodite consists of two lobes, the proximal with four and the distal with ten to twelve setae respectively on their inner margins.

The endopodite consists of five segments with three, two, one, two, and three setae respectively. The exopodite is indistinctly four-segmented, the second segment bears three densely plumose setæ on the outer margin and the last four terminal setae.

Second maxilliped (Fig. 10 *h*).—The endopodite is five-segmented, first four segments carry three, three, two and two setae on the inner margin, but the fourth segment has on its outer margin one long and two short setae. The last segment bears four long and a small setae.

The exopodite is three-segmented with seven terminal setae.

Third maxilliped (Fig. 10 *i*).—The exopodite is two-segmented, first segment has one seta and the second six terminal setae.

The endopodite is now five-segmented. The number of setae on each segment is as follows: two each on the inner margin of the first and second segments, two on the outer margin of the third, a row of setae at the anterior margin of the fourth and seven terminal setae on the last segment.

Pereiopods.—The first three pairs bear small exopodites with six terminal setae. The first pair is distinctly chelate.

Chelipeds (Fig. 11 *j*).—The carpus has three spines on the anterior margin. The fixed finger has three teeth, on the finger gap there are also three teeth on the distal margin of the propodus at its articulation with the dactylus.

Second pair of legs (Fig. 11 *k*).—The merus and propodus bear four plumose setae on the inner margins.

Third pair (Fig. 11 *l*).—The dactylus has three distinct spines on the outer margin.

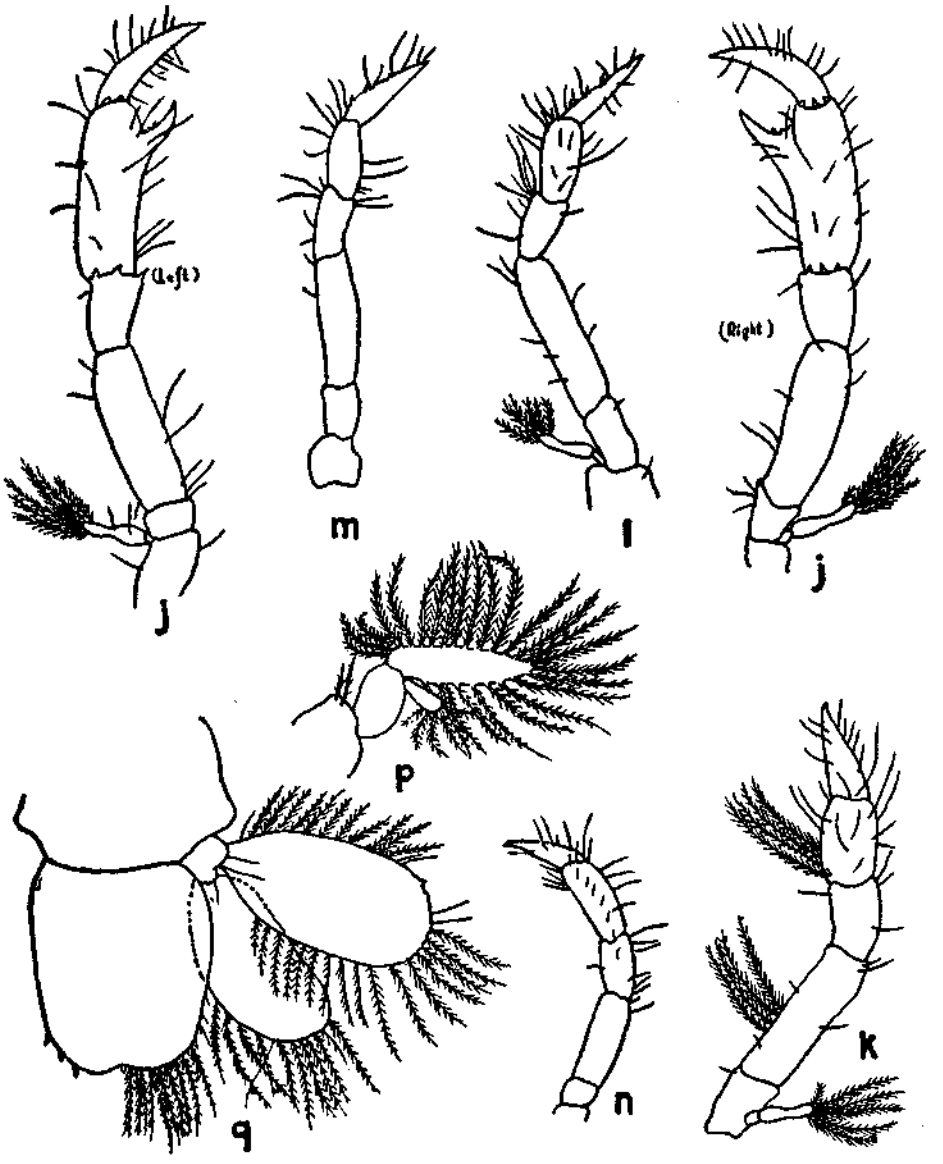

FIG. 11. *Upogebia* (*Upogebia*) *kempi* n. sp., first post-larva. (*j*) first leg; (*k*) second leg; (*l*) third leg; (*m*) fourth leg; (*n*) fifth leg; (*p*) pleopod; (*q*) uropod with telson.

Fourth pair (Fig. 11 *m*).—It is similar to the third but without exopodite.

Fifth leg (Fig. 11 *n*).—It is rather small with no spines on any of the segments. There is no exopodite.

Abdomen (Fig. 10 *a*).—It is 6-segmented with four pairs of pleopods on segments two to five. Each pleopod (Fig. 5 *p*) consists of a short penduncle with a large exopodite and a small endopodite. The number of setae on the exopodite and endopodite is 26 and 5 respectively in the first two pleopods and 27 and 4 on the others.

Uropods (Fig. 11 *q*).—The exopodite bears several setae all over the margins, but the endopodite is without any setae on its outer lateral margin, though it bears on the inner margin nineteen plumose setae intermingled with fine setae.

Telson (Fig. 11 *q*).—It is roughly rectangular in outline, and slightly broader at the base. The posterior margin has a broad shallow notch in the middle and is armed with a small tooth in the centre. There are four pairs of teeth on its postero-lateral margins. Either half of the hind border bears seven plumose and three small setae. On the proximal half of the lateral margin there are five setae. A few setae are also present on the dorsal surface.

Second post-larva (Fig. 12)

The first post-larva metamorphoses into two types of second post-larvae, fringed and non-fringed forms, the former can be easily distinguished by the dense fringe of long setae on the maxillipeds and first two pairs of legs. In the latter, though it is non-fringed, traces of several future setae can still be seen within the cuticle, thus indicating that the 2nd non-fringed post-larva may give rise to a fringed 3rd post-larva.

The appendages of the non-fringed larvae, on the whole, are similar to those of the fringed forms, though the non-fringed forms are smaller in size.

The following is the description of the fringed form:

Antennule (Fig. 12 *b*).—The peduncle, the inner and outer rami are all three-segmented. The inner ramus bears one long plumose seta on the outer margins of the first and second segments. The terminal segment of the outer ramus has four aesthetascs and two terminal and one proximal setae.

Antenna (Fig. 12 *c*).—The scale is highly reduced. In the peduncle, the second segment bears six long and one small setae on the outer margin, the third segment has a number of setae medially and a few on the outer margin. The flagellum is twenty-four-segmented.

Mandible (Fig. 12 *d*).—The palp is three-jointed, the second joint bears a single seta and the third nine to ten short, bristle-like setae. The cutting edge is provided with three to five fine teeth and a strong proximal tooth. The ventral plate bears a single tooth.

First maxilla (Fig. 12 *e*).—The palp is reduced, still shows traces of segmentation and bears a small seta. The distal endite bears ten bristle-like and nine simple setae. The proximal endite bears a few short setae and its anterior margin is fringed with numerous long setae.

Second maxilla (Fig. 12 *f*).—The scaphognathite bears about nineteen setae. The palp shows slight segmentation, bearing four setae. The two bilobed endites are fringed with a double row of setae on their anterior margins.

First maxilliped (Fig. 12 *g*).—The proximal lobe of the protopodite bears eight setae. The distal lobe is fringed with two rows of long setae on the outer margin.

The endopodite is two-segmented bearing six and three setae on the inner margins of the first and seond segments respectively. The second segment has three terminal setae also.

The exopodite is indistinctly two-segmented, basal segment is flattened and bears eleven plumose setae on its outer margin and the distal segment has three terminal setae.

Second maxilliped (Fig. 12 *h*).—The endopodite is five-segmented and is fringed along its inner margin. The terminal segment has four bristle-like and a number of simple setae.

The exopodite is two-segmented. There are a number of setae on the inner margin of the first segment, whereas, there are three long plumose setae and two small delicate hair-like setae on the second segment.

Third maxilliped (Fig. 12 *i*).—The five-segmented endopodite is fringed with long setae on the inner margin.

The exopodite is two-segmented, the first segment carries five setae on the inner margin and the second has four terminal setae.

Cheliped (Fig. 12 *j*).—The chelipeds of both the sides are similar and subequal. The exopodite of the previous stage is absent. All the segments are fringed with setae on the inner side. The

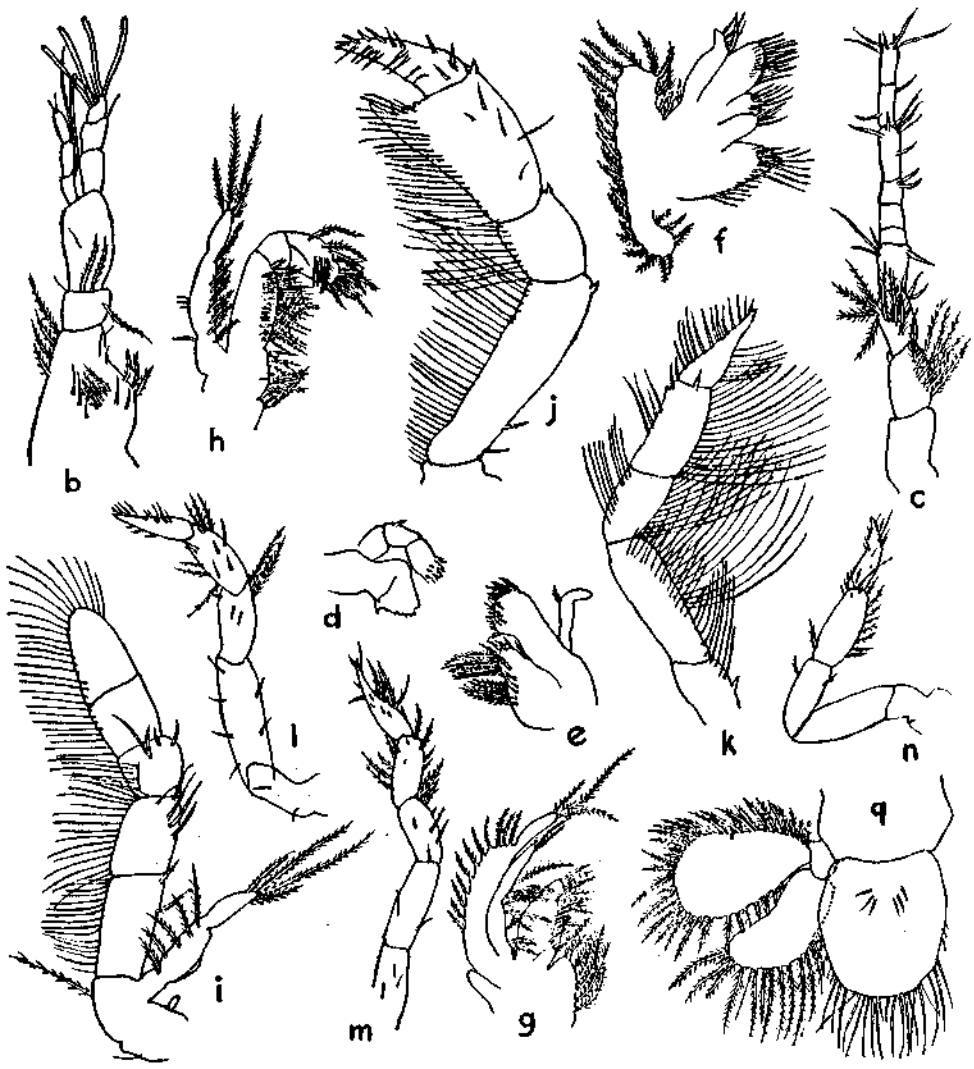

FIG. 12. *Upogebia* (*Upogebia*) *kempi* n. sp., second post-larva. (*b*) antennule; (*c*) antenna; (*d*) mandible; (*e*) first maxilla; (*f*) second maxilla; (*g*) first maxilliped; (*h*) second maxilliped; (*i*) third maxilliped; (*j*) first leg; (*k*) second leg; (*l*) third leg; (*m*) fourth leg; (*n*) fifth leg; (*q*) uropod with telson.

merus has a small spine on the posterior margin, and the carpus bears a similar spine distally on either of the posterior and anterior margins. The propodus bears three to four teeth-like tubercles on its cutting edge and a spine on the distal end of the posterior margin.

Second leg (Fig. 12 *k*).—The exopodite is absent. There is a small spine on the posterior margin of the ischium, and also on the anterior margin of the propodus. The last four segments have on their inner margins and also on the outer margin of the carpus, long, dense fringes of setae. The propodus and dactylus are provided with many short setae.

Third and fourth legs (Fig. 12 *l, m*).—These are alike in structure. There are many setae on the propodus and dactylus, but very few on the remaining segments. There is a small spine on the propodus and three similar spines on the dactylus.

Fifth leg (Fig. 12 *n*).—There is a strong spine and a row of setae on the inner margin of the propodus whereas the dactylus bears three small spines.

The last three pairs of legs do not bear any fringe of setae.

Pleopods.—There is no change except for the increase in the number of setae on their exopodites and endopodites. The exopodite of the first three pairs bears twenty-seven setae, and that of the last pleopod bears thirty-one setae. The endopodite of the first two pairs bears sixteen setae and that of the last two has fourteen setae.

Telson (Fig. 12 *q*).—It is longer than broad. The posterior margin is slightly convex and bears a few hairs and eleven pairs of setae. There is a group of about six small setae in the distal median portion of the dorsal surface.

Uropods (Fig. 12 *q*).—The exopodite now bears a few short bristle-like setae on the posterior margin and several long, plumose setae along its entire margin. The endopodite is bordered along the inner margin with about twenty setae, some of which are simple and others are long and plumose. There are no setae on its outer margin.

Discussion

Webb (1919) described two types of larvae, class A and class B, from II zoea onwards, in the development of *U. deltura* and *U. stellata*. These classes were based on differences in certain morphological characters, *i.e.*, in the number of setose exopodites and the development of endopodites on the walking legs. Her III zoea B moults directly into 1st post-larva B, whereas the III zoea A has an additional stage of IV zoea A before moulting to 1st post-larva A which gives rise to a single type of 2nd post-larva. But the 1st post-larva of class B moults into two types of 2nd post-larvae, *i.e.*, fringed and non-fringed forms.

In the present case, such a differentiation into two classes was not possible, though, in general, the larvae showed resemblance to class B larvae of Webb and the III zoea did not directly moult into the 1st post-larva. The III zoea, however, went through a IV zoeal stage before moulting into the 1st post-larva. This was confirmed by repeating the experiments three times. It was only the 1st post-larva that moulted into two types of 2nd post-larvae, *i.e.*, fringed and non-fringed forms, as observed by Webb.

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STUDIES ON LARVAL DEVELOPMENT IN ANOMURA (CRUSTACEA, DECAPODA)—III

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ABSTRACT

Laboratory study of the larval development of the porcellanid crab, *Petrolisthes boscii* (Audouin) reveals two distinct zoeal stages before the megalopa.

The presence of 4 plumose setae on the expodites of first two maxillipeds can be taken as indicative of stage I larvae since this is a common feature in *P. boscii* and the other porcellanid larvae described so far. However, in stage II the number of plumose setae varies from 10–16 in all species.

Considering the telson character of the larvae, the present study bears out that the larval stages described by Menon (1937) ascribed to *Petrolisthes* (sp. I and sp. II) are incorrect as has been already pointed out by Lebour (1943) and Sankolli (present publication); stage I and especially stage II of *Porcellanella* of Menon (*op. cit.*) appears to be *Petrolisthes* as per the present study.

Lebour (*op. cit.*) shows the presence of a central spine while illustrating the telson of stage II of presumably *Petrolisthes armatus* (after Gurney, 1938) but in the present study, stage II has a central plumose seta instead of the spine, as also observed by Menon (*op. cit.*), in stage II of *Porcellanella*.

THIS part incorporates a study on the life-history of the porcellanid crab, *Petrolisthes boscii* (Audouin), as worked out in the laboratory.

Very little work has been done on the larval development of the Indian porcellanids (Menon, 1937 and 1940 and Sankolli, 1967 present publication). Menon's identification was provisional since he could not get the early larvae in the laboratory or late post-larvae from his planktonic material whereas Sankolli obtained the early larval stages of five species of porcellanids in the laboratory including that of *Petrolisthes lamarckii* and hence his identification is reliable.

Besides the work of Menon and Sankolli there are several others on the development of *Petrolisthes*. Gurney (1938, *vide* Lebour, 1943) described an early and a late stage of a Porcellanid from the Red Sea, which he provisionally assigned to *Petrolisthes* and suggested that it is not the number of pleopods but the characteristics of the telson of the larvae which indicate the generic character. Lebour (1943) observed that Gurney's *Petrolisthes* is probably *P. armatus* (Gibbes), her observations being based on the studies of its 1st stage obtained in the laboratory. She also discussed the relationship between the larvae of *Porcellana* and *Petrolisthes*. Gohar and Al-Kholy (1957) described the life-history of *P. rufescens* (Heller) by obtaining the pre-zoea to the 2nd zoea in the laboratory, and the 2nd zoea to the megalopa from the plankton.

The life-history of *P. boscii*, comprises a pre-zoeal, two zoeal and a megalopa stages.

MATERIAL AND METHODS

Berried females of *P. boscii* were collected from Bombay (Chawpaty and Cuff-parade) and kept in aquarium tanks until the eggs hatched into the pre-zoeal stage. To provide a suitable environment, a few stones and coarse sand were placed at the bottom of the tank. This was necessary since the zoeae hatched out from specimens kept in such tanks were invariably healthier and stronger than those obtained from the females kept without stones and sand. The first zoeae

obtained from the latter, were less active and in all cases, died before moulting to 2nd zoeal stage, whereas the 1st zoeae got from the former were more active and were successfully reared upto the megalopa stage with little difficulty.

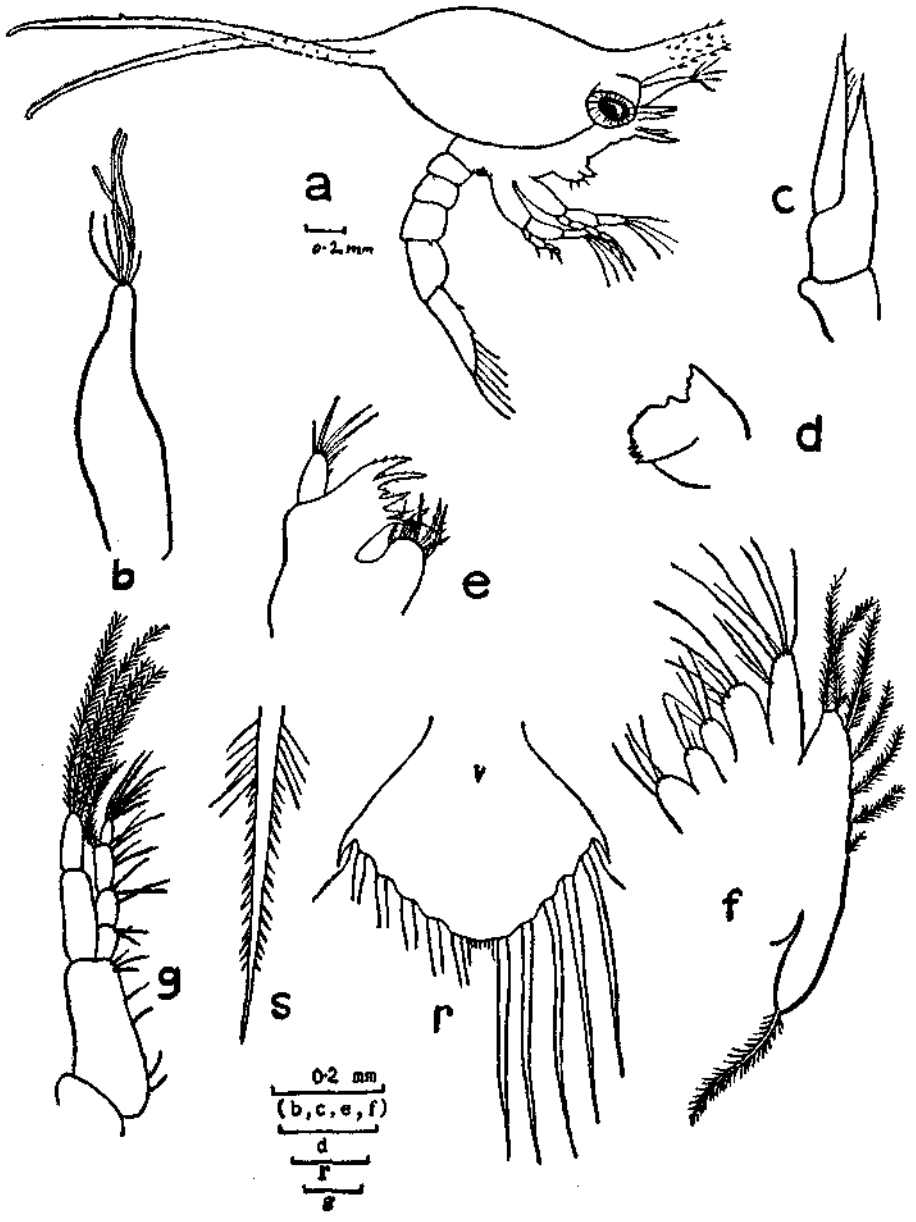

FIG. 1. *Petrolisthes boscii* (Audouin), first zoea. (*a*) entire larva; (*b*) antennule; (*c*) antenna; (*d*) mandible; (*e*) first maxilla; (*f*) second maxilla; (*g*) first maxilliped; (*r*) telson; (*s*) telson process (magnified).

Method of rearing and feeding the larvae was more or less similar to that suggested by Rees (1959).

OBSERVATIONS

Table I shows the average time required by each stage to moult into the next stage.

TABLE I

Stage	I	II	Megalopa
Average number of days spent in each stage	6	7	Lived for 2–3 days

P. boscii passes through two zoeal stages before moulting into the megalopa. Percentage of larval mortality was more during the intermoult period from 1st zoea to 2nd zoea and practically nil from the 2nd zoea to the megalopa.

Though every attempt was made to make the surroundings natural, the megalopa did not moult to the next instar in the laboratory.

DESCRIPTION OF THE STAGES

Pre-zoea

The eggs hatched out into pre-zoeae which swam sluggishly for 3–4 hours before moulting to the first zoeal stage. Whenever dissections of the appendages were attempted, the cuticle used to get invariably damaged, thereby rendering the study of pre-zoeal characters a difficult task. This kind of difficulty was also experienced by Lebour (1943) and Sankolli (*op. cit*).

First zoea (Fig. 1 *a*)

The rostrum is very long, nearly four times the length of the posterior spine, with about ten longitudinal rows of minute spines all around, the ventral spines being the most prominent. The posterior spine has minute, blunt, elongated processes all around, almost to the tip which is slightly bent inwards. The eyes are stalked but not free from the carapace.

Antennule (Fig. 1 *b*).—It is unsegmented with three aesthetascs and three unequal setae at its tip.

Antenna (Fig. 1 *c*).—The basipodite bears two styliform processes, the inner one is stout bearing a small seta at its tip and the outer has three delicate setae and a minute distal tooth on its inner side.

Mandible (Fig. 1 *d*).—The incisor part of the cutting edge bears four to five strong teeth and the molar is provided with several sharp and small teeth.

First maxilla (Fig. 1 *e*).—It consists of two endites and an unsegmented palp. The proximal endite is small bearing six bristle-like setae and one simple seta; the distal endite bears on the inner edge six bristle-like and three simple setae. The palp has at its distal end five setae, of which the inner three are plumose and the outer two smooth. There is also one minute seta near the distal end on the inner side.

Second maxilla (Fig. 1 *f*).—It consists of four endites, an unsegmented palp and a long, narrow scaphognathite. The palp bears two groups of setae, six distal and three marginal. The scaphognathite bears seven marginal plumose setae on the distal half and a long, plumose seta posteriorly.

First maxilliped (Fig. 1 *g*).—The basipodite has seven setae of which three are in a group. The endopodite is four-segmented and the inner margin of the first three segments bear three, three and six setae respectively. There is one seta on the outer margin of the third segment. The last segment bears seven to eight setae.

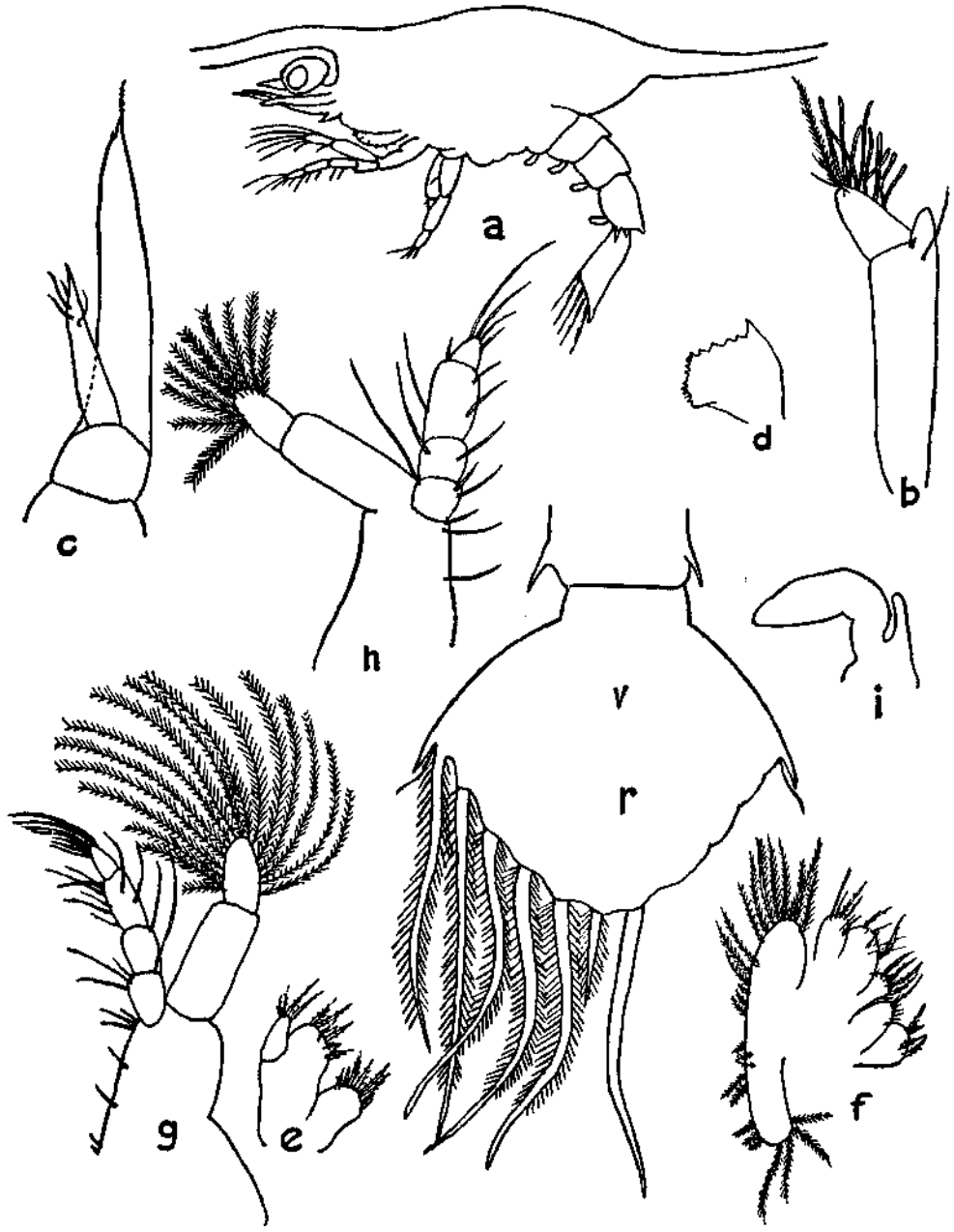

FIG. 2. *Petrolisthes boscii* (Audouin), second zoea. (*a*) entire larva; (*b*) antennule; (*c*) antenna; (*d*) mandible; (*e*) first maxilla; (*f*) second maxilla; (*g*) first maxilliped; (*h*) second maxilliped; (*i*) third maxilliped; (*r*) telson.

The exopodite is two-segmented, bearing four terminal plumose setae.

Second maxilliped.—The basipodite bears two to three setae, on its inner margin. The endopodite is four-segmented bearing on the inner margin, one to two, two, three setae respectively from first to third segments. As in the first maxilliped, the third segment has one prominent seta on outer margin also. The last segment has four terminal and one proximal setae. On the outer margin of the third segment, there are fine hairs in the proximal part. The exopodite is similar to that of the first maxilliped.

Other appendages.—Rudiments of thoracic appendages are present in the form of small buds and those of the third maxilliped are biramous.

Abdomen (Fig. 1 *a*).—It is 5-segmented, the 6th segment is fused to the telson. The fourth and fifth segments have distinct postero-lateral spines.

Telson (Fig. 1 *r* and *s*).—The telson process formula is 7 + 7. The 1st process is a fairly long spine, the 2nd is a delicate plumose hair, 3rd to 7th long plumose setae, the distal ends of which are armed with peculiar tooth-like spines on both the margins as shown in figure, these being longer in the 5th telson process. The posterior end of the central prominence is almost straight bearing about ten minute, short delicate hairs, in the middle visible under high magnification. The 7th process (= 5th long telson seta of Lebour) is situated on the central prominence. Anteriorly there is an anal spine on the ventral side.

Second zoea (Fig. 2 *a*).

The larva increases in size considerably with the eyes becoming stalked and movable. The pleopod buds develop on the second to the fifth abdominal segments.

Antennule (Fig. 2 *b*).—The exopodite is now distinctly articulated to the basal segments, bearing on the outer margin, eleven aesthetascs and three setae of which one is long and plumose. The endopodite is a small conical process, not separated from the basal segment and bears a single proximal seta. There is a minute spine on the basal segment.

Antenna (Fig. 2 *c*).—The endopodite is now nearly double the length of the exopodite and has distally, in addition to the terminal seta, one small papilla-like process.

Mandible (Fig. 2 *d*).—The teeth of the cutting edge are now stronger. A rudimentary pulp develops.

First maxilla (Fig. 2 *e*).—The number of setae on both the endites is increased to ten and there is general increase in size.

Second maxilla (Fig. 2 *f*).—The number of setae on the endites, from proximal to distal, is sixteen, five, eleven, and nine respectively. The palp bears two additional simple setae. The scaphognathite becomes longer bearing a distal group of fourteen plumose setae, an outer group of eight small setae and four long plumose setae in the proximal part.

First maxilliped (Fig. 2 *g*).—In the endopodite, there is an increase in the number of setae on the segments. The exopodite is now distinctly two-segmented, the second segment bearing sixteen setae.

Second maxilliped (Fig. 2 *h*).—The two-segmented exopodite bears ten terminal setae.

Third maxilliped (Fig. 2 *i*).—It is still rudimentary but has increased in size.

Pereiopods.—These are now better developed. The first pair (Fig. 2 *j*) shows its chelate nature. The spines on the posterior margin of the propodus of the second to the fourth legs could be seen through the cuticle in some of the advanced larvae.

Abdomen (Fig. 2 *a*).—Four pairs of biramous pleopod buds are present on 2nd to 5th abdominal somites.

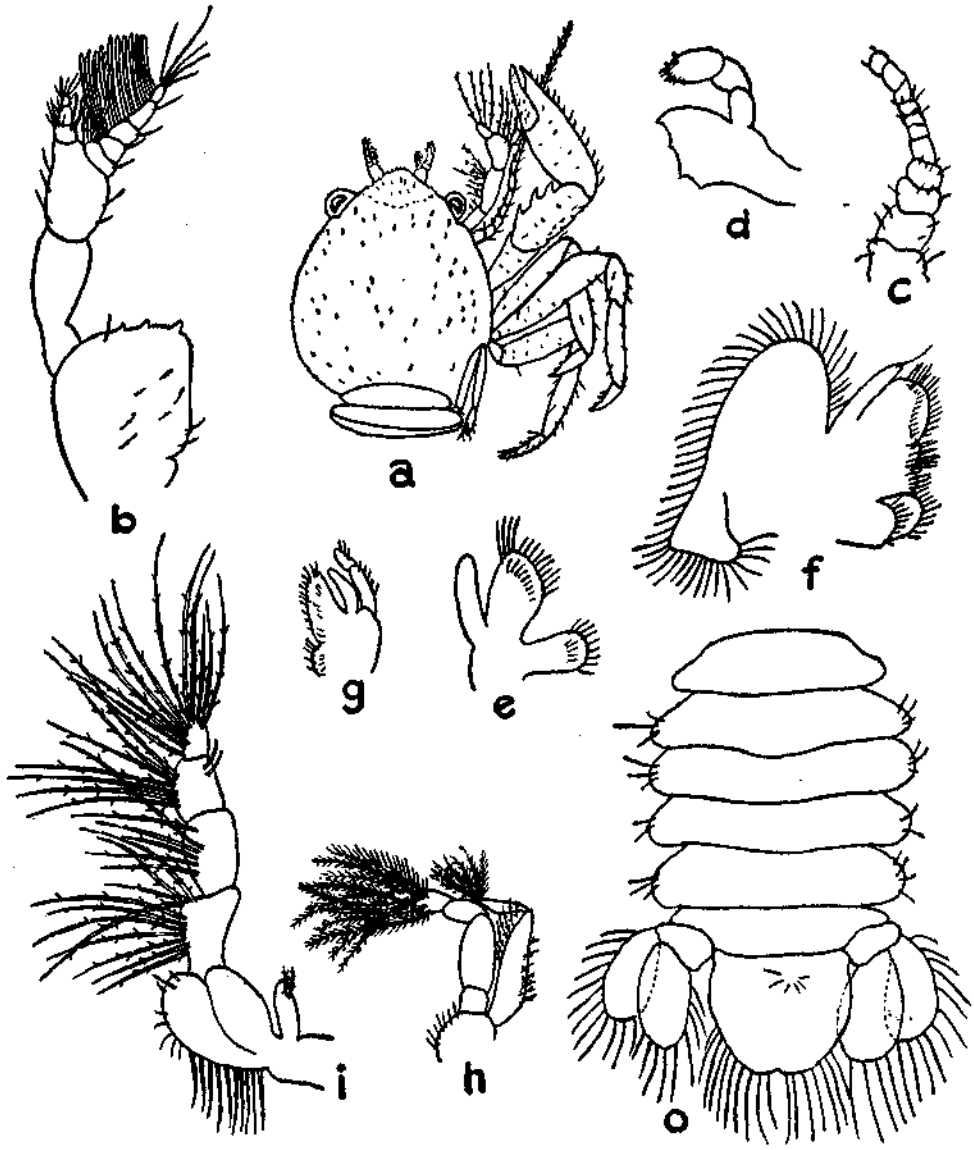

FIG. 3. *Petrolisthes boscii* (Audouin), Megalopa. (*a*) entire post-larva, (*b*) antennule, (*c*) antenna, (*d*) mandible, (*e*) first maxilla, (*f*) second maxilla, (*g*) first maxilliped, (*h*) second maxilliped, (*i*) third maxilliped, (*o*) abdomen.

Telson (Fig. 2 *r*).—Telson process formula is 7 + 1 + 7. There is no structural change in the processes except for the addition of a small, plumose seta which arises from the middle of the central prominence.

Anal spine continues to be present.

Megalopa (Fig. 3 *a*)

The post-larva closely resembles the adult in many morphological characters. It is pinkish in colour.

The carapace is longer than broad and is covered sparsely with small delicate setae all over. The front is somewhat triangular with minute serrations. The lateral margin is devoid of any serrations though in a very few specimens, it was found to be indistinctly serrated. The abdomen is folded underneath the carapace and is extended only when swimming.

Antennule (Fig. 3 *b*).—The peduncle is three-jointed. The basal joint is swollen and globular bearing on its anterior border three to five small unequal teeth and provided with a few delicate setae. The second joint is without any setae, and the third bears two to three setae on both margins. The outer flagellum is five-segmented; the segments bear on their inner margin in all about thirteen aesthetascs, of which six are present on the first segment and the remaining seven are on the other segments. Each segment bears a single small seta on its outer margin but the last segment has two long and three short setae terminally. The inner flagellum is three-segmented, the first segment bears five long setae on the inner and six on the outer margins, second segment has two setae on both margins, the last segment bears seven setae.

Antenna (Fig. 3 *c*).—The peduncle is four-jointed, each segment bearing a few setae. The flagellum is composed of about thirty-five segments which bear circlets of small setae.

Mandible (Fig. 3 *d*).—The cutting edge is armed with a few small teeth. The palp is developed and is three-jointed, the terminal joint has sixteen bristle-like setae along its anterior margin.

First maxilla (Fig. 3 *e*).—The number of setae on the endites is increased. The proximal endite bears twenty-six and eleven setae on the outer and inner margins respectively. The distal endite has five long and nineteen short setae on the outer margin and only ten on the inner. The palp is unsegmented without any setae.

Second maxilla (Fig. 3 *f*).—There are numerous setae on the endites. The palp is unsegmented with a single, terminal seta. The scaphognathite is well developed and is fringed with numerous setae.

First maxilliped (Fig. 3 *g*).—The protopodite is produced into a small proximal and a large distal lobe provided with numerous setae on the outer margin. The endopodite is unsegmented, bearing a few microscopic hairs on the proximal outer margin. The exopodite is two-jointed; the proximal joint bears five and the distal bears three setae respectively.

Second maxilliped (Fig. 3 *h*).—The basal segment is setose on its inner margin. The endopodite is five-segmented. The second segment bears ten setae on its inner margin and the fourth and fifth segments are provided with tufts of plumose setae. The exopodite is two-segmented, the proximal segment is long, bearing seven setae on either margin, the distal segment is flagelliform bearing six terminal and three distal small setae on the inner margin.

Third maxilliped (Fig. 3 *i*).—The endopodite is five-segmented, first segment is much flattened and the remaining less flat; first segment has eleven setae on the inner margin and a few short setae scattered all over the surface, second to fourth segments bear numerous sparsely plumose setae on their inner margin. The last segment has several setae on its inner margin and twelve terminal setae of which two are small. The second segment has two small distal setae on the outer margin.

The exopodite is small and unsegmented with two short, plumose setae near its distal end.

Chelipeds (Fig. 4*j*).—The right cheliped is slightly larger than the left. The dorsal surface is minutely rugose. The carpus is much longer than broad with carinate anterior margin which is armed with three broad teeth as in the adult. The outer margin of the propodus is bordered with small spine-like teeth and setae. The anterior margin of the dactylus is also armed with well spaced spine-like teeth. The cutting edge of both the fingers is armed with a few blunt teeth in the distal part.

Ambulatory legs.—The second, third and fourth pairs of pereiopods (Fig. 4*k–m*) are similar. The merus and propodus are the longest segments and more or less of the same length. There is a row of fine setae on the anterior margin of both segments. Minute rugae are present on the dorsal surface, these being more distinct on the merus and carpus. The posterior margin of the propodus bears distally three unequal spines. The dactylus is claw-like, short and stout with three short spines on its posterior margin.

The fifth leg (Fig. 4 *n*) is minutely chelate and small. The merus and carpus are the longest segments. The propodus bears setae in the distal half and the dactylus is also furnished with setae which are plumose on one side and on the distal part only.

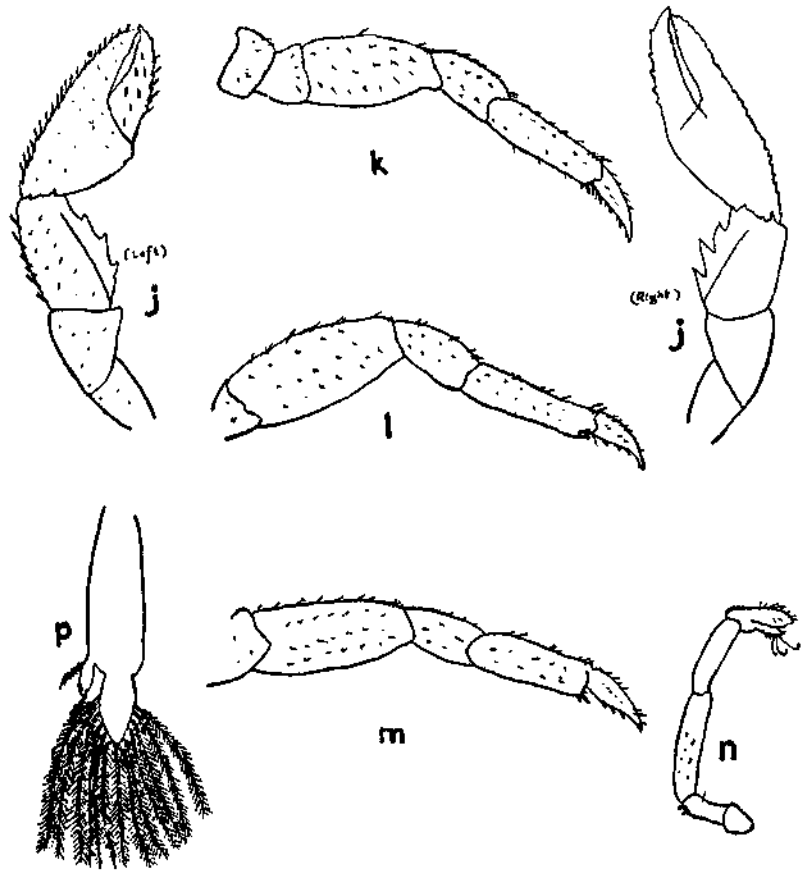

FIG. 4. *Petrolisthes boscii* (Audouin), Megalopa. (*j*) first leg, (*k*) second leg, (*l*) third leg, (*m*) fourth leg, (*n*) fifth leg, (*p*) pleopod.

Abdomen (Fig. 3 *o*).—It is folded underneath the carapace and consists of six dorso-ventrally flattened segments, the segments 2–5 bear biramous pleopods. Each pleopod (Fig. 4 *p*) consists of a large, oval exopodite and a smaller endopodite borne on a long peduncle. The exopodite of the first pleopod bears twelve to fourteen plumose setae whereas there are thirteen to fifteen setae on the others. The endopodite of the second to the fourth pleopods bears basally two setae on the inner side but that of the first has only one and there is a single, apical seta in all except the third which has two. The endopodite at its tip bears several minute hooks, ranging from twelve to fourteen in number.

Uropods (Fig. 3 *o*).—The uropods are articulated to the 6th abdominal segment by a short peduncle, which bears flat oval exopodite and endopodite bordered with numerous, long, plumose setae. The exopodite is slightly longer than the endopodite.

Telson (Fig. 3 *o*).—It is slightly broader than long. The lateral margin shows a shallow notch anteriorly. Also there is a median notch on the posterior margin which bears many long, plumose setae. There are a few groups of small setae on the dorsal surface of the telson.

Discussion

The 1st zoea of *P. boscii* has four plumose setae on the exopodite of the first two maxillipeds and this is true for all the known porcellanid larvae, except in *P. rufescens*, where it is 4 + 2 as described by Gohar and Al-Kholy (*op. cit.*). In the 2nd zoea, the number varies from ten to sixteen; eleven in *Porcellana longicornis*, thirteen in *P. platycheles* (Lebour, *op. cit.*), ten in *Petrolisthes refuscens* (Gohar *et al.*, *op. cit.*), eleven, ten and sixteen in Menon's (*op. cit.*) *Petrolisthes* (sp. I and II) and *Porcellanella* (equivalent to *Petrolisthes*) respectively; ten to twelve in *Petrolisthes armatus* (Lebour, *op. cit.*, after Gurney) and ten to sixteen in the present species. Hence, the presence of four plumose setae on the first two maxillipeds may be taken as characteristic of stage I larvae, though this character cannot be relied upon for stage II larvae. The telson process formula 7 + 7 for stage I of porcellanid larvae, as suggested by Lebour, is also applicable for 1st larva of *P. boscii*.

Gurney (*op. cit.*) working with the Red Sea species of porcellanids, stressed the importance of the characters of the telson in the identification of the larvae. This has been further supported by Lebour (*op. cit.*) who suggested that the 7th pair of setae arising from the central prominence of the posterior margin of the telson in stage I is a distinguishing character of *Petrolisthes*. In stage II, there are seven pairs of setae and a central tooth, the latter becoming an indicative character. The larval stages of *P. boscii* conform to these characters except that in stage II, instead of the central tooth recorded in the Red Sea species, there is a central plumose seta. State II of *Porcellanella* (equivalent to *Petrolisthes*) of Menon (*op. cit.*) has also a similar central seta. Considering the 2nd larva of the Indian and the Red Sea species of the genus *Petrolisthes*, it may be stated that the presence of either a central tooth or a seta on the posterior margin of the telson is a characteristic feature.

The only available description of the megalopa of the genus *Petrolisthes* is that of *P. rufescens* by Gohar and Al-Kholy (*op. cit.*). Since their account of the megalopa is somewhat confusing a detailed comparison is not attempted.

Acknowledgements

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SOME RECENT ADVANCES AND OUTSTANDING PROBLEMS IN THE STUDY OF LARVAL CRUSTACEA

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ABSTRACT

The paper deals mainly with larvae of the Decapoda and excludes laboratory rearing from consideration. Prior to 1939 most of the taxonomic work on decapod larvae was done with European coastal species; since 1939 the bulk of such work has concerned coastal species from the remainder of the world, with a continuing limited study of oceanic species. More hatching and rearing work at sea would be profitable. Some recently described larvae of particular taxonomic interest are mentioned, and families whose larvae remain totally unknown are listed.

Some interesting results have been published on factors controlling the number of zoeal stages and the length of larval life, but few species have yet been studied. There is need for more work on foods, methods of feeding, on the functional value of different body shapes and of modified appendages, and on factors controlling orientational behaviour.

Most of the problems of larval "navigation" remain unsolved. Some coastal and estuarine species probably make use of tidal currents to move shorewards in the late larval stages. The difficulties of returning to a suitable settling area are particularly great in the Palinuridae, where the phyllosoma stages may last up to 11 months and most of the larval development takes place well away from the hatching area. There is wide scope for studies on the distribution of larvae in relation to ocean currents, concentrating on (1) comparison of the larval and adult distribution of holopelagic species (*e.g.*, Euphausiidae, Sergestidae, some Penaeidae, Oplophoridae, Disciadidae), and (2) the distribution of long-lived larvae of benthic species (*e.g.*, some Stenopodidae, Palinuridae, Axiidae, some Diogenidae, Hippidea, Stomatopoda). The samples from the International Indian Ocean Expedition could provide the basis for such studies.

INTRODUCTION

THIS paper considers rome recent trends in work on crustacean larvae and some lines along which considerable progress might be expected during the next decade. It is a personal selection of topics, and it makes no claim to be a comprehensive review of all modern work on crustacean larvae or to mention all worth-while fields for future research. There are passing references to larvæ of groups other than the Decapoda, but most of the paper is restricted to considerations of decapod larvæ. Many topics concerned with the laboratory culture of larvae have been omitted as they are covered by other papers to this symposium.

TAXONOMY

Larvae of rather less than 100 species of Decapoda have been described since 1939, compared with 600–700 species described previously (listed by Gurney, 1939). This represents no spectacular change in the rate of publication of descriptions of larvae, but there has been a marked change in the geographical areas of activity in this sphere. Of the authors listed in Gurney's (1939) bibliography nearly three-quarters were working in Europe, and, although several of these published papers on non-European larvae, almost two-thirds of the larvae described were from European coastal waters. By contrast, in the last 25 years only about one-third of those working on decapod larvae have been attached to European institutions and considerably less than one-third of the larvae described have been from European waters.

By 1939 it was possible, from the existing literature, to obtain specific identifications of the great majority of zoeas encountered in the waters around the British Isles. "Mopping-up operations" have continued on the comparatively few undescribed zoeas, but the spectacular advance in larval identification in this area has concerned not zoeas but nauplii. It is now possible to identify to species the majority of the nauplii of both balanoid Cirripedia and calanoid Copepoda encountered in the coastal waters of north-west Europe. Most of the relevant literature has been published since 1945 (Crisp, 1962, with refs.; Ogilvie, 1956; Lovegrove, 1957).

Returning to taxonomic work on larval Decapoda, there has been a recent trend towards more detailed descriptions. Many of the older descriptions are of one zoeal stage only, with no descriptions or figures of the appendages; many recent papers describe not only all larval stages of a species but all appendages in each larval stage. This is to some extent a reflection of more successful laboratory rearing methods, giving the author sufficient material to make such detailed descriptions possible. This type of paper is to be welcomed in that it greatly enlarges the number of characters which can be considered in any taxonomic work. It means, however, that the larval development of any one species described in this detail fills a moderate sized paper, and one cannot envisage the 8,000-9,000 papers which would be necessary to cover the known Decapoda in this way. This is obviously not a situation in which rigid rules can be formulated or applied. Authors and editors will have to exercise their discretion as to the amount of detail which is desirable or practicable in each case, but in cases of doubt it is to be hoped that they will err on the side of too much detail rather than too little. Far too frequently one finds that a character of potential taxonomic or phylogenetic importance is neither described nor figured.

Most revisions of the classification of the Decapoda have taken some account of larval characters, but all have been greatly handicapped by the incompleteness of the larval evidence. The gaps in our knowledge of larval forms are, however, steadily disappearing, and a number of genera may be mentioned whose larvae are of particular taxonomic interest and which have recently been described or identified for the first time. These include *Leontocaris* Stebbing (Hippolytidae) whose larva appears to be the spectacular *Problemacaris* Stebbing (*see* Gordon, 1964); *Campylonotus* Bate (Campylonotidae), larvae hatched by Pike (unpublished); *Glyphocrangon* A. Milne Edwards (Glyphocrangonidae), described from plankton by Kurata (1964) but a different form of larva has been hatched from an American species by Dobkin (unpublished); *Thalassina* Latreille (Thalassinidae), described by Sankolli, 1967; *Parapagurus* S. I. Smith (Paguridae), described by Dechance (in press) and by Williamson and Levetzow (in preparation); *Uroptychus* Henderson (Chirostylidae), hatched by Pike (unpublished); *Dromidia* Stimpson (Dromiidae), described by Rice and Provenzano (in press); *Lyreidus* de Haan (Raninidae) described by Williamson (in press); *Mictyris* Latreille (Mictyridae), hatched by Cameron (unpublished). The number of recently described brachyuran larvae encourages us to look forward to definitions of larval characters of the families of this group in the near future. The report of a hymenosomatid crab with no megalopa stage by Al-Kholy (1959) deserves further investigation.

Some notable variations within genera have been demonstrated recently: the number of zoeal stages in different species of *Pandalus* Leach (Pandalidae) ranges from one to six or more (Pike and Williamson, 1964); some species of *Pagurisles* Dana (Diogenidae) have abbreviated development and the zoeal mouth-parts are not functional while others pass through a normal series of carnivorous larval stages (Provenzano, in press); equally striking variations in the length of larval life occur within what was until recently regarded as a single species, *Thor floridianus* Kingsley (Hippolytidae) (Dobkin, 1962).

The most obvious gaps in decapod larval taxonomy concern those families for which no larvae have been described. Using the classification of Balss (1957), there are nine such families: Stylodactylidae, Eugonatonotidae, Physetocarididae, Psalidopodidae, Gnathophyllidae, Pylochelidae, Lomisidae, Dynomenidae and Retroplumidae. It should be noted, however, that the position of several subfamilies and genera in Balss' classification has been questioned and in some cases new

families have been proposed for them, *e.g.*, Ogyrididae (*see* Holthuis, 1955), Tymolidae (*see* Gordon, 1964).

Knowledge of the larvae of no family can be said to be fully adequate, and every uninvestigated genus or species is liable to show features which may shed light not only on its own taxonomic position but also on the groupings of higher taxa. Examples of families whose larvae are very inadequately known include the Polychelidae, whose early larvae are undescribed. Much more knowledge is needed on the larvae of the Dromiidae, and descriptions of the newly-hatched animal in cases where development is abbreviated could be of considerable interest. In many cases the young is said to resemble the parent, but we do not know whether this resemblance extends to the mouth-parts or whether any vestigial zoeal characters remain. The examples of *Pandalus*, *Thor* and *Pagurisles* mentioned above show that when development is abbreviated in some members of a genus it is not necessarily so in all members. There is still no published description of the full larval development of any member of the Homolidae. Studies on the larvae of the Stenopodidae, particularly of genera other than *Stenopus* Latreille, may shed light on the relationships of this puzzling family.

Attempts to hatch and rear larvae at sea on the larger research vessels are likely to be rewarding, and a welcome move in this direction has been taken by biologists on R.R.S. "Discovery" (*see* Foxton, 1964). It is only from work with live material at sea that we are likely to obtain information on the larvae of deep-sea and open ocean Crustacea and obtain the identities of the many oceanic larvae which cannot yet be assigned to adult genera.

Physiology and Behaviour

The steadily growing volume of experimental work on factors which modify the number of larval stages and the length of larval life is covered by papers to this section of the Symposium on laboratory rearing. It will be of great interest to see this work extended to some of the species which can produce very large larvae, presumably after many stages, such as *Aristaeomorpha* Wood-Mason (Penaeidae) and some Stenopodidae and Pandalidae.

Decapod larvae were the first invertebrates to be shown to react to changes in hydrostatic pressure (Hardy and Bainbridge, 1951) and this work has recently been extended by Rice (1964). Changes in orientation behaviour during larval development and during metamorphosis have been demonstrated much more clearly in barnacle larvae (*e.g.*, Moyse and Knight Jones, 1967) than in decapods.

Many species of zoea will feed on *Artemia nauplii* in the laboratory, but there is evidence that this food is inadequate or not fully adequate in many cases (*e.g.*, Rust and Carlson, 1960; Inoue and Nonaka, 1963; Williamson, in press). Very little is known of the natural foods of larvae. It seems likely that some species are highly specialised feeders, and a detailed investigation of the associations between phyllosomas and medusae (reported by Thomas, 1963) is required. It may well be that the shape of a phyllosoma is primarily an adaptation for catching medusae and not for slowing down passive sinking as is often suggested. The resemblances between *Amphion* H. Milne Edwards and a phyllosoma, particularly in the form of the stomach, may reflect similar feeding habits, either convergent or inherited. The peculiar modifications of the trachelifer larva of *Jaxea* Nardo (Laomediidae) may also be related to specialised feeding, for they affect not only the shape of the head but also the form of the mandibles. *Eretmocaris* Bate (? Hippolytidae) is an example of another type of larva with morphological modifications for which there is, as yet, no functional explanation. It seems possible that the expanded peraeopods may be spread to slow down sinking and trailed to offer little resistance when swimming upwards, or they may have a sensory function, or is their use in some way connected with the very long eye-stalks found in larvae of this type?

DISTRIBUTION

To what extent are planktonic larvae passive drifters and to what extent navigators? What proportion of larvae are lost through being carried into unsuitable environments? How far can a larva travel before settling and metamorphosing? These are questions which have interested biologists since the beginning of the century at least, but as yet we can produce only very incomplete answers for a very few species and no answer at all for the great majority. However as Thorson (1961) has pointed out, information on length of larval life is becoming available for many more species and the water movements of many regions have been described in some detail. Much more information is required on the behaviour of larvae at various stages of development and many more studies of larval distribution are needed, but we now seem to be entering an era in which questions on larval dispersal will not only be asked but also answered.

Larvae of estuarine species usually disperse seawards very rapidly after hatching and only re-enter estuaries at a late larval stage (Gurney, 1942, with refs.; Chamberlain, 1962; Jones, 1963). Tidal currents must be used to re-enter the estauries in most cases, and the behaviour of the larvae must either depend on the salinity of the water or show a rhythm similar to that of the tides. As yet, no one has made a detailed study of the factors influencing the orientation of developing decapod larvae; studies on estuarine species may be particularly rewarding.

Ocean-going larvae face different navigational problems. The larvae of most holopelagic Crustacea appear to live nearer the surface than do the adults, and the water layers occupied by different stages may be moving at different rates or even in different directions. Detailed studies of distribution which include larval stages have mostly concerned the Euphausiidae (*e.g.*, Fraser, 1936; Einarsson, 1945; Marr, 1962). Similar investigations could profitably be carried out in other areas and extended to include such groups as the Sergestidae, pelagic Penaeidae, Oplophoridae and Disciadidae. The results should shed light on ocean currents at different depths as well as on the life-history, ecology and behaviour of the species investigated.

A number of adult Decapoda with a restricted benthic distribution give rise to larvae with a planktonic life of several months in areas where there is a regular current of several miles or even tens of miles per day. Such larvae may travel many hundreds or even several thousands of miles before metamorphosis. Two obvious questions arise: to what extent can such larvae cross the oceans? and how do sufficient numbers of larvae remain in the spawning area or return to it for the stock to be replenished?

Perhaps the most striking examples come from the Palinuridae. The duration of the pelagic phase was thought by Gurney (1942) to be not more than three months, but recent estimates for several species are all considerably longer. The average time taken to complete the phyllosoma stages is probably 5 months for *Jasus lalandii* (H. Milne Edwards) in south-eastern Australia (Olsen, 1960), 6 months for *Panulirus argus* (Latreille) in the Caribbean (Lewis, 1961), 8 months for *P. interruptus* (Randall) off California (Johnson, 1960) and 10 months for *P. cygnus* George off Western Australia (George and Cawthorn, 1962). In each case the pelagic phase may probably be extended by over a month by the puerulus, and it should be emphasised that these are all average values. The times for the slowest growing larvae are probably some 25% greater in all cases.

Some idea of the distances covered by phyllosomas is provided by those species of Palinuridae whose total adult range is considerably greater than their breeding range, due to the larvae drifting into regions which are suitable for metamorphosis and growth but too cold for reproduction. A well-documented case is provided by *Palinurus elephas* (Fabricius) in north-west Europe (Tambs-Lyche, 1958; Rae and Lamont, 1963). This species regularly breeds in south-west England and further south and also in Ireland, except the north. Very few ovigerous females have been taken in Scottish waters, and the most northerly record of eggs is in the Inner Hebrides. The range of non-breeding adults, however, extends to northern Scotland, the Orkney and Shetland Islands and western Norway (Fig. 1). The shortest route from the most northerly breeding record to the Norweigan coast is about 500 nautical miles, but it seems more likely that the Norwegian specimens

were hatched in western Ireland, where breeding is common, and that the larvae travelled at least 800 miles. This transport is achieved with comparatively modest currents, averaging between 5 and 10 miles per day.

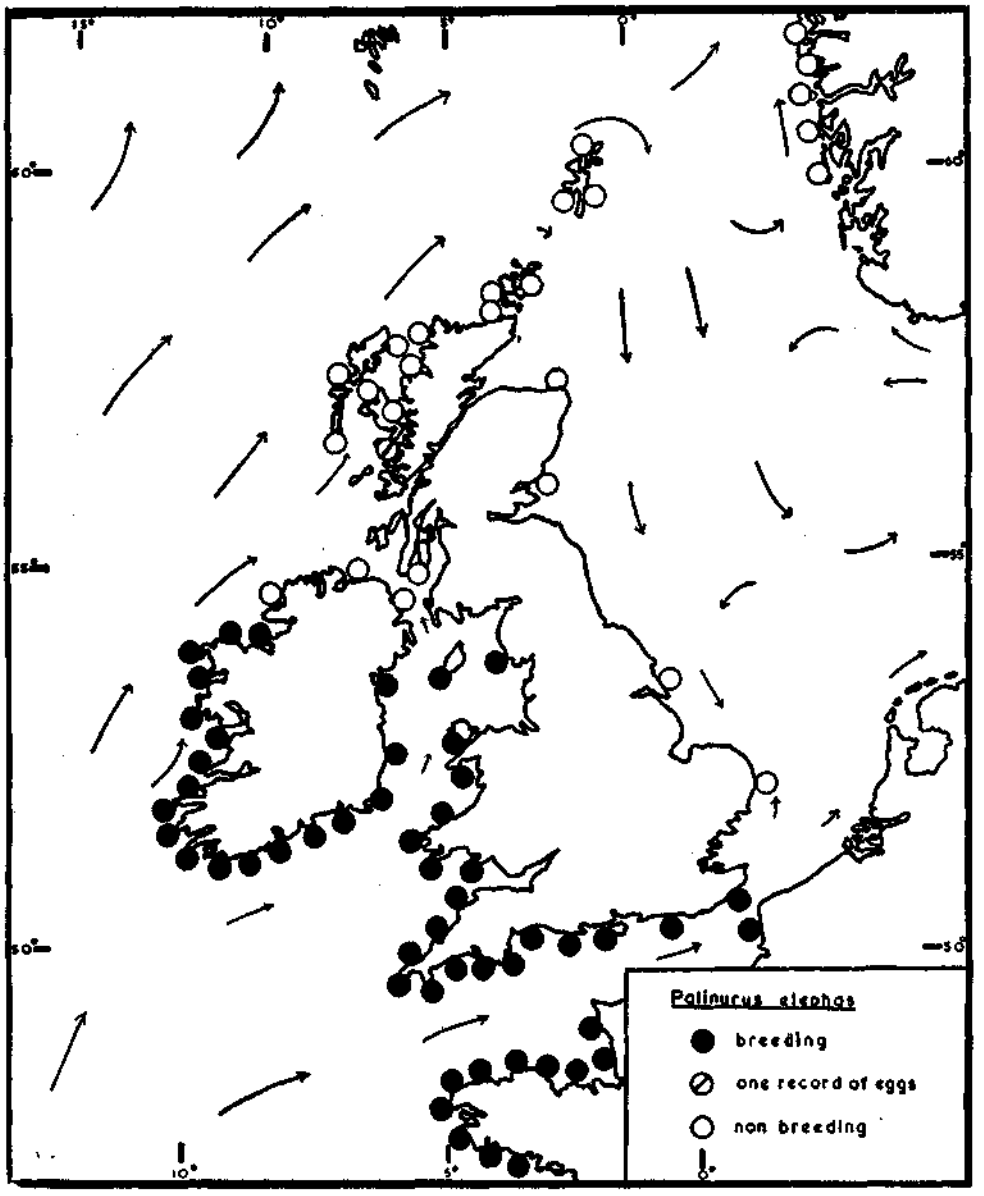

FIG. 1. Distribution of *Palinurus elephas* (Fabricius) in north-west Europe, and surface currents. Distribution after Tambs-Lyche (1958); currents after Lee, in Fraser (1962).

I am indebted to Dr. A. A. Racek, Sydney, for bringing to my attention the interesting distribution of the species of *Jasus* Parker in eastern Australia and New Zealand. *J. verreauxi* (H. Milne Edwards) extends at least 500 miles south of its breeding range in both countries, and in New Zealand ovigerous females are restricted to the most northerly regions (Fig. 2). It seems doubtful

whether the New Zealand stocks could be maintained from the small breeding area in that country, and it seems likely that they are regularly replenished from Australia. The currents of the Tasman Sea make it possible for larvae hatched on the Queensland coast of Australia to reach the New Zealand coast within three months, while only exceptionally would larvae from the New Zealand spawning grounds be carried to the western coasts of that country. The lack of morphological difference between the New Zealand and Australian stocks is consistent with the idea that there is considerable recruitment from Australia to New Zealand (Racek, personal communication).

If larvae of *J. verreauxi* cross in considerable numbers from Queensland to the North Island of New Zealand then we should expect an even greater transport of larvae of *J. lalandii* (s.l.) from Tasmania to the South Island, for the distance is slightly shorter and the currents seem to be at least as favourable. There are, however, morphological differences between the adults of the two countries, sufficient for Holthuis (1963) to regard them as specifically distinct. If Holthuis' view is accepted then it raises the question: what keeps the Australian species out of New Zealand? Certainly an 800 miles stretch of sea with an east-going current of about 15 miles per day should provide no serious obstacle to the larvae. The subtropical convergence will provide a partial barrier to some of the Austral an larvae, but it seems likely "that the Subtropical Convergence is formed by several strips, in which convergent movements take place, rather than in a continuous line, and it may even be temporarily absent" (Wyrtki, 1960). It apparently never occurs far enough south to interfere with the transport towards New Zealand of larvae hatched in southern Tasmania.

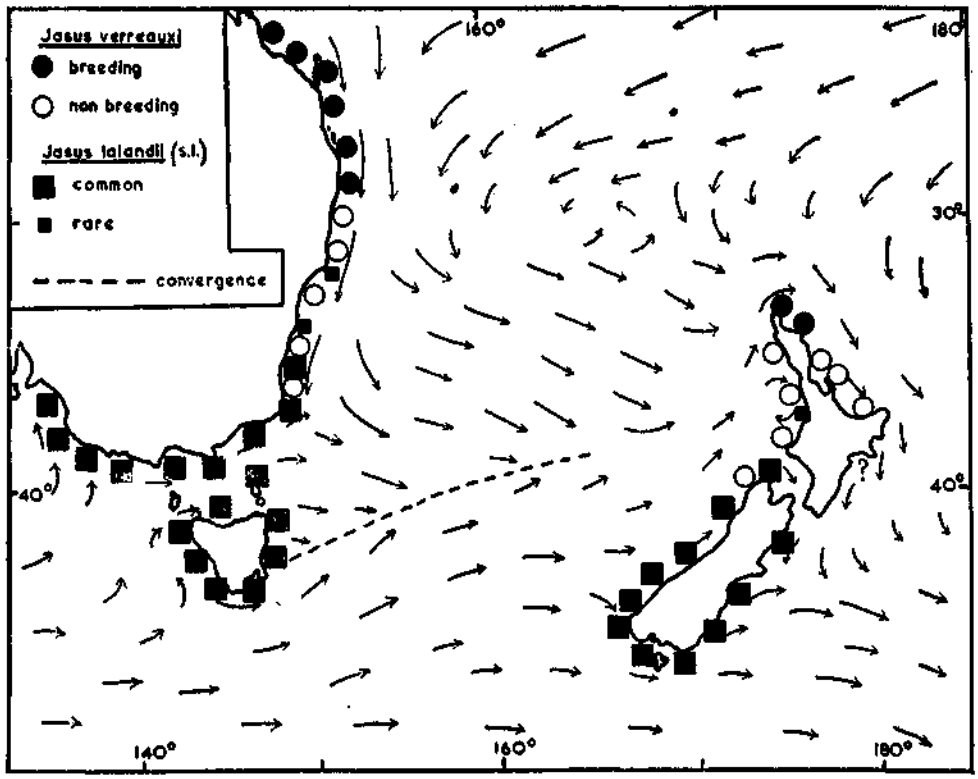

FIG. 2. Distribution of *Jasus verreauxi* (H. Milne Edwards) and *J. lalandii* (H. Milne Edwards) (s.l., including *J. novaehollandiae* Holthuis and *J. edwardsii* Hutton) in south-eastern Australia and New Zealand, and surface currents. Distribution data from Olsen (1960); N.S.W. State Fisheries Department (personal communications) and Dr. R. B. Pike (personal communication); currents after Wyrtki (1960).

Success in the laboratory culture of phyllosomas has, so far, been only limited, but the time when it will be possible to rear *J. lalandii* from egg to adult in the laboratory should not be far distant. Rearing from a late phyllosoma or puerulus stage to adult should present no great difficulties, even without the introduction of new techniques. Such rearing studies, under controlled conditions, could give valuable information on the differences between *J. novaehollandii* Holthuis, *J. edwardsii* (Hutton) and the other subdivisions of *J. lalandii* (s.l.), indicating to what extent they are genetic and to what extent environmental. Whatever the outcome of such work, however, studies on the distribution of phyllosomas in the Tasman Sea should be of the greatest interest. The samples from the International Indian Ocean Expedition should provide valuable information on the distribution of larvae of *Panulirus cygnus*, hatched in Western Australia, in relation to water movements, and also on the larval distribution of several other species of *Panulirus* and *Jasus*. The fact that the adult distribution of many Palinuridae of commercial importance is accurately known should make studies on their larval distribution of interest not only to the biologist but also to the physical oceanographer.

In spite of their long planktonic phase, the geographical distribution of most species of Palinuridae appears to be quite restricted, while species of some other families have probably made use of a prolonged larval life in achieving a very wide distribution. An example of this second type is *Stenopus hispidus* (Olivier) (Stenopodidae) which occurs very widely in the warmer waters of both the North Atlantic and the Indo-Pacific; its distribution is, however, probably discontinuous (Balss, 1957). Several other Stenopodidae and several Axiidae may have similar distributitions to *S. hispidus*, although their detailed distribution is not yet known. The species in question are known only as larvae and were described by Gurney (1936, 1938) from North Atlantic material; many of the same species occur plentifully in the plankton of the Coral Sea, south-west Pacific (personal observations). It is hoped that plankton from the International Indian Ocean Expedition will provide further data on these species and that their distributions in the Atlantic and Pacific will also be studied and compared with those of pan-oceanic Euphausiidae (*see* Brinton, 1962). Other long-lived larvae of benthic adults occur in the Diogenidae, Hippidea and Stomatopoda, and their distributions should repay study.

To conclude in a sentence, this paper is a reminder that, as biology expands rapidly into new fields, the older fields of taxonomy, behaviour and distribution are still fertile.

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DISCUSSION

Dr. V. Hansen: With reference to the last sentence of Dr. Williamson's paper, *i.e.*, "The samples of the International Indian Ocean Expedition could provide the basis for such studies", the problem of oceanic transport of larvae is very curious. I am confident that when the plankton samples are assorted and studied, they might show some distribution pattern of these larvae. Also decapod larvae can be checked and confirmed by studies on actual rearings in the laboratory as done by these workers.

AN ACCOUNT OF THE POST-LARVAL DEVELOPMENT, MOULTING AND GROWTH OF THE COMMON STOMATOPODS OF THE MADRAS COAST

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ABSTRACT

In a series of earlier contributions the author has reported on the stomatopod larvae of the Madras plankton, identifying them with the respective adult species by successfully holding pelagic larvae in laboratory aquaria, getting them metamorphosed into post-larvae and rearing the latter to the adult stage. The following 13 species of *Squilla*, one species of *Harpiosquilla*, two species of *Lysiosquilla* and three species of *Acanthosquilla* were, in this manner, positively correlated with their larval forms:

Squilla nepa, Squilla holoschista, Squilla wood-masoni, Squilla interrupta, Squilla quinquedentata, Squilla gonypetes, Squilla boops, Squilla hieroglyphica, Squilla scorpio, Squilla latreillei, Squilla fasciata, Squilla lata, Harpiosquilla raphidea, Lysiosquilla maculata, Lysiosquilla sulcirostris, Acanthosquilla multifasciata, A. tigrina and *A. acanthocarpus.*

607 larvae representing the above 18 species metamorphosed in laboratory aquaria and were reared for varying periods. Detailed observations made on the assumption of adult characters, moulting and growth during post-larval stages are presented in this paper.

INTRODUCTION

KEMP'S (1913) excellent monograph on the Indo-Pacific stomatopods, followed by contributions by Kemp and Chopra (1931) and Chopra (1934, 1939) among others have given a comprehensive though still incomplete picture of the stomatopod fauna of Indian waters. Detailed accounts of the stomatopod larvae of the Madras plankton have already been given in a series of contributions (Alikunhi and Aiyar, 1942; Alikunhi, 1944 *a*, *b*; 1952) and the successful rearing from planktonic larvae of as many as six species which had not been recorded from the Indian coast (Alikunhi, 1952) clearly demonstrated that our knowledge of this interesting group in our waters is markedly incomplete. The positive correlation of the common stomatopod larvae in the Madras plankton with the respective adult species that has been successfully achieved in the above studies has facilitated specific identification of at least the common larval forms occurring in other areas along the Indian coast also. This has been demonstrated in a recent account (Alikunhi, 1958) of a small collection of stomatopod larvae from the Bay of Bengal, off the Mahanadi estuary.

Our knowledge of the natural history, food and feeding habits, moulting, growth and attainment of maturity in the different species of this interesting group is, at present, extremely meagre. Brief observations on the habits of *Squilla empusa* subjected to artificial lighting in the aquarium have been given by Bigelow (1941). In a recent contribution the present author (Alikunhi, 1950) has given some notes on the habits (including feeding habits, moulting, etc.) of certain larval and post-larval stomatopods of the Madras coast. Brief accounts of the post-larval growth of *Squilla holoschista* and five other species (Alikunhi and Aiyar, 1943), *Lysiosquilla tigrina* (Alikunhi, 1944) and a description of the early post-larva of the rare species, *Squilla hieroglyphica* (Alikunhi, 1944) have also been available. Serene (1952) has described the habits of *Lysiosquilla sulcirostris* under natural conditions.

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In continuation of the detailed account of the pelagic larvae of the common stomatopods of the Madras coast (Alikunhi, 1952) an exhaustive study of the early post-larval stages, the assumption of adult characters during successive stages, the frequency of moults and growth of the following 18 species of stomatopods of the Madras coast has been made:

1. *Squilla nepa* Latreille (Bigelow).
2. *Squilla holoschista* Wood-Mason.
3. *Squilla wood-masoni* Kemp.
4. *Squilla interrupta* Wood-Mason.
5. *Squilla quinquedentata* Brooks.
6. *Squilla gonypetes* Wood-Mason.
7. *Squilla boops* Kemp.
8. *Squilla hieroglyphica* Kemp.
9. *Squilla scorpio* Latreille.
10. *Squilla latreillei* (Eydoux & Souleyet).
11. *Squilla fasciata* De Haan.
12. *Squilla lata* Brooks.
13. *Harpiosquilla raphidea* (Fabricius).
14. *Lysiosquilla maculata* (Fabricius).
15. *Lysiosquilla sulcirostris* (Kemp).
16. *Acanthosquilla multifasciata* (Wood-Mason).
17. *Acanthosquilla tigrina* (Nobili).
18. *Acanthosquilla acanthocarpus* (Miers).

The experimental work connected with these studies was carried out at the Zoological Research Laboratory, Madras, during the years 1941-43. The author is deeply indebted to Prof. R. Gopala Aiyar, then Director of that laboratory, for the invaluable help he rendered and the facilities provided to carry out these studies and also for kindly going through the manuscript. Thanks are due to the Marine Biological Association of India for kindly undertaking publication of this paper.

Material and Methods

Except for *S. scorpio*, the first post-larval stage of all the other 17 species described in this paper was obtained by rearing the final pelagic larva through metamorphosis in laboratory aquaria. This metamorphosis generally took place within 24 hours after collection of the larvae from the sea; in the majority of cases the larvae undergoing metamorphosis overnight (Alikunhi, 1950). The habits and appearance of these post-larvae were observed by studying live specimens in aquaria and small cement cisterns. By daily renewal of water and regular feeding with live specimens or minced meat of *Emerita asiatica* the post-larvae were reared to the adult stage. No running water was provided in the cisterns and aquaria.

It has already been reported that under aquarium conditions the post-larvae are often cannibalistic in habit (Alikunhi, 1950). In rearing speciemns in the laboratory this particular habit of the post-larvae often led to disappointing results, as, when more specimens than one were necessarily kept in a container, out of practical considerations such as lack of adequate number of containers, the smaller specimens and those newly moulted were frequently attacked and killed by others. In certain instances specimens were observed to die, a day or two after a moult for no apparent reason. In still others some of the moults were not complete and this often resulted in death. Several died in the act of moulting also. Perhaps the rather sedentary life in the very limited space of the aquarium might well be one of the main reasons for these instances of unexpected mortality. All

these added to the difficulties of rearing specimens successfully to the adult stage. As one of the aims of the present study was to rear the specimens for the maximum number of days possible, they could not be subjected to detailed examination and study during the progress of rearing except for brief periods under a low power binocular microscope. After each moult, however, the specimens were kept in flat bottom glass dishes with just sufficient water to keep the body about three-fourth immersed, and, when they remained quiet, were quickly measured approximately, with the help of a scale placed beneath the dish. The total length from the anterior margin of the ophthalmic segment to the tip of telson was recorded. Separate records were maintained of the frequency of moults in the different species. As far as possible the moults were carefully retrieved and were extremely useful in studying the details of carination and also the dimensions of the different parts of the body. For purposes of comparison with the laboratory reared material and for observations on the size at maturity in certain species, adult specimens and other material collected from Bombay, Cochin and some other parts of the country have also been examined. The description of the first post-larval stage of *Squilla scorpio* is based on a small collection from the Barbalong Estuary, Chandipur, Orissa, made on 17th May, 1950.

As no details relating to age, growth, moults, etc., of stomatopods seem to be on record and as post-larval stages are found to differ from the adults in several important features, detailed descriptions and measurements of parts of the available stages of the different species have been included so as to facilitate comparison and relatively easy identification. The total length at different post-larval stages of specimens reared through a number of moults was generally taken on the day of moulting. When the moult took place at night the measurement was taken the following morning, between 10 and 11 A.M., and when moults took place in the morning after 8 A.M. the measurements were taken within 2–4 hours after moult.

All the figures have been made out of camera lucida sketches. Certain minor details of little taxonomic significance have been left out in most of the figures.

The following abbreviations have been used in the course of this report, particularly in tabular statements of measurements or proportions of parts:

AWC	..	Anterior width of carapace.
F	..	Female.
LE	..	Length of eye.
LR	..	Length of rostrum.
LRP	..	Length of raptorial propodus.
M	..	Male.
MLC	..	Median length of carapace.
MLT	..	Median length of telson.
MWC	..	Maximum width of carapace.
TL	..	Total length.
WE	..	Width of eye.
WR	..	Width of rostrum.
WRP	..	Width of raptorial propodus.
WT	..	Width of telson.

Descriptive Account

Squilla nepa Latreille (Bigelow) (Text-Figs. 1–22)

The larvae of *Squilla nepa* being very common in the Madras plankton, quite a number of them could be successfully metamorphosed into post-larvae and, a few, reared to the adult stage

in the laboratory. Several specimens were reared up to the 5th–6th post-larval stage by which time the majority of them succumbed to predation by other specimens in the aquarium. Only a few specimens, therefore, survived after the 5–6th moult.

Post-larval Stage I (Text-Figs. 1–8)

The remarkable changes that take place in the structure and appearance of the different organs during the final larval moult which is accomplished in a relatively short time have been described in detail (Alikunhi, 1950). In the early post-larva the eyes are conspicuous, though the corneal portion is not markedly broader than the stalk. The cornea is not set fully transverse to the stalk (Fig. 3). The corneal index varies from 2·91 to 4·10. In specimens soon after metamorphosis the eyes are relatively larger than in those a few days older (Fig. 2). The rostrum is conical in shape. The antero-lateral corners of the carapace are smoothly rounded, being devoid of spines (Fig. 1). The width of carapace immediately behind the antero-lateral corners is about $\frac{2}{3}$ its maximum (posterior) width, and a little over half its median length including rostrum. The median carina of carapace is well indicated though its anterior bifurcation is thin and almost obsolete (Fig. 1). The raptorial dactylus has six teeth including the terminal one, and has a small inconspicuous tubercle externally near the base. The carpus is weakly carinate, with a smooth prominence mid-way along its dorsal keel and is nearly straight at the carpus-propodus joint (Fig. 4).

The lateral processes of the fifth thoracic segment seen from above are bifid, the two lobes being short and almost equal in size (Fig. 5). In the sixth segment also the lateral process is bifid but the lobes are blunt and unequal, the anterior one being very much smaller than the posterior. On the seventh segment the lateral process appears as a flat lobe with just a smooth tubercle anteriorly. Carinae are present on all the abdominal segments but only the following ones terminate in spines:

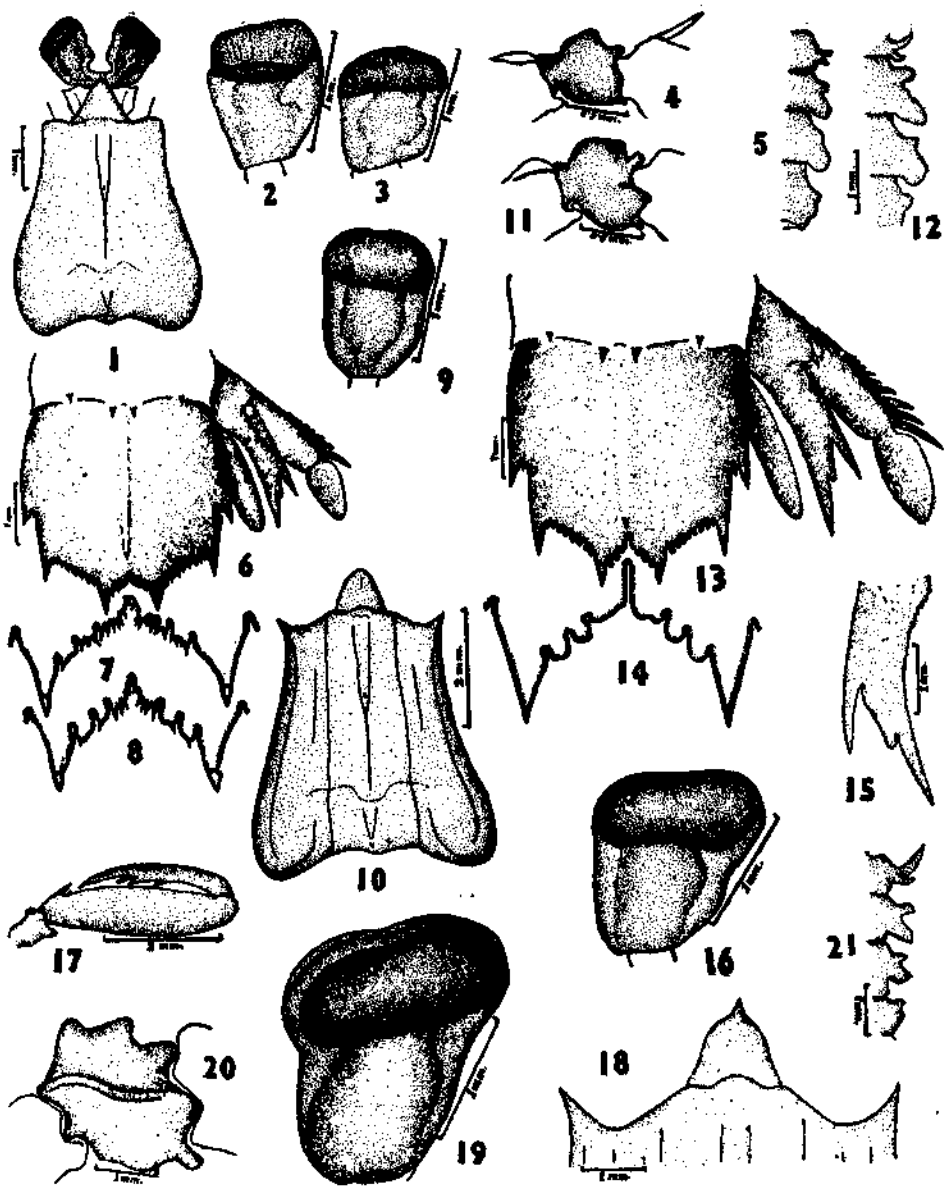
Carina ending in spines	On abdominal segments
Marginal	.. 1, 2, 3, 4, 5
Lateral	.. 2, 3, 4, 5, 6
Intermediate	.. 3, 4, 5, 6
Submedian	.. 5, 6

The marginal spines of telson are well developed, moderately long and fairly stout (Fig. 6). The submedian spines are terminally articulated. There is a stout, median dorsal carina on telson terminating in a short spine distally. The denticles number 1 lateral, 8 intermediate and 7–12 submedian on each side. All the denticles are acutely pointed. The submedian denticles show some variation in their number and arrangement (Figs. 7, 8). In the uropod the basal segment of the exopod has 9 movable spines. The outer spine of the ventral prolongation of telson is more than half the length of the inner which has a smooth tubercle proximally. The outer aspect of this tubercle is almost straight, while the inner margin of the ventral prolongation is finely serrated (Fig. 6).

Colouration.—The body has become stout and opaque, with a number of chromatophores distributed all over the dorsal aspect. There is, however, no distinct concentration of these chromatophores on any particular part of the body which has a general pale brown colour. By the third or fourth day after metamorphosis more chromatophores of a deeper brown colour appear.

Post-larval Stage II (Text-Figs. 9–15)

With the first moult after metamorphosis the specimen enters the second post-larval stage. The eyes are of almost the same shape as in the previous stage (Fig. 9). Rudimentary antero-lateral spines appear on the carapace which has the median carina also distinct and fully formed,



FIGS. 1–21. *Squilla nepa*. Figs. 1–8. First post-larval stage: Fig. 1. Carapace and rostrum, dorsal view. Fig. 2. Eye, twelve hours after metamorphosis. Fig. 3. Eye, in a specimen 14 days old. Fig. 4. Carpus of the raptorial limb. Fig. 5. Lateral processes of thoracic segments V–VIII. Fig. 6. Telson and right uropod, dorsal view. Fig. 7. Sub-median spines and denticles of telson, magnified. Fig. 8. Same, a common variation. Figs. 9–15. Second post-larval stage: Fig. 9. Eye, soon after first moult. Fig. 10. Carapace and rostrum, dorsal view. Fig. 11. Carpus of the raptorial limb. Fig. 12. Lateral processes of thoracic segments V–VIII. Fig. 13. Telson and right uropod, dorsal view. Fig. 14. Sub-median spines and denticles of telson, magnified. Fig. 15. Ventral prolongation of the uropod. Figs. 16 and 17. Fourth post-larval stage: Fig. 16. Eye, dorsal view. Fig. 17. The three terminal segments of a regenerated raptorial claw. Figs. 18 and 19. Sixth post-larval stage: Fig. 18. Anterior portion of carapace and rostrum showing median point on the latter. Fig. 19. Left eye, dorsal view. Figs. 20 and 21. Seventh post-larval stage: Fig. 20. Carpus of the raptorial limb. Fig. 21. Lateral processes of thoracic segments V–VIII.

though perhaps not yet so very conspicuous as in the adult (Fig. 10). The rostrum has become broader terminally than in the earlier stage and, in some specimens, has an obsolete median carina distally. The carpus of the raptorial limb is more strongly carinate than in the first post-larval stage and has its distal margin against the carpus-propodus joint produced into a smooth prominence (Fig. 11). The anterior lobe of the bifid lateral process of the 5th thoracic segment is very much longer than the posterior and is also anteriorly directed (Fig. 12). In the 6th segment the two lobes are still unequal and blunt. The anterior tubercle on the lateral process of the 7th segment has now become a short spine; while, in the 8th segment the lateral process is just a smooth prominence.

The submedian carinae of the fourth abdominal segment end in rudimentary spines.

The general shape of telson is different from that in the first post-larval stage, and the marginal spines have grown larger, the intermediate spines now being the largest (Fig. 13). The submedian spines, though actually pointed, are not terminally articulated. A rudimentary pre-lateral denticle is indicated in some specimens on each side of the telson. The lateral denticles are pointed but the intermediate and submedian denticles have become blunt (Figs. 13, 14). Only three pairs of submedian denticles, with large smoothly rounded tips are present in between the two submedian spines. The median pair of these denticles is often insipiently notched.

The outer aspect of the basal tubercle on the inner spine of the ventral prolongation of uroped is convex basally but becomes almost straight distally. The inner margin of the ventral process is weakly serrated (Fig. 15).

Colouration.—A transverse band of dark brown pigment has appeared on the second abdominal segment dorsally. More chromatophores have appeared on the dorsal aspect in general and consequently the specimen has a deeper brown colour than in the earlier stage.

Post-larval Stage III

The median dorsal carina of the carapace is fully formed and the antero-lateral spines are also strongly developed. The cornea of the eye is distinctly (though not very much) wider than the stalk. Spines on the carinae of the abdominal segments are better developed, as in the adult. The pigmentation has become brighter, with the pigment band on the second abdominal segment a little more conspicuous than in the earlier stage.

Juvenile Stages (Text-Figs. 16–21)

As most of the adult features have appeared by the third post-larval stage, very few structural changes, other than growth, take place during the subsequent moults. The eyes get progressively smaller with each moult till about the ninth or tenth when the width of cornea will be approximately 1/7 the median length of carapace (Figs. 16, 19). In some cases the rostrum terminates in a median sharp spine which persists even upto the sixth or seventh post-larval moult (Fig. 18). The raptorial carpus becomes strongly carinate and develops a third tubercle along its dorsal keel behind the first two (Fig. 20). The lateral processes of the last four thoracic segments are fully formed and attain adult shape and proportion by the fifth to seventh moult (Fig. 21). After the fifth-sixth moult the submedian carinae of the third abdominal segment also end in rudimentary spines which remain short and weak during the subsequent stages also. In specimens in the fourth-fifth post-larval stage another characteristic but less conspicuous pigment band appears on the fifth abdominal segment. This and the larger one on the second abdominal segment become prominent and characteristic during the subsequent stages when a general ashy tinge also develops on the body.

Frequency of Post-larval Moults

Fed regularly, the young post-larva undergoes the first moult 5–7 days after metamorphosis. Subsequent moults, usually up to the fourth, take place at regular short intervals, after which the

intervening period between successive moults lengthens. If the post-larva is not fed regularly, the moults are also considerably delayed. A specimen kept in the aquarium without regular feeding took nearly 56 days to undergo the first post-larval moult. Available data on the age at successive moults in respect of seven specimens metamorphosed and reared in the laboratory with regular feeding are given in Table I.

TABLE I

Moulting and age of Squilla nepa *after metamorphosis of pelagic larva*

Specimen No.	Age in days after metamorphosis at moult											
	1	2	3	4	5	6	7	8	9	10	11	12
1	5	10	18	..	..	..	..	..	..		..	..
2	6	12	19	26	..	..	..	..	..	..	..	..
3	7	14	22	30	38	46	..	..	..	..	..	..
4	7	14	22	31	38	46	53	..	..	..	..	..
5	6	13	20	28	35	43	61	..	..	..	..	..
6	6	11	16	26	33	44	58	81	102	129	..	..
7	6	10	15	21	26	34	44	77	114	146	176	215

It is seen from Table I that the duration of the successive post-larval stages, in this species, is as in Table II.

TABLE II

Duration of successive post-larval stages of Squilla nepa

	Post-larval stages											
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Duration in days:												
Range ..	5–7	4–7	5–8	6–10	5–8	8–11	7–18	23–33	21–37	27–32	30	39
Average ..	6·14	5·86	6·86	8·0	6·8	8·6	12·25	28·0	29·0	29·5	30	39

Thus, ordinarily within a month after metamorphosis the post-larva undergoes at least 4 moults. The duration of the later post-larval stages gradually increases to about a month or over from the 8th stage onwards. The first 5–6 moults are very regular, taking place at short intervals which ordinarily do not exceed a week. The interval between the sixth and the seventh moults is longer, averaging over 12 days; while from the eighth moult onwards the intervening period extends to 28–35 days. This continued up to the 12th moult which took place in just over seven months after the final larval moult, and might continue so for a few subsequent moults also, though no actual observations are available.

Post-larval Growth

The early post-larva measures 16·0–17·0 mm. in total length. It grows appreciably in length following each moult. The maximum growth takes place soon after moulting when the new chitinous armature is soft. The latter, however, gets hardened within a few hours after moulting and hence actual growth in length during the later part of each post-larval stage is very limited. The

specimens under observation in aquaria were measured after each moult and the data so gathered are furnished in Table III.

TABLE III

Squilla nepa: *Total length after successive post-larval moults*

No.	Length of final pelagic larva* (mm.)	Length of post-larva in mm.												
		Before moult	After moult											
			1	2	3	4	5	6	7	8	9	10	11	12
1	21·3	17·0	20·0	22·5	27·5	..	..	..	..	..	..	..	..	..
2	20·9	17·0	21·0	23·5	30·0	34·0	..	..	..	..	..	..	..	..
3	21·3	17·0	21·0	24·5	28·5	31·0	34·0	41·0	..	..	..	..	..	..
4	20·2	16·5	21·0	24·5	29·0	32·0	35·0	41·0	49·0	..	..	..	..	..
5	21·0	17·0	20·5	24·5	29·0	35·0	43·0	53·0	64·0	..	..	..	..	..
6	20·3	16·5	20·0	23·5	29·0	35·5	42·0	50·0	60·0	70·0	80·0	93·0	..	..
7	20·0	16·0	20·0	23·0	29·0	35·5	41·5	52·5	65·0	72·0	83·0	96·0	106·0	116·8

*Excluding rostrum.

Even when total length of the final pelagic larva excluding the rostrum is considered there is appreciable reduction in length, to the extent of 3·7–4·3 mm., taking place during the final larval moult. Besides individual variations, the actual growth in length during the different post-larval stages also varies as given Table in IV.

TABLE IV

Squilla nepa: *Growth in length after successive post-larval moults*

	Growth in mm. after moult											
	1	2	3	4	5	6	7	8	9	10	11	12
Growth in length: Range	.. 3·0–4·5	2·5–4·0	4·0–6·5	2·5–6·5	3·0–7·5	6·0–11·0	8·0–12·5	7·0–10·0	10·0–11·0	13·0	10·0	10·8
Average	.. 3·8	3·2	5·14	4·83	5·2	8·4·	10·37	8·5	10·5	13·0	..	..

Thus the average growth which is the minimum during the first two moults, increases to about 5 mm. during each of the next three successive moults and thereafter ranges from 8·0 to 13·0 mm. upto the 12th moult. The 16·0–17·0 mm. long post-larva attains a length of over 100·0 mm. in just under six months. In the absence of any data on the age and growth of this or of any other stomatopod in its natural habitat it is not now possible to assess what relation to the natural growth of the species is represented by the growth under laboratory conditions reported here. It is, however, probable that as ample live food was always provided in the aquarium and as the water was renewed regularly to maintain hygiene in the environment, the conditions for growth would have been favourable as demonstrated by the regular moults and growth. If this is really the case the growth under such conditions should be comparable to or perhaps even better than that in the natural habitat where hazards and competition for food would certainly be more than under laboratory conditions.

From the above data on the age, frequency of moulting and growth of post-larvae an attempt could reasonably be made to assess the age of and possibly even the number of moults undergone by specimens of different size from natural habitats. From this aspect the available data could be summarised as in Table V.

TABLE V

Squilla nepa: *Age after metamorphosis of and moults undergone by specimens of different size*

Length of specimen (mm.)	Approximate age after metamorphosis (days)	Probable number of moults undergone after metamorphosis
16·0–17·0	1– 7	Nil
20·0–21·5	5– 14	1
22·5–24·5	10– 22	2
27·5– 30·0	15– 31	3
31·0–35·5	21– 38	4
34·0–43·0	26– 46	5
41·0– 53·0	34– 61	6
49·0–65·0	44– 81	7
70·0–72·0	77–114	8
80·0–83·0	102–146	9
93·0–96·0	129–176	10
106·0	177–215	11

As already mentioned, during the first 3-4 moults the post-larva attains most of the adult features but the eyes are rather slow to reach the adult proportions. The corneal index (Kemp, 1913, p. 6) for the species during different stages of growth tabulated in Table VI demonstrates this point clearly.

TABLE VI

The corneal index for Squilla nepa *during successive post-larval stages*

Post-larval stage ..	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Corneal index ..	2·91	3·57	..	4·33	4·54	5·57	5·41	5·52	6·84	7·12	7·34
	4·10	4·23		4·45	5·26		6·33	5·82			

As specimens become sexually mature by the 10th–11th post-larval moult (*vide infra*) they should then be considered to have attained all adult characters. Corneal index 7·0 or above might therefore be taken as the adult condition. The relatively large eyes of the early post-larva become progressively smaller with successive moults. Kemp (1913) has also found the corneal index in this species ranging from 4·5 in specimens about 30·0 mm. long, to 7·0 in those 80·0–90·0 mm. long and upto 8·0 in the largest specimens. The present observations are in complete accord with the above data.

TABLE VII

Squilla nepa : *Post-larval stage, age, total length and measurements of selected parts of body**

Post larval stage	Age after metamorphosis (days)	Total length	Carapace			Rostrum		Telson		Raptorial propodus		Eye	
			Median length	Anterior width	Maximum width	Length	Width	Length	Width	Length	Width	Length	Width of cornea
I	0–7	15·4–	3·15–	1·95–	2·70–	0·53–	0·69–	2·70–	3·02–	2·72–	0·78–	1·13–	0·87–
		16·8	3·57	2·33	3·54	0·63	0·80	2·86	3·23	2·96	0·89	1·23	1·08
II	5–14	18·0–	3·51–	2·40–	3·39–	0·53–	0·75–	2·81–	3·21–	3·09–	0·89–	1·05–	0·93–
		19·5	4·02	2·57	3·65	0·56	0·86	3·00	3·68	3·38	0·99	1·28	1·05
IV	15–31	26·0–	5·43–	3·30–	4·58–	0·66–	1·02–	3·87–	4·67–	4·39–	1·25–	1·47–	1·23–
		27·3	5·55	3·48	5·28	0·74	1·13	4·32	4·80	4·68	1·32	1·56	1·28
V	21–38	36·5–	7·45–	4·68–	7·36–	0·91–	1·36–	5·64–	7·18–	6·09–	1·82	1·70–	1·45–
		38·0	7·64	4·82	7·64	0·95	1·45	5·91	7·27	6·23		1·82	1·64
VI	26–46	42·0–	8·64–	4·95–	8·18–	0·95–	1·45	6·64–	7·73–	6·82–	1·82–	2·27	1·91
		49·0	10·64	5·91	10·32	1·05		7·91	8·59	8·50	2·09		
VII	34–61	46·5–	9·36–	5·45–	8·50–	1·14–	1·64–	6·68–	7·91–	8·09–	2·09–	2·09–	1·73–
		63·0	13·55	7·82	12·86	1·72	2·18	8·36	11·23	10·77	2·86	2·50	2·14
VIII	44–81	51·0–	11·05–	6·00–	9·55–	1·23–	1·73–	6·82–	9·55–	8·50–	2·27–	2·18–	2·00–
		65·0	13·91	8·36	10·36	1·73	2·27	10·64	12·45	11·64	3·14	3·18	2·45
IX	77–114	70·0–	13·55–	7·91–	12·36–	1·43–	2·18–	9·64–	12·27–	11·45–	3·00–	3·27	2·55
		72·0	17·45	10·59	16·68	1·82	2·77	11·09	14·82	14·41	3·82		
X	102–146	80·0– 83·0	14·82– 19·27	8·82– 11·55	14·09– 18·64	1·82– 1·91	2·36– 2·95	11·36– 12·68	13·45– 15·45	12·00– 16·23	3·36– 4·18	3·73	2·68
XI	129–176	96·0	21·00	11·73	18·41	2·09	3·14	15·00	17·45	18·09	4·45	3·91	2·86

* All measurements in mm.

Other important organs of the body also show progressive growth with each moult and a study of this is helpful in determining the exact stage at which dependable adult characters and body proportions are well established [Pl. I (i).C-*f*). A series of measurements of the various parts of the body in specimens of different sizes reared in the laboratory are given in Table VII. Considerable variations in the size of the different parts in individuals of the same age and stage are evident. From these measurements the relative proportions of the various parts of the body during different stages are calculated in Table VIII.

As only specimens reared in the laboratory were studied for purposes of compiling Table VIII, the number examined is far too inadequate for drawing any inference. Nevertheless the limited data now available might indicate specific differences which could be of much help in the taxonomy of closely allied species or varieties and is discussed elsewhere.

A careful study of Table VIII shows that while the carapace, excluding rostrum, is about 1/5 the total length of the specimen, it is perhaps a little smaller in the females than in the males. The raptorial propodus is always shorter than the median length of carapace; is almost $\frac{1}{6}$ the total length of the specimen, and like the carapace, appears smaller in the females than in the males. The length-width ratio of the raptorial propodus varies only to a very limited extent during the different post-larval stages, even though in either sex, the propodus is relatively wider in the early post-larval stages than in the adult. The width of carapace between the antero-lateral corners is greater in the early post-larval stages than in the adult. Likewise, during the first two stages the rostrum is appreciably larger than in the succeeding stages. In the eye also the width of cornea is, perhaps, a little more in the males than in the females. In most other features more or less adult proportions are found in the early post-larval stages.

Sexual Maturity and Breeding

Sexes are easily distinguished, even in the first post-larval stage, by the presence (in the male) or absence (in the female) of the slender appendage at the base of the last pair of walking legs. In the fresh condition the ovaries are reddish-brown in colour and extend dorsally from the posterior region of the carapace right upto the telson. When fully developed it appears like a band, about 12 mm. in width and having segmental constrictions. A few branched chromatophores are distributed over the ripe ovary; immature ovaries appear pale, with the chromatophores more prominent than in the mature ones. Ovaries are fairly well developed in specimens 72·0 mm. long. 82·0–87·0 mm. long specimens had the ovaries almost fully developed. Under laboratory conditions the ovaries are fully developed by the 10th post-larval moult when the specimen is only 129 days old (post-larval life only) and about 93·0 mm. long. On the 156th day when a female specimen died in the aquarium it had the ovaries fully ripe and reddish in colour. It would, therefore, appear that in this species sexual maturity is attained within 5 months after the pelagic larval life.

While no direct observations or data on breeding are available a study of the occurrence of larvae in plankton hauls seems to indicate generally the breeding season of this species. Considered as a group the stomatopod larvae in the Madras plankton do not exhibit any marked seasonal abundance; the larvae of different species being available in plankton almost throughout the year (Alikunhi, 1952). However, a species-wise analysis of the collections made during the different months for a five years period (1938–42) is given in Ttable IX.

As the number of collections made during the different months varied widely and consequently the number of larvae collected, the average number of larvae per collection for each month is given in Table IX. There were no collections or were only very few collections during the months May, June and November. From the available data, also represented in Fig. 22, it is seen that the larvae are most abundant during August–September; while, during February–March also they are quite common. However, as the above information relates only to advanced pelagic larvae, mostly in the final pelagic stage and as we do not now have any definite idea as to the exact duration of their larval life in our coastal waters, it seems premature to infer anything on the probable

TABLE VIII

Squilla nepa: *Proportionate size of various parts of the body during different stages*

		Post larval stage I	II	IV	V	VI	VII	VIII	IX	X	XI
TL/MLC	M	4·97	4·80	4·97	4·90	4·60–4·86	4·62–4·96	4·61–4·67	4·12	4·30	4·57
	F	4·31–4·78	4·85–4·93	4·74–4·92	4·97	..	5·00	5·15	5·16	5·40	..
TL/MLT	M	6·22	6·40	6·92	6·17	6·19–6·32	6·34–7·73	6·11–7·48	6·49	6·54	6·40
	F	5·26–5·57	6·16–6·84	6·02–7·05	6·73	..	6·54	6·84	7·26	7·04	..
TL/LRP	M	5·67	5·62	6·13	5·85	5·76–6·15	5·74–5·85	5·58–6·00	5·00	5·11	5·33
	F	5·39–5·69	5·76–5·98	5·83	56·24	..	5·84	6·16	6·11	6·66	..
MLC/LR	M	5·36	6·70	8·00	7·84	8·22–11·20	7·87–10·04	8·04–9·00	9·58	10·08	10·04
	F	5·08–6·51	6·62–7·17	7·50–8·30	8·40	..	7·57	9·46	9·47	8·14	..
MLC/AWC	M	1·45	1·51	1·64	1·59	1·74–1·80	1·63–1·73	1·66–1·84	1·66	1·66	1·79
	F	1·50–1·63	1·45–1·62	1·58–1·59	1·58	..	1·66	1·67	1·71	1·68	..
MLC/MWC	M	0·95	1·03	1·18	1·01	1·03–1·05	1·05–1·10	1·12–1·15	1·04	1·03	1·14
	F	1·05–1·32	1·03–1·14	1·03–1·07	1·00	..	1·06	1·12	1·09	1·05	..
MWC/AWC	M	1·51	1·47	1·38	1·57	1·65–1·74	1·52–1·64	1·47–1·59	1·58	1·61	1·57
	F	1·23–1·42	1·32–1·41	1·49–1·53	1·58	..	1·56	1·49	1·56	1·59	..
WR/LR	M	1·26	1·44	1·50	1·43	1·38–1·52	1·26–1·69	1·31–1·40	1·52	1·54	1·50
	F	1·12–1·51	1·41–1·62	1·52–1·63	1·59	..	1·44	1·62	1·52	1·30	..
LE/WE	M	1·14	1·22	1·19	1·03	1·18	1·16–1·21	1·09–1·30	1·28	1·39	1·36
	F	1·14–1·22	1·13–1·32	1·21–1·23	1·25	..	..	1·34	..	..	..
WT/MLT	M	1·15	1·14	1·19	1·21	1·08–1·16	1·18–1·37	1·17–1·40	1·33	1·21	1·16
	F	1·06–1·12	1·09–1·29	1·09–1·24	1·28	..	1·25	1·26	1·27	1·18	..
LRP/WRP	M	3·32	3·22	3·49	3·42	3·74–4·06	3·76–3·87	3·70–3·74	3·77	3·88	4·06
	F	3·43–3·49	3·35–3·55	3·38–3·74	3·34	..	3·76	3·63	3·81	3·57	..
MLC/LRP	M	1·14	1·17	1·23	1·19	1·25–1·26	1·15–1·25	1·19–1·30	1·21	1·18	1·16
	F	1·13–1·31	1·13–1·20	1·18–1·22	1·25	..	1·16	1·19	1·18	1·23	..

breeding period, though it could more reasonably be stated that the species perhaps breeds throughout the year, with two peak periods, one much higher than the other. It may be mentioned in this connection that under laboratory conditions a pelagic larva which metamorphosed into the early post-larva during the last week of September became sexually ripe by the first week of February; within 129 days after the final larval moult.

TABLE IX

Squilla nepa: *Average number of larvae caught in townet hauls during different months*

Year	Average number of larvae per collection during											
	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1938	16	1	2	X	—	—	7	30	17	28	9	—
1939	5	X	18	14	—	—	31	38	9	12	—	—
1940	X	18	13	6	—	—	1	7	90	8	—	8
1941	8	22	13	10	X	15	7	82	90	9	—	1
1942	13	18	19	1	—	—	55	85	107	49	5	7

X : no larvae in the collection; — : no collection during the month.

Remarks

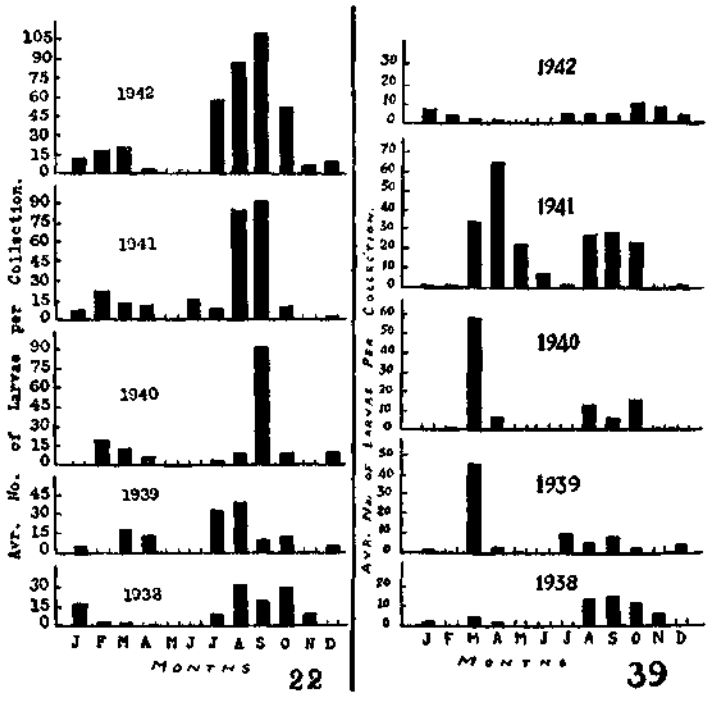
This widely distributed, Indo-Pacific species, is perhaps the commonest stomatopod in Indian waters. The pelagic larvae of this species constitute more than half the total catch of stomatopod larvae from the Madras coast (Alikunhi, 1952). During the final larval moult there is appreciable shrinking of the telescoped antenna—labral region of the larva with the result that the young post-larva is definitely smaller than the final pelagic larva. Two important features of the early post-larvae are the absence of antero-lateral spines on the carapace and the possession of a terminal movable piece on the submedian spines of telson. Both these features disappear with the first post-larval moult, specimens in the second post-larval stage showing hardly any indication of these features. The raptorial dactylus is provided with the full complement of teeth even in the first post-larval stage. Most other adult features are formed by about the third or fourth post-larval stage.

Fed regularly, growth is also regular with successive moults. Lack of food results in poor growth and irregular moults. Occasionally during moults one or other of the appendages are dropped off, but new ones are soon regenerated in place. In a particular instance, one of the raptorial limbs dropped off during the second post-larval moult and a miniature one was regenerated after the third moult, seven days after (Fig. 17). In the regenerated limb the propodus was 3·36 mm. long as compared to the normal length of 4·45 mm. and had only 4 rudimentary teeth on the dactylus.

Kemp (1913, p. 63) has referred to *S. nepa* a number of young individuals, 20–30 mm. long, and in which the antero-lateral spines have not developed on the carapace. According to the present observations the early post-larvae of *S. nepa* do not ordinarily exceed 17·0 mm. in length and specimens 20·0–30·0 mm. long should be in the second to the fourth post-larval stage. It has also been shown that the antero-lateral spines on the carapace are developed almost invariably with the first post-larval moult, when the specimen attains a length of 18·0–21·0 mm. In view of these it is quite possible that the young specimens mentioned by Kemp do not really belong to *S. nepa* but to some closely allied species like *S. holoschista* in which the early post-larva has been found to be appreciably longer than in *S. nepa*.

Squilla holoschista Wood-Mason (Text-Figs. 23–39)

Several larvae of this common species metamorphosed in the laboratory and a few were reared to the adult stage.



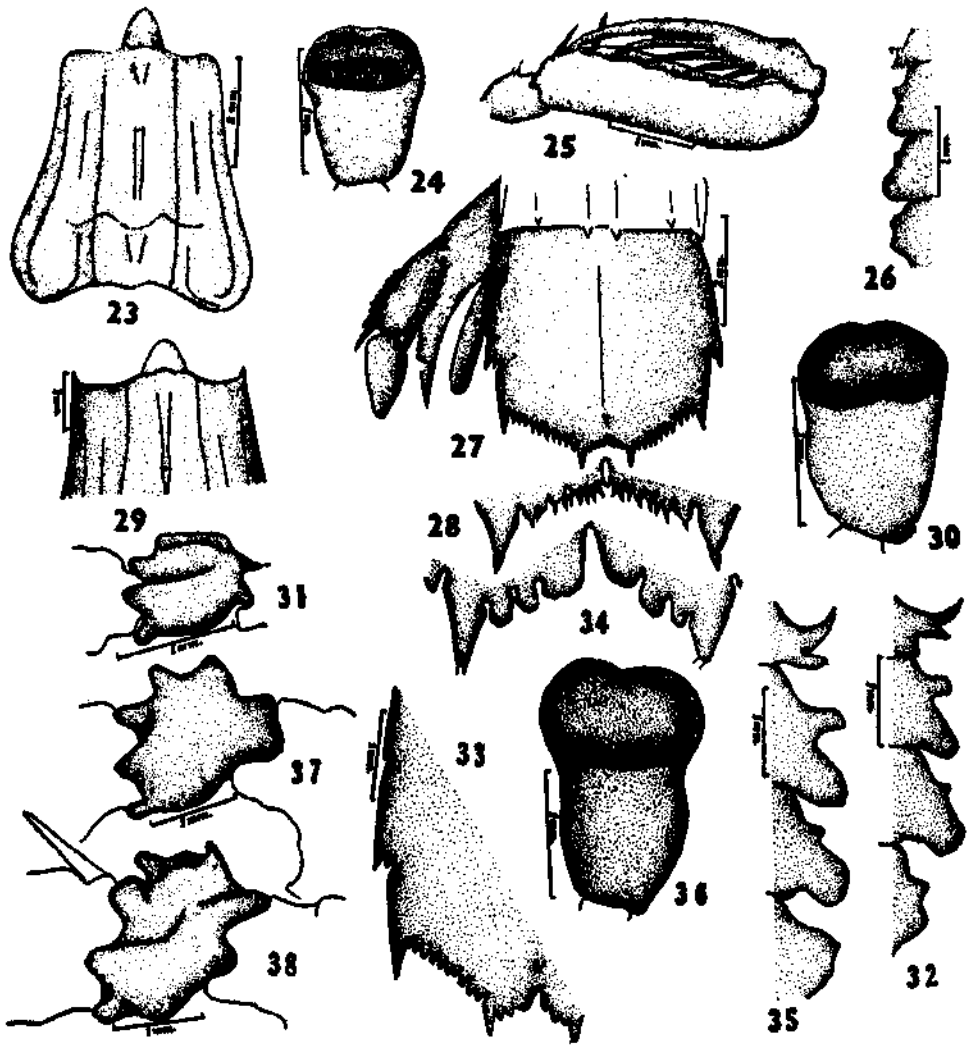
FIGS. 22 and 39. Histograms showing the average number of larvae per collection (of plankton from the Madras coast) during different months in a period of five years from 1938–1942.
Fig. 22. *Squilla nepa.* Fig. 39. *Squilla holoschista.*

Post-larval Stage 1

The early post-larva is 18·00–20·00 mm. long. It is pale or light opaque brown in colour, due to scarcity of pigment, particularly during the first day after metamorphosis; but gradually becomes more brownish owing to the appearance of chromatophores, which, however, are not grouped into any characteristic pattern. The antero-lateral spines are wanting on the carapace which has the anterior bifurcation of the median carina also obsolete in front of the median dorsal pit (Fig. 23). In some specimens the terminal portion of the anterior bifurcation is weakly indicated but the portion between this bifurcation and the dorsal pit is entirely wanting in all specimens. The bicarinate portion behind the dorsal pit is clearly indicated as also the portion behind the cervical groove. All other carinae of the carapace are clearly indicated. The rostrum is conical in shape which is very much different from the condition in the adult. The eyes, directed forwards, reach the tip of the basal segment of the antennular peduncle. The corneal portion of the eye is not very much broader than the stalk (Fig. 24).

In the raptorial claw the carpus has its dorsal keel entire without any distinct tubercle or spine (Fig. 25). The dactylus has six teeth and has the outer margin sinuous, with a fairly distinct basal lobe. The lateral process of the fifth thoracic segment seen from above is bifid, with the two spinous processes almost equal, though the anterior one is a trifle more slender than the other (Fig. 26). The lateral processes of the sixth and seventh segments are insipiently bifid, with the

anterior process very short and small, and the posterior one comparatively very large and foliaceous.



FIGS. 23–38. *Squilla holoschista*. Figs. 23–28. First post-larval stage: Fig. 23. Carapace and rostrum, dorsal view. Fig. 24. Eye, second day after metamorphosis. Fig. 25. The three terminal segments of the raptorial claw. Fig. 26. Lateral processes of thoracic segments V–VIII. Fig. 27. Telson and left uropod, dorsal view. Fig. 28. Sub-median spines and denticles of telson, magnified. Figs. 29–34. Second post-larval stage: Fig. 29. Anterior half of carapace, with rostrum, dorsal view. Fig. 30. Eye, soon after first moult. Fig. 31. Carpus of the raptorial limb. Fig. 32. Lateral processes of thoracic segments V–VIII. Fig. 33. Marginal spines and denticles of telson. Fig. 34. Sub-median spines and denticles of telson, magnified. Figs. 35. Third post-larval stage: Lateral processes of thoracic segments V–VIII. Fig. 36. Fourth post-larval stage: Eye, dorsal view. Fig. 37. Sixth post-larval stage: Carpus of the raptorial limb of a female specimen. Fig. 38. Seventh post-larval stage: Carpus of the raptorial limb of a male specimen.

The abdominal segments are very much broader than in the final pelagic larva and have four pairs of carinae on each of the first five and three pairs on the sixth. The following carinae terminate in spines:

Carina ending in spines	On abdominal segments
Submedian	5, 6 (Rudimentary on 5th)
Intermediate	4, 5, 6
Lateral	3,4, 5, 6
Marginal	1, 2, 3, 4, 5

The telson is almost as long as broad and has the marginal spines, particularly the lateral and intermediate, fairly well developed. The submedian spines are terminally articulated (Fig. 27). The dorsal carina of telson terminates distally in a small spine which does not reach the distal margin of telson. The denticles are all finely pointed. There are 1 lateral and 9–10 intermediate denticles on each side (Fig. 27). The submedian area between the two spines is notched medially and has three main denticles on either side. These denticles are provided with upto 20 fine, pointed processes or denticles (Fig. 28). Often a pre-lateral denticle is indicated on the margin above the lateral spines.

The ventral process from the base of the uropod is bifid and the outer spine is almost half the length of the inner, the external margin of which, above the small lobe, being almost straight or somewhat concave, but never convex. The exopod is provided with nine movable spines.

Post-larval Stage II

With the first post-larval moult several of the adult characters appear. Antero-lateral spines are formed on the carapace. The median carina of carapace is also fully formed, including the anterior bifurcation (Fig. 29). The rostrum has become much shorter. The shape of the eye is unchanged, with the cornea relatively small and not much wider than the stalk (Fig. 30).

The dorsal keel of the carpus of the raptorial claw stops abruptly before reaching the carpus-propodus joint, terminating in a sub-acute process (Fig. 31). The outer margin of the dactylus is sinuous, with a basal lobe also, as in the earlier stage.

The anterior spine of the lateral process of the fifth thoracic segment is very much longer than the posterior one; is acutely pointed, slender and curved forwards. The posterior one is short and directed straight laterally (Fig. 32). The lateral process of the sixth segment is distinctly bilobed, with the anterior process short, truncate and not pointed, while the posterior one is large and foliaceous. Both these processes are much more conspicuous than in the first post-larval stage. The corresponding process of the seventh segment is only insipiently bilobed, though the anterior projection is a trifle more conspicuous than in the preceding stage.

The carinae on the abdominal segments are quite distinct, the following ones terminating in spines:

Carina ending in spines	On abdominal segments
Submedian	5, 6
Intermediate	(3), 4, 5, 6
Lateral	2, 3, 4, 5, 6
Marginal	1, 2, 3, 4, 5

In the telson the pre-lateral denticles are distinct; the intermediate spines have grown larger; the submedian spines have lost their terminal articulations; and all the denticles have lost their terminal points, having consequently become smooth and rounded at the tip (Figs. 33, 34). In the basal prolongation of the uropod the outer margin of the inner spine, above the tubercle is distinctly concave.

No characteristic pigmentation has developed on the body though chromatophores are numerous and scattered over the carapace and the abdominal segments.

Post-larval stage III

Except for growth in size, very little of structural changes take place during the third post-larval stage when the specimen is fairly easily identifiable.

The spine on the dorsal keel of the raptorial carpus has become prominent. The anterior spine of the lateral process of the fifth thoracic segment is stout, acutely pointed, curved anteriorly and very much larger than the posterior spine which is almost straight and sub-acutely pointed (Fig. 35).

No characteristic pigmentation has developed on the body.

Juvenile stages

Though easily identifiable as *S. holoschista* even at the third post-larval stage, the adult body proportions are only gradually attained (*cf.* Post-larval growth). As shown in *S. nepa*, in this species also, in certain specimens the rostrum is provided with a terminal, median, sharp, pointed spine which has been observed even in the V–VI post-larval stage. Even during the fourth stage the eyes have assumed the characteristic adult appearance (Fig. 36). The outer margin of the raptorial dactylus becomes less sinuous than in the earlier stages. Two prominent spinous processes are formed on the dorsal keel of the raptorial carpus by the VI–VII stage (Figs. 37, 38), when it resembles the adult condition.

Post-larval moults

When regularly fed the early post-larva undergoes the first moult six to seven days after metamorphosis. The interval between successive moults gradually lengthens thereafter till about the eighth, after which the moults are, probably at much longer intervals. Details about post-larval age and moults of seven specimens reared in the laboratory for one to four months are furnished in Table X.

TABLE X

Age and moults of Squilla holoschista *after metamorphosis of pelagic larva into post-larva*

No.	Age in days after metamorphosis at moult								
	1	2	3	4	5	6	7	8	9
1	6·5	12·5	20·5	28·5	..	..	..	..	..
2	6·0	14·0	26·0	35·0	44·0	..	..	..	..
3	7·0	13·0	21·0	31·0	43·0	54·0	..	..	..
4	6·5	11·5	19·0	25·0	35·0	48·0	65·0	..	..
5	6·0	14·0	24·0	35·0	45·0	56·0	68·0	82·0	120·0
6	8·0	18·0	26·0	35·0	43·0	51·0	..	..	..
7	7·0	15·0	23·0	32·0	41·0	52·0	..	..	..

From the above data as also from observations on the early moults of several other specimens which died in the laboratory, the duration of the successive post-larval stages in *S. holoschista* would appear to be as in Table XI.

TABLE XI

Duration, in days, of successive post-larval stages in Squilla holoschista *under laboratory conditions*

	Post-larval stages								
	I	II	III	IV	V	VI	VII	VIII	IX
Duration in days:									
Range	.. 5·5–	5·0–	7·5–	6·0–	8·0–	8·0–	12·0–	..	..
	8·0	10·0	12·0	11·0	12·0	13·0	17·0		
Average	.. 6·5	6·5	8·6	8·8	9·8	10·8	14·5	14·0	38

Ordinarily, within 4–5 weeks after metamorphosis the specimen undergoes at least four moults and assumes most of the adult features. The average duration of the first post-larval stage is six and a half days, though some specimens moult on completion of five days after metamorphosis. The duration of the successive post-larval stages gradually increases reaching about two weeks during the seventh and the eighth stages. The duration of the ninth post-larval stage was much longer (38 days). Though only one specimen could be reared up to this stage and hence the duration of this particular stage could not be verified, the relatively longer intervals between successive later moults could well be the normal feature in this species also, if the observations on *S. nepa* could be any indication.

It has already been stated that when the pelagic larvae are blinded they metamorphose into almost albino specimens of post-larvae, which moult and thrive like normal specimens (Alikunhi, 1950). Two such specimens which were reared upto the third moult had the post-larval stages as follows:

No.	Duration in days		
	1st stage	2nd stage	3rd stage
1	5·5	6·0	6·0
2	5·5	6·0	7·0

Post-larval growth

As in the case of *S. nepa*, post-larval growth commences with a marked decrease in length as compared to the final pelagic larva which measures 34·5 mm. with the rostrum and just over 30·0 mm. excluding it (Alikunhi, 1952). The early post-larva, immediately after the final larval moult measures 21·0–23·0 mm. in length, thereby showing a shrinkage in length to the extent of 7·0–9·0 mm. in the course of six to eight hours. During the first two days after metamorphosis also this shrinking phase continues, but to a much less extent, the post-larva at the end of the phase measuring only 18·5–20·0 mm. in total length. The total decrease in length following the final larval moult is thus 10·0–11·5 mm.

Fed regularly, the young post-larva grows rapidly, the maximum growth, as in the other species, taking place soon after moulting when the new shell is soft. Growth records of six specimens reared in the laboratory are furnished in Table XII.

TABLE XII

Squilla holoschista: *Total length attained after successive post-larval moults*

Specimen No.	Length of final pelagic larva* (mm.)	Length of post-larva in mm.									
		Before moult	After moult								
			1	2	3	4	5	6	7	8	9
1	30·2	19·5	23·5	28·0	32·0	41·0	..	..	..	..	..
2	30·2	19·5	24·5	29·0	35·5	42·5	49·5	..	..	..	..
3	30·3	18·5	23·0	27·0	33·0	39·0	46·0	55·0	..	..	..
4	30·2	19·0	24·0	29·0	35·0	42·0	49·0	58·0	68·0	..	..
5	30·1	19·0	24·0	28·0	35·0	43·0	49·0	59·0	67·0	76·0	87·0
6	30·4	19·5	24·0	28·5	35·5	42·5	49·0	56·0	..	..	..

* excluding rostrum.

Some individual variations in size must necessarily be expected and excepting this the length of post-larva at different stages appears to be quite characteristically constant, showing a very low range. Though kept in the laboratory aquaria, the almost uniform environmental conditions such as availability of food, under which they were reared should, to some extent at least, account for this uniformity of size at the different stages. The actual growth in length following successive moults as gleaned from Table XII is furnished in Table XIII.

TABLE XIII

Squilla holoschista: *Growth in length (mm.) after successive post-larval moults*

	After moult								
	1	2	3	4	5	6	7	8	9
Growth in length (mm.):									
Range	.. 4·0–5·0	4·0–5·0	4·0–7·0	7·0–9·0	6·0–7·0	7·0–10·0	8·0–10·0	9·0	11·0
Average	.. 4·7	4·4	6·1	7·3	6·7	8·75	9·0	..	..

As in *S. nepa* growth is the minimum after the first moult, but steadily increases with the subsequent moults, being about 9·0 mm. or over from the sixth moult onwards.

From the data now available on the age, frequency of moulting and growth of post-larva it should be possible to assess the age of and possibly even the number of moults undergone by any given medium size specimen of this species, provided we consider the growth under laboratory conditions normal. The data considered as a whole may be tabulated as in Table XIV.

The size of the pelagic larva and the young post-larva, as also the rate of growth of the latter seem to indicate that *S. holoschista* is probably a larger species than *S. nepa*. However, the largest specimen of *S. holoschista* recorded by Kemp (1913) is only 95·0 mm. long. The 87·0 mm. long specimen reared in the laboratory is only just four months old after metamorphosis and has attained all the adult characters of the species. On the basis of the rate of growth of this specimen, the 95·0 mm. long specimen recorded by Kemp would probably be only about five to six months old after the final larval moult and would have, in the meantime, undergone at least 10 moults. The

TABLE XIV

Squilla holoschista: *Age after metamorphosis of and number of moults undergone by specimens of given size*

Length of specimen (mm.)	Approximate age after metamorphosis (days)	Probable number of moults after metamorphosis
18·0–20·0	1– 8	Nil
23·0–25·0	6– 18	1
27·0–29·5	12– 26	2
32·0–35·5	20– 35	3
39·0–43·0	29– 45	4
46·0–49·5	35– 56	5
55·0–59·0	48– 68	6
67·0–68·0	65– 82	7
76·0	82–120	8
87·0	120–150	9

maximum size the species can attain therefore appears to be appreciably more than the maximum size so far recorded.

Though from general features the post-larva could be correctly identified to the species even during the second or the third stage, the different parts of the body assume adult proportions only gradually. The eyes are relatively large in the young post-larva but with each moult get gradually smaller. The proportionate size of the eye in terms of the corneal index and the length-width ratio during the different post-larval stages are given in Table XV.

TABLE XV

Squilla holoschista: *Corneal index and length-width ratio of eyes during successive post-larval stages*

Post-larval stage	I	II	III	IV	V	VI	VII	VIII	IX
Cornal index*	3·4–3·6	4·53–5·12	5·99–	6·00–6·10	5·82–6·48	6·17–·6·63	7·15	..	7·07
Length of eye / Width of cornea	1·25–1·42	1·25–1·48	1·58	1·43–1·52	1·40–1·49	1·30–1·35	1·35		1·37

* Median length of carapace excluding rostrum divided by the maximum width of cornea of eye (*vide* Kemp, 1913, p. 9).

It is evident from the above that the relative width of cornea of the eye in the early post-larva is exactly double that of a specimen after the sixth moult (seventh post-larval stage). Compared to *S. nepa* the corneal index in *S. holoschista* is invariably higher at all stages, showing that the eyes in the latter are relatively smaller than those of *S. nepa*. According to Kemp (1913) specimens of *S. holoschista*, 80·0–90·0 mm. in length have the corneal index at about 9·0; whereas it is about

TABLE XVI

Squilla holoschista: *Measurements of selected parts of body of specimens reared in the laboratory*

Post-larval stage	Age after metamorphosis (days)	Total length	Carapace			Rostrum		Telson		Raptorial propodus		Eye	
			Median length	Anterior width	Maximum width	Length	Width	Length	Width	Length	Width	Length	Width of cornea
I	2– 8	18·5–19·8	3·66–4·67	2·65–2·97	4·49–4·76	0·62–0·73	0·87–1·00	3·66–3·85	3·74–4·12	3·20–3·66	0·91–1·09	1·28–1·83	1·00–1·32
II	6– 18	24·0–25·5	4·12–5·12	2·93–3·30	4·49–4·76	0·64–0·73	0·83–1·01	3·75–3·94	4·21–4·49	4·03–4·30	1·01–1·09	1·28–1·46	0·92–1·09
III	12– 26	28·0–29·4	5·86–6·78	3·66–4·03	5·77–6·32	0·74–0·82	0·95–1·28	4·58–5·31	5·04–6·41	4·76–5·77	1·19–1·47	1·60	1·01
IV	20– 35	37·0–37·5	6·96–8·24	4·12–4·85	6·05–7·88	0·83–0·92	1·19–1·47	5·31–6·32	6·32–7·24	5·95–6·94	1·19–1·83	1·74–1·92	1·14–1·28
V	29– 45	42·4–48·3	8·25–9·53	4·67–5·31	7·79–8·89	1·01–1·10	1·37–1·56	6·41–7·51	7·33–8·61	6·96–8·43	1·65–2·11	1·92–2·20	1·37–1·51
VI	35– 56	42·0–51·0	9·07–10·35	4·67–6·14	7·24–10·26	1·01–1·28	1·47–1·65	7·05–7·79	8·06–9·43	7·51–9·43	1·83–2·29	1·92–2·11	1·47–1·56
VII	48– 68	55·0–60·0	11·45–13·10	6·41–7·33	10·44–12·10	1·28–1·37	1·83–1·97	8·24–9·62	9·71–10·81	10·08–11·54	2·38–2·84	2·47	1·83
VIII	65– 82	67·0–68·0	13·46	7·24	12·73	1·74	2·14	9·89	10·99	12·18	2·84	..	..
IX	82–120	76·0	15·57	8·34	13·46	1·92	2·29	10·99	12·64	..	..	3·02	2·20

7·0 in examples of *S. nepa* of similar size. The length-width ratio of the eye remains fairly constant from the sixth post-larval stage.

Other important organs like the carapace, raptorial claw, telson, etc., also undergo remarkable changes during metamorphosis and growth [Pl. I (2)] and some idea of the size and growth of these during the different stages would be of help not only in taxonomic considerations but also in elucidating the stage at which adult proportions are attained. A series of measurements of important parts of the body of specimens reared in the laboratory are given in Table XVI together with the post-larval stage and approximate age of each.

As specimens reared in the laboratory only were taken for this study adequate number representing each stage could not be examined to arrive at conclusions. A casual glance at the table shows that in the second post-larval stage the carapace has the same maximum width posteriorly as in the first, even though the latter is smaller in total length and has a smaller carapace than the former. The carapace, thus, continues to shrink up to the second post-larval stage. In the eye also the width of cornea shows progressive shrinkage upto the third post-larval stage, though the specimen itself is steadily increasing in length at every moult. Growth proper, of the eye, thus starts from the fourth stage only. The exact nature of these changes would be celarly seen from the relative size of the various parts given in Table XVII.

TABLE XVII

Squilla holoschista: *Proportionate size of selected parts of the body during successive post-larval stages*

Post-larval stage ..	I	II	III	IV	V	VI	VII	VIII	IX
TL/MLC	4·28– 5·24	4·89– 5·82	4·27– 4·63	4·43– 5·38	4·84– 5·22	4·63– 4·92	4·58– 4·60	4·97	4·88
TL/MLT ..	5·14– 5·24	6·23– 6·66	5·55– 6·41	5·77– 6·81	6·20– 6·82	5·95– 6·54	6·23– 6·55	6·77	6·91
TL/LRP ..	5·46– 6·00	5·93– 6·20	5·02– 6·17	5·24– 5·96	5·60– 6·09	5·19– 5·59	5·20– 5·21	5·50	..
MLC/LR ..	5·72– 7·24	6·40– 7·53	7·61– 8·69	8·32– 9·26	7·50– 8·66	8·08– 9·52	8·88– 9·56	7·73	8·10
MLC/AWC ..	1·38– 1·64	1·54– 1·69	1·56– 1·73	1·63– 1·82	1·65– 1·87	1·68– 1·94	1·71– 1·82	1·85	1·86
MLC/MWC ..	0·94– 1·00	0·98– 1·13	0·98– 1·10	0·95– 1·14	1·00– 1·13	1·01– 1·25	0·98– 1·12	1·05	.
MLC/LRP ..	1·11– 1·29	1·13– 1·30	1·11– 1·33	1·16– 1·21	1·13– 1·18	1·08– 1·20	1·13	1·10	..
WR/LR ..	1·21– 1·56	1·13– 1·57	1·15– 1·64	1·43– 1·60	1·24– 1·45	1·29– 1·63	1·38– 1·43	1·23	1·19
WT/MLT ..	1·04– 1·07	1·09– 1·19	1·10– 1·27	1·14– 1·21	1·14– 1·20	1·13– 1·21	1·12– 1·23	1·11	1·15
LRP/WRP ..	3·27– 3·62	3·61– 4·07	3·55– 4·00	3·60– 4·10	3·60– 4·31	3·88– 4·11	4·04– 4·23	4·28	..

As sufficient number of male and female specimens in the different stages were not available it is not known whether there are differences in the size of any of the body structures in the two sexes. The carapace and telson in the young post-larva are appreciably bigger proportionately and get gradually reduced with growth. Approximately 1/5 the total length of the early post-larva, the telson after the seventh moult measures only about 1/7 the total length. The early post-larva would also appear to have a stouter raptorial propodus, almost quadrate telson, the maximum width of carapace not exceeding or slightly less than its median length (excluding rostrum) and the anterior width of carapace greater than in the later stages.

Breeding season

Though no direct observations on breeding are available the occurrence of planktonic larvae as in the case of *S. nepa*, seems to indicate that during certain months breeding activity is perhaps much more than during the other months. In tow-net hauls the larvae are less common than those of *S. nepa* and the maximum number (average) encountered in a collection is only 65 as compared to 119 in *S. nepa*. The average number of larvae per collection during the different months of the years 1938–42 are given in Table XVIII and are represented in Fig. 39.

TABLE XVIII

Squilla holoschista: *Average number of pelagic larvae per collection during different months for the years*, 1938–42

Year	Average number of larvae per collection											
	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1938	2	X	4	1	..	..	..	13	14	11	5	..
1939	1	X	45	2	..	..	9	4	7	1	..	..
1940	X	1	50	6	...	..	X	12	5	15	..	X
1941	1	1	34	65	22	8	1	27	28	23	..	1
1942	7	4	2	1	..	..	4	4	4	10	8	4

X—No larva in the collection.

——No collection during the month.

From the available data it would appear that the larvae are more abundant during March–April and August–September than during other months of the year. March–April collections are richer than those of August–September. These observations relate only to larvae in the final pelagic stage. In the absence of any information regarding the duration of pelagic larval life the present data only lead to the inference that the species, though perhaps a perennial spawner, has probably two peak periods of spawning in a year. These peak periods of occurrence of advanced larvae happen to follow the north-east and the south-west monsoons. It is tempting to suggest, though entirely presumptuous, that breeding probably takes place immediately preceding commencement of monsoons, but this in its turn, presupposes that the duration of pelagic larval life does not exceed about three months.

Remarks

S. holoschista has a restricted distribution and except for a specimen recorded by Sunier (1918) from the Sunda Straits, it is so far known only from the east coast of India. It is common along the Madras coast and, as already mentioned, in the abundance of pelagic larvae also it comes next to *S. nepa* in the Madras waters.

The larva, one of the largest in the Madras plankton, is of the typical *Alima* type. The antenna-labral region is extremely telescoped and the total reduction in length during final larval moult is about 10·0–11·5 mm., even when the length of larva excluding its rostrum is taken into consideration.

Absence of antero-lateral spines on carapace and the presence of a small terminal articulated piece on the submedian spines of telson are characteristic of the first post-larval stage which has the bicarinate median carina of carapace also indicated. As in *S. nepa* both the above features disappear with the first post-larval moult. The raptorial dactylus has the full complement of teeth at the beginning of post-larval life itself.

Growth is regular, and at least during the early stages quicker, than in *S. nepa*. The first post-larval stage itself is almost as big as the second post-larval stage of *S. nepa* and this initial difference appears to be maintained during the subsequent stages also. Frequency of moulting is very similar to that in *S. nepa* but the average duration of each stage up to the seventh is a little higher than that in the latter. Thus, while the seventh moult in *S. nepa* takes place on the 44th to 61st day after metamorphosis, in *S. holoschista* the seventh moult takes place on the 65th to 68th day. The interval between the seventh and eighth moults in *S. nepa* is longer than that in *S. holoschista* with the result that at the eighth moult the age of post-larva is almost the same in both the species.

Excepting body proportions, most of the adult features are indicated even during the second post-larval stage. The lateral processes of the fifth thoracic segment show progressive development during the early stages and the anterior spine becomes stout, acutely pointed, curved anteriorly and much longer than that shown in one of the type specimens (Kemp, 1913, Fig. 50). The raptorial carpus in a female specimen in the sixth post-larval stage shows a second tubercle along the dorsal keel, though only one such tubercle is shown in Kemp's Fig. 53. In the case of the male, even in the seventh stage the spinous tubercles on the carpus are not as prominent as shown in the adult specimens.

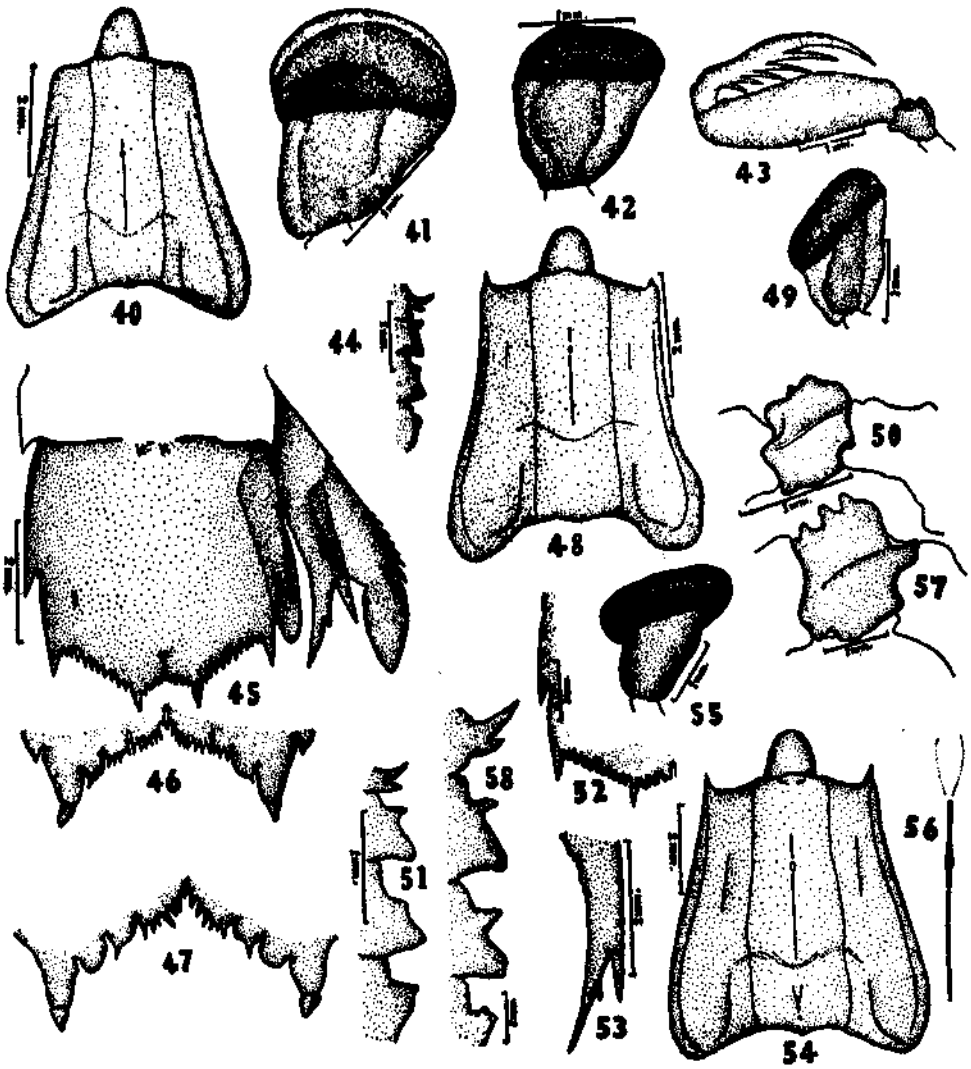
The remarkable similarity between *S. nepa* and *S. holoschista* is clearly brought out by a comparison of Tables VIII and XVII. A close scrutiny of these tables, however, reveals that *S. holoschista* has (*a*) a smaller carapace (at least in some specimens) in the early stages and a somewhat larger one in the later stages; (*b*) a larger telson; (*c*) somewhat smaller and narrower raptorial propodus, and (*d*) the maximum width of carapace quite often less than its median length, as compared to *S. nepa*. The raptorial propodus in both the species is shorter than the median length of carapace. In both again, the anterior width of carapace is a little greater than half its median length including the rostrum, though in *S. holoschista*, in the later stages the anterior width tends to equal or become even a little less than the median length.

It is interesting that blind specimens of post-larvae also moult and grow very much like the normal specimens. The two specimens which survived upto the third moult, however, attained an appreciably larger size than the normal specimens and the frequency of moults was also perhaps a little greater than in the latter. Unless more specimens are reared these indications cannot be confirmed.

The two peak periods in the occurrence of larvae differ in their height but unlike *S. nepa* the higher peak occurs in March–April in *S. holoschista*.

Squilla wood-masoni Kemp (Text-Figs. 40–58)

Next in abundance to *S. nepa* and *S. holoschista*, is *S. wood-masoni* which is fairly common along the Madras coast. Several larvae of this species metamorphosed and were reared in the laboratory during the present study.



FIGS. 40–58. *Squilla wood-masoni*. Figs. 40–47. First post-larval stage: Fig. 40. Carapace and rostrum, dorsal view. Fig. 41. Eye, soon after metamorphosis. Fig. 42. Eye, three days after metamorphosis. Fig. 43. The last three segments of the raptorial limb. Fig. 44. Lateral processes of thoracic segments V–VIII. Fig. 45. Telson and right uropod, dorsal view. Fig. 46. Sub-median spines and denticles of telson, magnified. Fig. 47. Magnified view of the sub-median spines and denticles showing a common variation in the number and arrangement of denticles. Figs. 48–53. Second post-larval stage: Fig. 48. Carapace and rostrum, dorsal view. Fig. 49. Left eye, dorsal view. Fig. 50. Carpus of the raptorial limb. Fig. 51. Lateral processes of thoracic segments V–VIII. Fig. 52. Left half of telson showing the marginal spines and denticles. Fig. 53. Ventral process of the uropod. Fig. 54. Third post-larval stage. Carapace and rostrum, dorsal view. Fig. 55. Fourth post-larval stage: Left eye, dorsal view. Fig. 56. Fifth post-larval stage: The median carina of carapce, magnified. Fig. 57. Carpus of the raptorial limb. Fig. 58. Sixth post-larval stage. Lateral processes of thoracic segments V–VIII.

Post-larval stage I

The young post-larva is 20·0–22·0 mm. long, opaque-white in colour and has conspicuous eyes which though quite different in appearance from the adult eye, have the corneal portion distinctly wider than the stalk and reach beyond the tip of the basal segment of the antennular peduncle, (Figs. 41–42). The cornea is almost transversely placed on the stalk. The carapace is devoid of anterolateral spines and has the median carina anterior to the dorsal pit entirely absent and the portion behind the pit up to the cervical groove, very slender. There is no trace of the median carina behind the cervical groove (Fig. 40). The rostrum is fairly large and broad terminally. In the raptorial limb the dorsal keel of the carpus terminates in a smooth prominence before reaching the distal margin (Fig. 43). The propodus is rather conspicuously broad, its maximum width being almost $\frac{1}{3}$ the length. The dactylus has six teeth including the terminal one and has its outer margin smoothly sinuous with a faint indication of a basal lobe.

The lateral process of the fifth thoracic segment seen from above is bifid, with an anterior larger, slightly anteriorly curved acute spine and a posterior, smaller, postero-laterally directed straight sub-acute spine (Fig. 44). The corresponding process of the sixth segment is insipiently bifid with a short, sub-acute anterior lobe and a broader posterior lobe. In the seventh segment the lateral process is almost entire though anteriorly it is raised into a small prominence.

Carinae are present on all the abdominal and the exposed thoracic segments and the following ones terminate in spines:

Carina ending in spines		On abdominal segments
Submedian	..	6
Intermediate	..	4, 5, 6
Lateral	..	(3), 4, 5, 6
Marginal	..	1, 2, 3, 4, 5

The telson is quite conspicuous, its width only very slightly exceeding the length and has the marginal spines long and acutely pointed (Fig. 45). The submedian spines have each a small, terminal articulated piece. The prelateral denticles are indicated. All the marginal denticles are acutely pointed. There are one lateral and 9–11 intermediate denticles on each side. Between the submedian spines there are altogether 23–25 denticles which are generally arranged in three groups on either side of the median line as shown in Fig. 46. Slight variations from this pattern are occasionally seen and in certain specimens the denticle nearest the submedian spine may be smoothly rounded (Fig. 47). The median dorsal carina of telson terminates in a spine distally. The outer spine of the ventral prolongation from the base of the uropod is about half the length of the inner one which has a small lobe on its outer aspect almost halfway. Above this lobe the outer margin of the spine is distinctly concave, while its inner margin is weakly serrated proximally (Fig. 45). The exopod of the uropod has nine movable spines.

Pigmentation of the post-larva is characteristic. In the very early post-larva, just about 10–12 hours after metamorphosis, quite a number of reddish-brown chromatophores are found all over the body. On either side the rostrum is coloured reddish-brown and on the carapace there are two longitudinal bands of similar though slightly deeper colour, on either side of the median line. The posterior half of the lateral margin of carapace is also similarly pigmented and between this lateral and the median bands there is a smaller, intermediate band on either side. On each of the exposed thoracic and abdominal segments there is a single band of reddish-brown chromatophores,

conspicuous at the hind border, particularly on the lateral third on either side. In the middle third also the chromatophores are grouped together into a distinct though lighter coloured area. The dorsal carina of telson is pigmented brown, particularly at its base and the distal end. Parallel, obliquely curved rows of chromatophores are present all over the telson. The tip of the uropod is reddish-brown.

On the second day after metamorphosis pigmentation is more pronounced and deeper brown. A number of light yellow chromatophores have appeared, mostly on the abdominal segments, medially in front of the brown band. On the first abdominal segment these yellow chromatophores are more prominent than on the other segments. On the telson yellow pigment is prominent at the anterolateral corners, on either side of the median carina and on the distal margin between the intermediate and the submedian spines. A few are present on the outer aspect of the terminal segment of the outer uropod also.

During the rest of the first post-larval stage very little change in pigmentation is noticed.

Post-larval stage II

With the first moult which takes place within four and a half to seven days after metamorphosis the second post-larval stage is reached, the specimen showing greater approximation to the adult condition than during the earlier stage. The shape of the eyes has markedly changed, the cornea having become very conspicuous and markedly obliquely set on the stalk (Fig. 49). Antero-lateral spines have appeared on the carapace which has the median carina indicated anterior to the dorsal pit also (Fig. 48). The anterior bifurcation of the median carina is, however, entirely lacking. A second spinous tubercle has appeared along the dorsal aspect of the raptorial carpus (Fig. 50). The lateral process of the fifth, sixth and seventh thoracic segments are larger and better differentiated than in the earlier stage (Fig. 51). The following carinae on abdominal segments terminate in spines:

Carina ending in spines		On abdominal segments
Submedian	..	5, 6
Intermediate	..	3, 4, 5, 6
Lateral	..	3, 4, 5, 6
Marginal	..	1, 2, 3, 4, 5

Thus, spines on the submedian carinae of the fifth abdominal segment, and on the intermediate and lateral carinae of the third segment appear after the first post-larval moult.

The lateral and intermediate marginal spines of telson are long and stout; the submedian spines are not terminally articulated, and the intermediate and submedian denticles are smooth with bluntly rounded tips (Fig. 52). The outer margin of the inner spine of the ventral prolongation of the uropod, above the lobe, is distinctly concave (Fig. 53).

Pigment on the body has become more prominent and characteristic than in the first post-larval stage. The distal half of the basal segment of the antennular peduncle is reddish-brown; while, the other two segments have a bluish-brown tinge. Of the antennular flagella, the long inner one is pale white, while the other two are brown. The antennal flagellum is white in colour and the antennal scale is bordered brown with bright yellow pigment centrally. The posterior third of the carapace has a marked concentration of brown pigment which on either side is continued as a linear patch between the lateral carina and the gastric groove. The expodites of the walking legs are yellow at the base and white distally. The ground colour of the body is dull brown, which

is concentrated into a distinct, roughly square patch along the mid-dorsal region in all the segments beginning from the sixth thoracic to the fifth abdominal. On the sixth thoracic segment there is a thin transverse streak of pale yellow, anterior to the brown patch but not quite reaching the sides. A similar but broader streak is present on the first abdominal segment. It is absent on the second abdominal but is represented on the third, fourth and fifth segments in a reduced form; that on the fifth segment being very inconspicuous. The median brown patch is very poorly developed on the sixth abdominal segment, which, however, has a yellow spot between the submedian carinae. The telson is uniformly brown, with a small pale patch at the antero-lateral corner and a brighter linear area at the intermediate marginal zone. The proximal end of the basal segment of uropod has a bright yellow spot; the exopod is bluish-black with a yellow area at the outer half of the terminal joint. The ventral prolongation and the endopod are dark brown.

Post-larval stages III–IV

The anterior bifurcation of the median carinae of carapace is entirely obsolete (Fig. 54). The eyes have become characteristic with the large, obliquely placed cornea (Fig. 55). The lateral carinae of the second abdominal segment also terminate in rudimentary spines, besides those observed in the earlier stages.

Post-larval stages V–VI

The anterior bifurcation of the median carina of carapace is very faintly indicated, not in the form of a carina but like a mere marking (Fig. 56). The dorsal keel of the raptorial carpus now bears three distinct tubercles (Fig. 57). The lateral processes of the fifth thoracic segment are acutely pointed, the anterior larger one curved and anteriorly directed; while, the short posterior one is almost laterally directed. The corresponding anterior process of the sixth and the seventh segments are short and subacutely pointed, with the posterior process large, broad and foliaceous (Fig. 58). Other structures do not show any marked change from the earlier stages. In most of the characters the post-larva now resembles the adult and with subsequent moults it attains the adult size fairly rapidly.

Frequency of post-larval moults

Under normal aquarium conditions the young post-larva undergoes the first moult four and a half to seven and a half days after the final larval moult and metamorphosis. As in the preceding species the interval between successive moults gradually increases with age. Details of the age and moults of larvae metamorphosed and reared in the laboratory are furnished in Table XIX.

TABLE XIX

Age and moults of Squilla wood-masoni *after metamorphosis of pelagic larva into post-larva*

Specimen No.	Age, in days, after metamorphosis, at moult									
	1	2	3	4	5	6	7	8	9	10
1	5·0	13·0	21·5	..	..	..	..	..	..	..
2	7·0	14·0	21·0	28·0	..	..	..	..	..	..
3	7·0	14·0	20·0	30·0	40·0	49·0	..	..	..	..
4	6·0	9·0	14·0	22·0	30·0	38·0	48·0	..	..	..
5	4·5	10·5	15·5	21·5	28·5	38·5	47·5	64·5	98·5	136·0
6	6·0	10·0	16·0	26·0	36·0	..	..	..	..	..

Besides the above specimens several others survived only the first 2–3 moults and then died. From the frequency of moulting of all these specimens reared in the laboratory the duration of the successive post-larval stages in this species is seen to be as follows (Table XX).

TABLE XX

Duration, in days, of successive post-larval stages of Squilla wood-masoni

	Post-larval stages									
	I	II	III	IV	V	VI	VII	VIII	IX	X
Duration in days:										
Range ..	4·5–7·5	3·0–8·0	5·0–8·5	6·0–10·0	17·0–10·0	8·0–10·0	9·0–10·0	17·0	34·0	37·5
Average ..	6·0	6·0	6·3	8·2	8·8	9·0	9·5	..	..	..

Frequency of moulting is rather rapid and in certain specimens the first moult takes place on the fifth day after metamorphosis. The average duration of the first two moults is six days, though in some cases the interval between the first and the second moults has been just three days. With successive moults the duration of the different stages also gradually increases, though it does not exceed 10 days up to the seventh stage. While adequate number of specimens have not been reared and studied from the seventh stage onwards, available data show that the duration of the eight stage is almost double that of the seventh and that the ninth and the tenth stages extend over a month each.

Post-larval growth

As in most other species of the genus, the final larval moult brings in remarkable structural changes including appreciable reduction in the total length of the specimen. The final pelagic larva usually measures about 35·5 mm. in total length including the rostrum (31·0 mm. excluding rostrum), but the young post-larva soon after metamorphosis measures only about 24·0 mm. in length. It undergoes further reduction in length during the first two days after metamorphosis when it measures only 20·0–21·0 mm. A reduction in length to the extent of 10·0–11·0 mm. (considering only the length of the larva excluding rostrum) thus takes place during metamorphosis. Positive growth in length commences with the first post-larval moult. The size of individuals after successive moults as seen from specimens reared in the laboratory is as follows (Table XXI.)

TALBE XXI

Squilla wood-masoni—*Total length attained after successive post-larval moults*

No.	Length of final pelagic larva (mm.)	Length of post-larva in mm.									
		Before moult	After moult								
			1	2	3	4	5	6	7	8	9
1	30·0	20·0	24·0	30·0	..	..	..	..	..	..	..
2	30·3	20·0	23·5	29·0	34·5	41·0	..	..	..	..	..
3	30·8	21·0	25·0	31·0	37·0	43·5	51·5	..	..	..	..
4	31·0	21·5	25·5	31·0	37·0	43·5	51·5	60·5	..	..	..
5	31·0	20·5	24·0	29·0	37·0	44·0	51·0	62·0	71·0	..	..
6	30·7	20·0	24·0	28·0	34·0	43·0	52·0	63·0	73·0	84·0	92·0

Except for limited individual variations the length of post-larva at the different stages is remarkably constant and shows only a very low range of variation. The actual growth following successive moults as seen from Table XXI is given in Table XXII.

TABLE XXII

Squilla wood-masoni: *Growth in length after successive post-larval moults*

	After moult								
	1	2	3	4	5	6	7	8	9
Growth in length (mm.)									
Range ..	3·5–4·0	4·0–6·0	5·5–8·0	6·5–9·0	7·0–9·0	9·0–11·0	9·0–10·0	11·0	8·0
Average ..	3·8	5·3	6·3	7·1	8·0	10·3	9·5	..	..

From the data given in Table XXII it is seen that growth after the first post-larval moult is the minimum but it steadily increases during subsequent moults. The maximum average growth of 10·3 mm. is recorded after the sixth moult. In the specimen that survived the 9th moult also growth was good following the 7th, 8th and 9th moults.

Considering the growth of post-larva under laboratory conditions as normal or akin to normal it should now be possible, as was done in the case of *S. nepa* and *S. holoschista*, to make a tentative assessment of the age and possibly also the number of moults undergone by any medium size specimen of this species. The data reviewed from this aspect could be tabulated as fallows:

TABLE XXIII

Squilla wood-masoni: *Age of and number of moults undergone by specimens of known size reared in the laboratory*

Length of specimen (mm.)	Approximate age after metamorphosis (days)	Probable number of moults after metamorphosis
23·0–24·0	0– 2	Nil
20·0–21·5	3– 7	Nil
23·5–25·5	5– 14	1
28·0–31·0	9– 21	2
34·0–37·0	14– 30	3
41·0–44·0	22– 40	4
51·0–52·0	29– 49	5
60·5–63·0	38– 49	6
71·0–73·0	48– 65	7
84·0	65– 98	8
92·0	99–136	9

As the number of specimens on which Table XXIII is based is very small the inferences therefrom could at best be considered as tentative only. However, it does facilitate assessment of the age of any specimen up to 100·0 mm. in total length.

The length of the pelagic larva and the young post-larva compare well with those of *S. holoschista*, though the latter appears to be a little smaller. Some of the recorded specimens of *S. woodmasoni* are much larger than the largest recorded specimen of *S. holoschista* (Kemp, 1913).

As in *S. nepa* and *S. holoschista*, within the first two or three moults the post-larva assumes most of the distinguishing features of the species though some of the important organs attain their adult proportions only gradually. The size and shape of the eye are characteristic in *S. woodmasoni* and the relative size of the eye during successive post-larval stages in terms of the corneal index is given in Table XXIV.

TABLE XXIV

Squilla wood-masoni: *Corneal index and length-width ratio of the eye during successive post-larval stages*

Post-larval stage	..	I	II	III	IV	V	VI	VII	VIII	IX
Corneal index	..	2·70–3·46	2·60–2·65	2·30	2·50	..	2·82–3·18	..	3·49	3·84
Length of eye / Width of cornea		1·06–1·30	1·10–1·29	1·03	1·07	..	1·05–1·15	..	..	..

While the proportion of the length of eye to the width of cornea appears to be constant, the corneal index varies considerably. With the first post-larval moult the width of the cornea increases markedly; this continues up to the third stage, after which it becomes proportionately smaller, the corneal index being 3·84 in the ninth stage when the specimen is about 92·0 mm. long. According to Kemp (1913, p. 74) the corneal index varies from 3·0 in young specimens, to 3·4 and 3·9 in specimens 80·0 and 90·0 mm. long and 4·2 in larger specimens. The smallest specimen examined by Kemp measures 34·5 mm. long. According to data furnished in the present paper a specimen 34·0 mm. long would be in the third post-larval stage when the corneal index hardly reaches 3·0 which, however, is attained in specimens over 50·0 mm. in length.

During metamorphosis other important organs also undergo remarkable changes in shape and, as in the eye, the adult proportions are attained only gradually. A series of measurements of selected structures during successive post-larval stages included in Table XXV would be of help not only for distinguishing the species from closely allied forms but also to ascertain the exact stage at which full adult proportions are attained.

The number of specimens of each size examined (single specimen in some) is far too inadequate for attempting generalisations. However, it is seen that throughout the early stages of growth the carapace has its maximum width near the hind margin, almost equal to or a little over its median length excluding the rostrum. The carapace in the first post-larval stage is comparatively narrow anteriorly, but during the subsequent stages the width increases to over $\frac{3}{4}$ the median length excluding the rostrum. The eyes, particularly the width of cornea, show steady growth with each moult. The exact growth of the different structures and the size at different stages in relation to the total length of the specimen could be seen from Table XXVI.

It is thus seen that the median length of carapace, length of telson and the length of raptorial propodus are all relatively longer in the early stages but become shorter or shrink up to about the fifth stage after which they show slight gradual increase in size. The width of carapace between its antero-lateral corners is relatively small in the first post-larval stage but from about the fourth stage onwards it is more or less constant being about 1·4 in the median length. The maximum width of carapace which in the first post-larval stage is almost invariably less than the median length of the same, is more than the latter from the seventh stage onwards. At this stage the length of

TABLE XXV

Squilla wood- masoni: *Measurements of selected parts of the body of specimens in different stages reared in the labcratory*

Post-larval stage	Total length	Carapace			Rostrum		Telson		Raptorial propodus		Eye	
		Median length	Anterior width	Maximum width	Length	Width	Length	Width	Length	Width	Length	Width
I	20·0–	4·03–	2·56–	3·85–	..	..	3·48–	3·76–	3·57–	1·01–	1·37–	1·19–
	22·5	4·76	2·84	4·03			3·85	4·12	3·85	1·19	1·83	1·60
II	23·5–	3·94–	2·97–	4·49–	0·92–	1·01–	3·48–	4·31–	3·89–	1·10–	1·92–	1·49–
	25·5	4·85	3·20	4·58	1·05	1·10	3·94	4·58	4·21	1·23	2·11	1·83
III	31·0–	5·68–	3·85	5·68–	1·01	1·28	4·12–	5·13–	4·76–	1·47–	2·56	2·47
	32·0	5·77		5·86			4·40	5·50	4·95	1·56		
IV	34·5	5·95	4·21	6·00	..	..	..	..	..	..	2·56	2·38
V	52·0	8·52	6·05	8·79	1·37	1·83	6·23	8·43	6·60	2·02	..	..
VI	54·0	10·08	6·41	9·30	1·56	2·02	7·60	9·62	8·43	2·66	3·66–	3·17–
VII	63·0	10·35	7·33	10·99	1·56	2·15					3·76	3·57
VIII	73·0	12·00	8·61	12–27	1·83	2·56	8·50	10·50	9·10	2·75	..	..
IX	84·0	14·38	10·17	15·20	2·29	2·93	9·34	12·09	10·44	3·02	..	..
X	92·0	16·21	11·45	16·58	2·56	3·21	11·26	14·84	13·00	3·66	..	4·12
							12·64	16·95	14·84	4·03	..	4·22

TABLE XXVI

Squilla wood-masoni: *Proportionate size of selected parts of the body during successive post-larval stages*

Post-larval stage	..	I	II	III	IV	V	VI	VII	VIII	IX
TL/MLC	..	4·66–5·11	5·14–5·96	5·45–5·54	5·80	6·10	5·27–6·08	6·08	5·84	5·67
TL/MLT	..	6·00–6·37	5·96–7·32	7·27–7·52	..	8·34	7·10–7·41	7·81	7·46	7·27
TL/LRP	..	5·58–5·84	5·82–6·19	6·46–6·51	..	7·88	6·40–6·92	7·00	6·46	6·20
MLC/LR		5·00	4·53–5·27	5·62–5·71	..	6·21	6·46–6·95	6·55	6·28	6·35
MLC/AWC	..	1·48–1·67	1·32–1·56	1·47–1·50	1·41	1·40	1·41–1·59	1·39	1·41	1·41
MLC/MWC	..	1·04–1·32	0·87–1·08	0·98–1·00	..	0·96	0·94–1·09	0·97	0·94	0·97
MLC/LRP	..	1·09–1·23	1·01–1·17	1·16–1·19	..	1·29	1·13–1·22	1·14	1·10	1·09
WR/LR	..	..	0·96–1·19	1·26	..	1·33	1·29–1·39	1·40	1·28	1·25
WT/MLT	..	1·05–1·12	1·09–1·31	1·16–1·33	..	1·35	1·21–1·31	1·29	1·31	1·34
LRP/WRP	..	3·23–3·81	3·38–3·74	3·17–3·23	..	3·26	3·17–3·44	3·45	3·55	3·68

telson is only 1·3 in its width, though in the earlier stages it was distinctly longer. The proportionate width of the raptorial propodus also becomes less with increase in size. The size of most of the structures during the eighth-tenth stages remains almost constant and could therefore be considered as representing the adult condition.

Breeding

No direct observations on the breeding habits or breeding season of *S. wood-masoni* are yet on record, as in the case of most other stomatopods. The species being less common than *S. nepa* and *S. holoschista* along the Madras coast, the larvae were also comparatively fewer in the tow-net collections. However, from the occurrence of even these limited number of larvae in the plankton hauls it would appear that as in the case of *S. nepa* and *S. holoschista* there is, probably, greater breeding activity during certain months of the year than in others. The details of occurrence of late pelagic larvae are given in Table XXVII.

Thus, the maximum incidence of larvae is in March–April and August–September, which coincides with the post-monsoon period in Madras. As suggested in the case of *S. holoschista* if the duration of pelagic larval life is short, breeding might be taking place just before the advent of monsoon.

Remarks

S. wood-masoni is a widely distributed species which has been recorded from the Bay of Bengal as well as the Arabian Sea. Third in the order of abundance along the Madras coast the advanced

pelagic larva of *S. wood-masoni* is, perhaps the longest stomatopod larva in the Madras plankton. A typical *Alima* with the antenna-labral region highly telescoped, it undergoes appreciable shrinkage in length, almost to the same extent as in *S. holoschista,* during the final larval moult and metamorphosis into post-larva.

TABLE XXVII

Squilla wood-masoni: *Average number of advanced pelagic larvae per collection during different months for the years* 1938–42

Year	Average number of larvae per collection during											
	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1938	X	X	X	1	..	..	1	2	1	X	X	..
1939	X	X	4	11	—	—	7	9	2	1	..	X
1940	X	X	3	3	—	—	X	1	19	X	..	X
1941	X	1	3	2	X	X	1	5	5	X	..	X
1942	5	1	5	1	—	..	4	4	5	1	1	..

X = No larva in the collection.

.. = No collection available.

As in the foregoing species (*S. nepa* and *S. holoschista*) the early post-larva of *S. wood-masoni* also is characterised by the absence of antero-lateral spines on the carapace and the presence of a terminal articulated piece on the submedian spines of telson. Both these features disappear with the first post-larval moult. The anterior bifurcation of the median carina of carapace is absent up to the sixth stage after which it appears as an absolete marking, but never becomes carinate even in the later stages. Right from the first post-larval stage the width of carapace at the antero-lateral angles is definitely more than half its median length including the rostrum. Anteriorly the carapace is characteristically broad, being 1·41 in the median length as compared to 1·86 in *S. holoschista* and 1·66–1·71 in *S. nepa,* during the ninth post-larval stage. The proportionate median length of carapace is comparable with that of *S. holoschista* only during the first stage after which it remains proportionately much smaller than in the latter species. The raptorial propodus is smaller and stouter than in the two foregoing species and the dactylus is provided with six teeth even at the first stage. The raptorial carpus attains the full adult structure in the fifth stage. From the second stage onwards the eyes gradually assume the characteristic shape of the adult.

The lateral processes of the fifth thoracic segment are unequal (anterior larger) even in the first post-larval stage and become longer and more acute in the subsequent stages; resembling more the corresponding processes in *S. interrupta* and appreciably different from what is shown by Kemp (*vide* Kemp's, Pl. V, Fig. 63) in one of the type specimens of *S. wood-masoni.* Similarly, the tubercle on the outer aspect of the inner spine of the ventral prolongation of the uropod appears to be somewhat more conspicuous than what is shown by Kemp in his Fig. 65, which condition might probably be attained in older specimens.

Fed regularly the moults are rather quick; the ninth moult taking place 98 days after metamorphosis. The corresponding stage in *S. nepa* is attained in 102–114 days and in *S. holoschista* in 120 days after metamorphosis. The interval between successive moults steadily lengthens with age and is similar to the condition in *S. holoschista.*

The early post-larva is a little longer than that of *S. holoschista* and the size attained by the same during successive moults shows that this initial difference in length is maintained during subsequent stages also. At the ninth moult the specimen attains a length of about 92·0 mm.;

the corresponding specimen of *S. holoschista* measures only 87·0 mm., and *S. nepa* will be still smaller, measuring only 80·0–83·0 mm. in total length. The actual increase in length following each moult is similar to that in *S. holoschista.*

In the occurrence of larvae the higher peak seems to be that during August–September, in which case *S. wood-masoni* differs from *S. holoschista* and resembles *S. nepa.* The larger size of the pelagic larva and the early post-larva, the larger size maintained during subsequent stages and the quicker growth probably indicate that *S. wood-masoni* is perhaps a larger species than *S. holoschista* and *S. nepa.* The size of the pelagic larva alone, however, cannot be considered an indication of the size of the adult form.

Squilla interrupta Wood-Mason (Figs. 59–76)

Far less common than any of the foregoing species in the Madras plankton, only a few larvae could be successfully metamorphosed in the laboratory but none of these thrived in the aquaria beyond the fifth post-larval stage. The early post-larval stages of the species are, however, described here in detail.

Post-larval stage I

The fairly stout post-larva measuring about 18·0 mm. long, has the eyes somewhat conspicuous with the corneal portion distinctly wider than the stalk (Fig. 59). The rostrum is broader than long and has the tip smoothly arched (Fig. 60). The antero-lateral corners of the carapace are fully rounded, without any trace of spines. Its width at the antero-lateral corners is only half its median length including rostrum. The median carina of carapace is seen anterior to the cervical groove and a little past the dorsal pit but the anterior bifurcation is wanting (Fig. 60). All the other carinae on the carapace are well indicated.

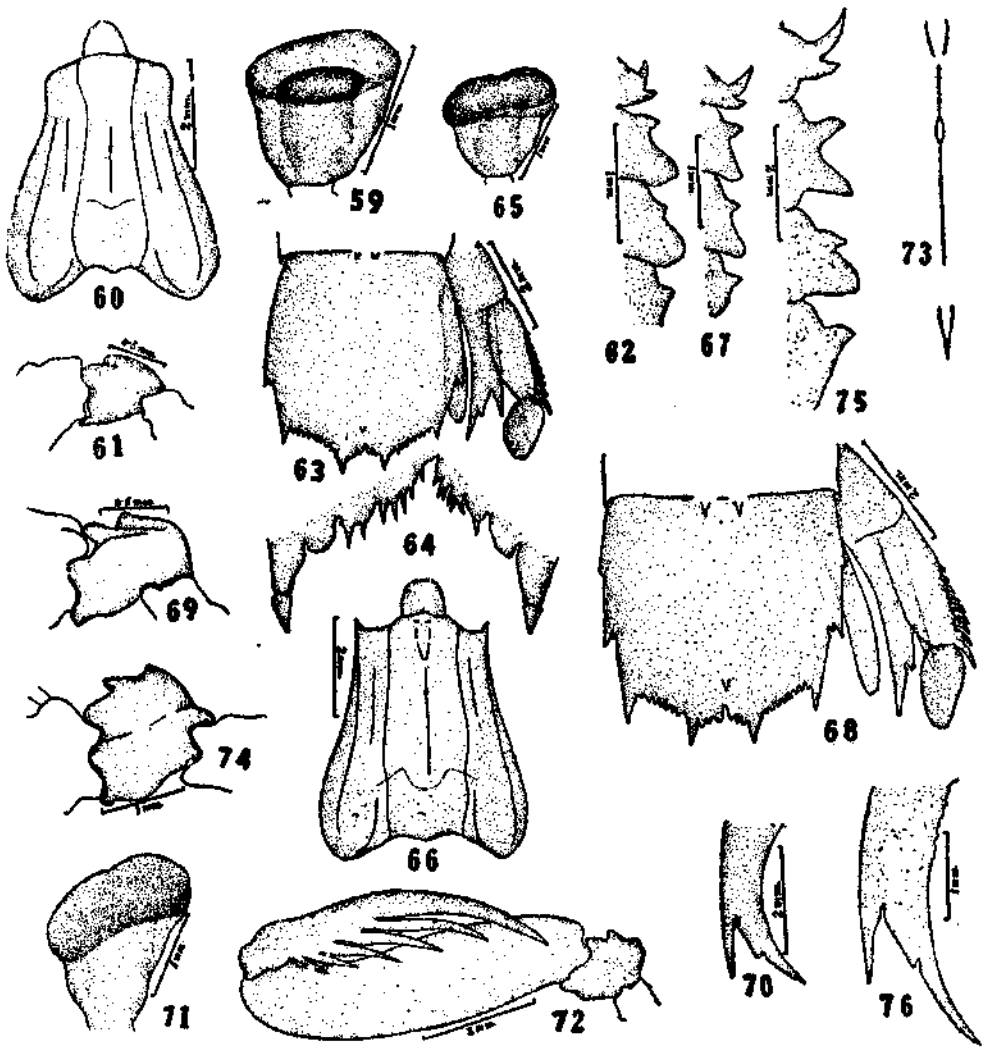
The raptorial dactylus has six teeth including the terminal one and has the outer margin sinuous, with an inconspicuous lobe also basally. The carpus is simple and has the dorsal keel ending in a smooth tubercular prominence (Fig. 61). The lateral processes of the fifth to seventh thoracic segments are bilobed. The anterior lobe in the fifth segment is larger than the posterior, acutely pointed and anteriorly directed; the posterior lobe is short, straight and sub-acute (Fig. 62). In the sixth and seventh segments the anterior lobe is short, that on the seventh being very small; while the posterior lobes on both these segments are broad and foliaceous.

There are four pairs of dorsal carinae on each of the first five abdominal segments and three pairs on the sixth. The following carinae terminate in spines:

Carina ending in spines		On abdominal segments
Submedian	—	6
Intermediate	—	4, 5, 6
Lateral	—	4, 5, 6
Marginal	—	1, 2, 3, 4, 5

The telson is almost as long as broad. The submedian spines have each a small, terminal, articulated piece. Between the two submedian spines there are three pairs of large denticles, the outermost pair smoothly rounded and the inner two pairs provided with 1 or 2 and 5 or 6 smaller, acutely pointed denticles respectively (Fig. 64). A small denticle may or may not be present in

the central notch in the submedian area. Besides the rudimentary pre-lateral denticle, there are one lateral and 8 intermediate denticles also on either side of telson (Fig. 63). The basal segment of the exopod of the uropod has 9 or 10 movable spines. The inner spine of the ventral process of the uropod has a conspicuous lobe half-way along its outer margin, which, above this lobe, is almost straight and not convex (Fig. 63).



FIGS. 59–76. *Squilla interrupta*. Figs. 59–64. First post-larval stage: Fig. 59. Left eye, dorsal view. Fig. 60. Carapace and rostrum, dorsal view. Fig. 61. Carpus of the raptorial limb. Fig. 62. Lateral processes of thoracic segments V–VIII. Fig. 63. Telson and left uropod, dorsal view. Fig. 64. Submedian spines and denticles of telson, magnified. Figs. 65–68. Second post-larval stage: Fig. 65. The left eye, dorsal view. Fig. 66. Carapace and rostrum, dorsal view. Fig. 67. Lateral processes of thoracic segments V–VIII. Fig. 68. Telson and right uropod, dorsal view. Figs. 69 and 70. Third post-larval stage: Fig. 69. Carpus of the raptorial limb. Fig. 70. Ventral prolongation from the base of the uropod. Figs. 71–73. Fourth post-larval stage: Fig. 71. The left eye, dorsal view. Fig. 72. The last three segments of the raptorial limb. Fig. 73. Median carina of carapace. Figs. 74–76. Fifth post-larval stage. Fig. 74. Carpus of the raptorial limb. Fig. 75. Lateral processes of thoracic segments V–VIII. Fig. 76. Ventral prolongation of the uropod.

The colouration of the young post-larva is very similar to that in the early post-larva of *S. holoschista.*

Post-larval stage II

With the first moult the eyes have grown in size and the cornea has become distinctly broader than the stalk and clearly obliquely placed (Fig. 65). The rostrum has become broad and truncate anteriorly; while the antero-lateral spines have appeared on the carapace which is now thoroughly changed in shape as compared to the first stage (Fig. 66). The anterior bifurcation of the median carina of carapace is clearly indicated though not yet raised up in the form of a carina. It is not only very faint at the middle but is interrupted at its (anterior bifurcation) base and is thus not continuous with the undivided hinder portion. The raptorial propodus has not developed any additional tubercle along its dorsal keel. The lateral processes of the fifth to the seventh thoracic segments are better formed; the posterior lobes of the sixth and seventh segments having become appreciably smaller than in the previous stage, though maintaining almost the same form (Fig. 67). The anterior lobes in both these segments are also more acute than in the earlier stage. On the abdominal segments the submedian carinae on the fifth and the lateral carinae on the third segment also terminate posteriorly in spines.

The intermediate pair of spines on the telson have become larger than the other two pairs; the submedian spines have lost their terminal joints (Fig. 68). The prelateral denticle is well indicated; other denticles numbering one lateral, eight intermediate and 3 submedian on each side are all smooth-tipped. On the inner spine of the ventral prolongation of the uropod the outer margin above the lobe appears slightly concave.

Numerous brown chromatophores have appeared on the body, those on the first five abdominal segments showing a low median concentration.

Post-larval stage III

There is hardly any change from the earlier stages, though in the raptorial carpus the dorsal keel shows a slightly sinuous outline, before abruptly terminating in the blunt tubercle (Fig. 69). In the ventral process of the uropod also the outer margin of the inner spine above the lobe is straight or slightly convex but definitely not concave (Fig. 70).

Post-larval stage IV

The eyes have assumed the characteristic shape with the cornea distinctly obliquely placed as in the adult (Fig. 71). In the raptorial limb a second tubercle has appeared behind the first one along the dorsal keel of carpus (Fig. 72). The dactylus still has a small, inconspicuous basal lobe externally. The median carina of carapace is well formed with the anterior bifurcation clearly separate from the hinder portion as in the adult (Fig. 73).

Concentrations of chromatophores are distinct over the terminal half of the rostrum, and, as a line, along the anterior border as well as the postero-lateral margin of carapace. Along the hind border of the last three thoracic segments the chromatophores form a dark, narrow band which is not very conspicuous. Pigment is more diffused on the first five abdominal segments though a thin transverse band along the hind margin and a median sparse concentration in each segment are distinct. At the base of the telson there is a clear brown spot. In the uropod the distal half of the endopod has a peripheral row of chromatophores. The inner margin of the ventral prolongation of the uropod is reddish-brown.

Post-larval stage V

The second tubercle on the raptorial carpus has become more pointed, though not quite so much as in the adult (Fig. 74). The lateral processes of the fifth-seventh thoracic segments have

also attained the adult condition (Fig. 75). The outer margin of the inner spine of the ventral process of the uropod, above the external lobe, has become slightly convex, approaching the adult condition (Fig. 76). On the telson the reddish-brown median spot at the base of the dorsal carina is more conspicuous and characteristic. Except probably in the relative size of the various parts the post-larva resembles the adult in most of the important features and could be fairly easily identified.

Frequency of early post-larval moults

The first post-larval moult takes place 5–8 days after metamorphosis. As in the other species already described the interval between successive moults up to the fifth stage does not show much variation (Table XXVIII).

TABLE XXVIII

Squilla interrupta: *Age at early post-larval moults*

No.	Age in days after metamorphosis at moult				
	1	2	3	4	5
1	7·0	14·0	22·0	29·0	37·0
2	5·0	13·0	20·0	...	...
3	8·0	14·0	21·0	28·0	...
4	8·0	14·0	24·0	..	...

From Table XXVIII the duration of each of the first five post-larval stages would appear to be 5–8, 6–8, 7–10, 7 and 8 days respectively. The moults, thus take place almost at weekly intervals upto the fifth. This is in agreement with the condition observed is *S. wood-masoni* and other allied species and on the same analogy it may be presumed that the duration of the subsequent post-larval stages in *S. interupta* also would follow approximately the same pattern.

Notes on early growth

As in other typical *Alima* larvae there is appreciable shrinking in length taking place during metamorphosis; the 25–26 mm. long larva (excluding rostrum) transforming itself into a post-larva measuring only 17·0–19·0 mm. in total length. The actual reduction in length is, thus, 6·0–8·0 mm. Following each post-larval moult appreciable growth in length takes place as given in Table XXIX.

The actual growth in length following each moult up to the fifth is thus 3·0–4·1; 4·5–5·5; 7·0–8·0 and 6·0–6·5 mm. respectively. As in the allied species the growth in length is the minimum following the first moult but gradually increases during the subsequent moults. The available data on the frequency of moulting and the size attained after each moult when considered together would indicate the age, size and moults undergone by the young post-larvae. (Table XXX).

Within a month after metamorphosis the post-larva thus undergoes at least four moults and attains a length of over 40·0 mm. Though most of the important adult features are attained by this period, certain body parts are yet to reach adult proportions. During the first five stages the corneal index changes as follows:

Post-larval stage ..	I	II	III	IV	V
Corneal index ..	3·30	3·47	3·52	3·70	4·05

TABLE XXIX

Squilla interrupta: *Total length attained after successive post-larval moults*
(All measurements in millimeters)

No.	Length of larva excl. rostrum	Length of post-larva				
		Before moult	After moult			
			1	2	3	4
1	26·0	19·0	22·0	27·0	34·0	40·0
2	25·0	17·5	21·0	26·5	34·5	..
3	26·0	18·4	22·5	27·0	35·0	41·5
4	25·5	18·0	22·0	26·5	34·0	..

TABLE XXX

Size, age and moults of early post-larvae of Squilla interrupta *as per aquarium observations*

Length of specimen (mm.)	Approximate age after metamorphosis (days)	Probable number of moults after metamorphosis
17·5–19·0	1– 8	Nil
21·0–22·5	6–14	1
26·5–27·0	13–24	2
34·0–35·0	20–29	3
40·0–41·5	28–37	4

Kemp (1913) found the corneal index ranging from 5·0 in the smallest examples in his collections, to 6·1 in the largest examples. Kemp's smallest specimen was 34·0 mm. long which, according to data furnished in Table XXX, would be in the fourth post-larval stage (after third moult). In the laboratory reared material of the same stage the corneal index is only about 3·7, the eye being distinctly larger. In two specimens, 32·5 mm. and 44·5 mm. long, recently collected from Bombay the corneal index is found to be 4·04 and 4·79 respectively. This would indicate that the eyes in specimens 35·0–45·0 mm. long are perhaps somewhat larger than that mentioned by Kemp, though not as large as in the laboratory-reared material. Since there is no doubt about the identity of the reared material the above difference is, probably, to be attributed to the artificial aquarium environment.

As *S. interrupta* is very closely related to *S. oratoria* and *S. oratoria* var. *inornata* and as the early post-larval stages of the former are likely to be easily mistaken for corresponding stages of the latter species the proportionate size of some of the important parts of the body of the early post-larvae of *S. interrupta* are given in Table XXXI to facilitate their easy identification.

It is seen from Table XXXI that, as in the other species, the carapace, telson and the raptorial propodus are all very much larger in the early post-larva than in the adult and that these become proportionately smaller with each post-larval moult. The width of carapace at the antero-lateral angles is about 1·75 times its median length excluding rostrum and this proportion remains

TABLE XXXI

Squilla interrupta: *Proportionate size of selected parts of the body during the first five post-larval stages*

Post-larval stage ..	I	II	III	IV	V
TL/MLC ..	4·52	4·54–4·62	4·21–4·26	5·23–5·30	4·98
TL/MLT ..	4·67–5·01	5·48–5·71	5·45–5·50	7·25–7·28	7·06
TL/LRP ..	5·04–5·15	5·24–5·58	5·00–5·25	5·70	5·65
MLC/LR ..	6·21	6·52–7·00	7·14	6·34–6·53	6·54
MLC/AWC ..	1·70	1·73–1·78	1·72	1·71–1·79	1·77
MLC/MWC ..	1·00	1·18–1·30	1·04	1·07–1·09	1·18
MLC/LRP ..	1·11–1·13	1·15–1·20	1·18–1·23	1·09	1·13
WR/LR ..	1·43	1·35–1·38	1·23	1·00–1·21	1·15
WT/MLT ..	0·97–1·00	1·02–1·07	1·04–1·08	1·11–1·21	1·21
LRP/WRP ..	3·43–3·80	3·31–3·46	3·47–3·61	3·85	3·94

almost constant during the first five post-larval stages. The maximum width of carapace in front of the posterolateral corners appears to be invariably less than its median length. The telson in the early post-larva is as long as or even a little longer than broad but in the subsequent stages it remains broader than long.

Remarks

S. interrupta is one of the common species of stomatopods in the Indian waters and is closely related to *S. oratoria* var. *inornata*. While the larva of the latter is still unknown, those ascribed to *S. oratoria* by Komai and Tung (1929) are very much smaller than the final pelagic larva of *S. interrupta* and have a somewhat different carapace shape also. The larva of *S. interrupta* is a typical *Alima* and as already shown, undergoes appreciable reduction in length during the final larval moult and metamorphosis.

The early post-larva has the antero-lateral corners of carapace smoothly rounded and the submedian spines of telson articulated. As in *S. nepa* and *S. wood-masoni* both these features disappear with the first post-larval moult. The anterior bifurcation of the median carina of carapace appears during the second post-larval stage. The eyes are invariably much smaller than in *S. wood-masoni* and larger than in *S. nepa* and *S. holoschista* of corresponding sizes. The median length of carapace is proportionately larger than in *S. wood-masoni* during the first five stages studied while it is comparable with that in *S. nepa* and *S. holoschista*. The anterior width of carapace is appreciably smaller than in *S. wood-masoni*. In *S. nepa* also the anterior width of carapace during the first five stages is proportionately greater than in *S. interrupta* though in the

later stages it attains almost the same proportion as in the early stages of the latter species. In the first two stages of *S. holoschista* the anterior width of carapace is relatively greater than in *S. interrupta* but in the subsequent stages it is considerably reduced and becomes even less than in the latter. In the raptorial limb the dorsal carina of the carpus merely terminates abruptly before reaching the distal end, during the first three post-larval stages but during the fourth stage two distinct, though rudimentary, tubercles appear on the same. By the fifth stage these tubercles are distinct and the specimens could be easily distinguished from *S. oratoria* var. *inornata* in which the dorsal carina of the carpus terminates abruptly before reaching the distal margin and apart from the above has no trace whatever of any dorsal tubercle (Kemp, 1913, p. 70). The fact that the structure of the carpus during the first three stages was exactly similar to the condition in the adult *S. oratoria* var. *inornata* clearly reflects the close relationship between the two species. The same close relationship is seen also in the structure of the ventral process of the uropod; during the first two stages the outer margin of the inner spine above the external lobe is faintly concave resembling the condition in *S. oratoria* var. *inornata* but during the subsequent stages it becomes clearly convex—a distinguishing feature of *S. interrupta* when compared with the former species. The lateral process of the fifth thoracic segment in the first post-larval stage resembles that of adult *S. oratoria* but with the first moult it becomes more prominent as in the var. *inornata*.

With normal feeding the frequency of early post-larval moults is similar to that in the foregoing species. The early post-larva is somewhat smaller than in *S. wood-masoni* and *S. holoschista* but is slightly larger than in *S. nepa*. This difference in size is maintained during the first five stages which shows that the actual growth following each moult is comparable in the four species.

Though nothing is now known about the size at sexual maturity or the breeding season of this species, examination of a number of specimens collected from Bombay during March and May shows female specimens 74·0 mm. and over in length with maturing ovaries in various stages of ripeness.

Squilla quinquedentata Brooks (Figs. 77–89)

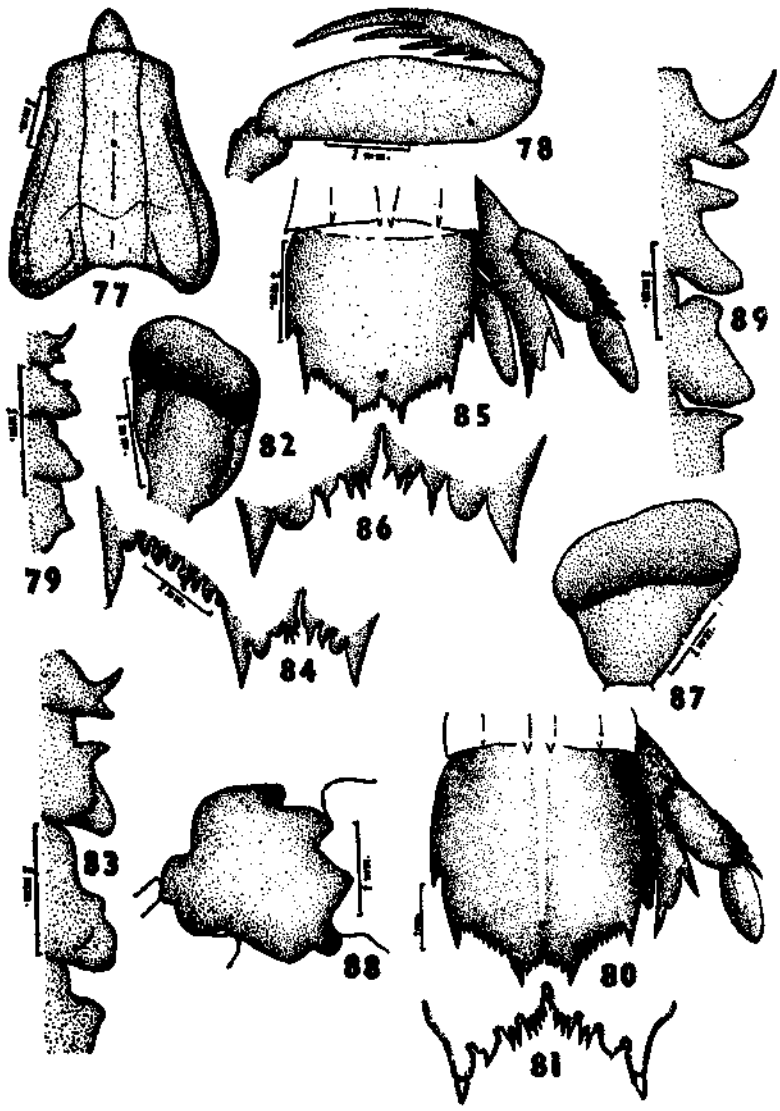
S. quinquedentata is not very common along the Madras Coast and the pelagic larvae are also only occasionally caught in the plankton hauls. The material for rearing and study was, thus, limited when compared with the more common species and though several larvae metamorphosed in the laboratory only two of them could be reared up to the 7th–8th post-larval stage.

Post-larval stage I

The medium sized, 15–16 mm. long, early post-larva is somewhat slender in appearance and opaque pale white in colour. The eyes are not very large though the cornea, which is slightly obliquely placed, is wider than the stalk. The antero-lateral corners of the carapace are smooth, the spines having not yet appeared (Fig. 77). The median carina of carapace is distinct in front of the cervical groove up to the dorsal pit beyond which it is not well differentiated, though visible for a short distance. There is no trace of any anterior bifurcation of the carina. The intermediate carinae are absent on the carapace but the laterals are distinct.

In the raptorial limb the dactylus has 5 teeth including the terminal one and a small external lobe basally (Fig. 78). The propodus appears fairly broad and is shorter than the median length of carapace. The dorsal keel of the carpus stops abruptly before reaching its anterior margin.

The lateral process of the fifth thoracic segment seen from above is bifid, with the anterior process acutely pointed and curved forwards and the posterior one short, sub-acute or smooth-tipped and directed laterally or postero-laterally (Fig. 79). The corresponding process of the sixth segment is also bifid with a short anterior and a large foliaceous posterior process. The lateral process of the seventh segment is hardly bifid, the anterior process being represented by a mere, smooth prominence.



FIGS. 77–89. *Squilla quinquedentata*. Figs. 77–81. First post-larval stage: Fig. 77. Carapace and rostrum in dorsal view. Fig. 78. The three terminal segments of the raptorial limb. Fig. 79. Lateral processes of thoracic segments V–VIII. Fig. 80. Telson and right uropod, dorsal view. Fig. 81. Sub-median spines and denticles of telson, dorsal view. Figs. 82–84. Third post-larval stage: Fig. 82. Right eye, dorsal view. Fig. 83. Lateral processes of thoracic segments V–VIII. Fig. 84. Intermediate and sub-median spines and denticles of telson, magnified. Figs. 85 and 86. Fourth post-larval stage: Fig. 85. Telson and uropod, dorsal view. Fig. 86. Sub-median spines and denticles of telson, magnified. Figs. 87–89. Seventh post-larval stage. Fig. 87. Left eye, dorsal view. Fig. 88. Carpus of the raptorial limb. Fig. 89. Lateral processes of thoracic segments V–VIII.

Carinae are distinct on the abdominal segments, the following ones terminating in spines:

Carina ending in spines		On abdominal somites
Sub-median	...	6
Intermediate	...	5, 6
Lateral	...	4, 5, 6
Marginal	...	1, 2, 3, 4, 5

The telson is quadrate or often a little longer than broad. The intermediate spines of telson are longer than the rest. The sub-median spines are terminally articulated (Figs. 80–81). There are 1 lateral and 7 or 8 intermediate denticles on each side, all acutely pointed. Between the two sub-median spines 6 large denticles are indicated, each provided with one or more acutely pointed processes (Fig. 81). The arrangement and number of these smaller denticles are subject to some variation. In the uropod the basal segment of the exopod bears 8 movable spines. The inner spine of the ventral prolongation has a prominent lobe externally above which its outer margin is convex (Fig. 80).

Pigment is scarce on the body soon after metamorphosis but within the next two days brown chromatophores appear mainly along the hind border of the abdominal segments.

Post-larval stage II

Rudimentary spines have appeared at the antero-lateral corners of the carapace which has the intermediate carinae also differentiated. The shape of rostrum is practically unchanged.

The intermediate carinae of the fourth abdominal segment terminate in spines which are rudimentary in some specimens.

The sub-median spines of telson are not terminally articulated. The intermediate and sub-median denticles are all pointed and the latter are less numerous than in the previous stage. The outer margin of the inner spine of the ventral process of uropod, above the lobe, is either straight or slightly concave.

Post-larval stage III

The cornea of the eye is obliquely placed and wider than the stalk (Fig. 82). The anterior one of the lateral processes of the fifth thoracic segment is a little longer than the hind one which is almost bluntly rounded at the tip (Fig. 83). In the sixth segment the anterior process is very much smaller and more acute than the posterior one. The lateral process of the seventh segment is practically single, as in the earlier stage. A pair of pre-lateral denticles are indicated on the telson. The intermediates are the longest of the marginal spines of telson. Some of the intermediate and sub-median denticles are blunt and rounded, while others are acutely pointed (Fig. 84).

Post-larval stage IV

The median carina of carapace in front of the dorsal pit is obsolete.

The sub-median carinae of the fifth abdominal segment also terminate in spines.

The lateral and a few of the intermediate and sub-median denticles of telson still remain acutely pointed (Fig. 86). In the uropod the outer margin of the inner spine of the ventral process above the lobe is distinctly concave (Fig. 85).

Post-larval stages V–VII

The eyes are characteristically broad but much less so than in *S. wood-masoni* or *S. interrupta* (Fig. 87). The outer margin of the raptorial dactylus is faintly sinuous. The carpus is very much the same as in the earlier stages, the carina along its dorsal keel stopping abruptly before reaching the tip (Fig. 88). The anterior spine of the lateral processes of the fifth thoracic segment is large, acutely pointed and turned forwards; while the posterior one is short, broad and sub-acute (Fig. 89). The corresponding processes of the sixth segment are also markedly unequal in size, the anterior small, short, finger-shaped and the posterior broad and foliaceous. The lateral process of the seventh segment is incipiently bifid, with a short, smooth anterior and a broad foliaceous posterior lobe. The number of abdominal carinae ending in spines remains the same as in the earlier stages.

The pre-lateral denticles on telson become distinct. All the intermediate and sub-median denticles are smooth and rounded.

The hind border of the last three thoracic and the first five abdominal segments is provided with a narrow transverse band of dark brown pigment, broad and more conspicuous medially. On the first abdominal segment this band is more conspicuous than on the succeeding ones. On the telson the distal end of the median carina, at the base of the terminal spine, is tinged dark brown. The distal half of the endopod and the inner half of the terminal piece of the exopod of the uropod are also brown in colour.

Frequency of post-larval moults

As in the species described earlier, young post-larvae frequently moult in aquaria when they are regularly fed; individual variations and variations depending on fluctuations in food are, however, noticeable. The age at successive moults after metamorphosis in respect of two specimens reared in the laboratory up to the 6th-7th moult is given in Table XXXII.

TABLE XXXII

Age and frequency of moulting during early post-larval stages of two specimens of Squilla quinquedentata

No.	Age in days after metamorphosis at moult						
	1	2	3	4	5	6	7
1	11	18	27	37	53	67	76
2	9	15	21	28	36	47	..

The duration of the successive early post-larval stages in respect of the above two specimens is as follows:

TABLE XXXIII

Duration in days of successive early post-larval stages of Squilla quinquedentata

	Post-larval stage						
	I	II	III	IV	V	VI	VII
Duration in days:							
Range ..	9–11	6–7	6–9	7–10	8–16	11–14	9
Average ..	10·0	6·5	7·5	8·5	12	12·6	..

The duration of the first post-larval stage appears to be appreciably longer than that of the three succeeding stages but this needs verification by rearing more specimens, particularly since in most other species hitherto studied the duration of the first stage is relatively short. The duration of the subsequent stages steadily increases and within a month after the final larval moult the post-larva undergoes about 4 moults. The trend of duration of the early post-larval stages appears to be similar to that in *S. nepa* and allied species.

Post-larval growth

As in other typical *Alima* larvae there is appreciable reduction in length during the final larval moult and the young post-larva usually measures only 15–16 mm. in total length, indicating a reduction of 8–9 mm. if the total length of the larva excluding rostrum is considered (Alikunhi, 1952). When fed regularly the post-larva grows rapidly after each moult, the actual growth being the maximum soon after the moult when the shell remains soft. The growth records of two specimens reared in the laboratory are furnished in Table XXXIV.

TABLE XXXIV

Squilla quinquedentata: *Total length attained after successive early post-larval moults*

Final pelagic larva: length excl. rostrum (mm.)	Length of post-larva in mm.						
	Before moult	After moult					
		1	2	3	4	5	6
24·0	16·4	19·5	24·0	28·0	31·0	34·0	..
24·3	16·5	19·5	23·5	27·0	32·0	38·5	44·0

The actual growth in length following successive moults is thus seen to be as given in Table XXXV.

TABLE XXXV

Squilla quinquedentata: *Growth in length in mm. after successive post-larval moults*

	After moult					
	1	2	3	4	5	6
Growth in length (mm.):						
Range	3·0–3·1	4·0–4·5	3·5–4·0	3·0–5·0	3·0–6·5	5·5
Average	3·05	4·25	3·75	4·0	4·75	..

As in the other species growth is the minimum after the first moult, but increases during the subsequent moults.

Though no conclusions are warranted on the data relating to the couple of specimens reared in the laboratory, when the available information on the age, frequency of moulting and growth of the early post-larva are put together the age of and possibly the number of moults undergone by young specimens of given size of the species would appear as given in Table XXXV.

TABLE XXXVI

Squilla quinquedentata: *Age and probable number of moults undergone by young specimens of given size*

Length of specimen (mm.)	Approximate age in days, after metamorphosis	Probable number of moults undergone after metamorphosis
16·0–16·5	1–11	Nil
19·5	9–18	1
23·5–24·0	15–27	2
27·0–28·0	21–37	3
31·0–32·0	28–53	4
38·5–43·0	36–67	5
44·0	47–76	6

Compared to other species the moults would appear somewhat delayed in this one; however, as only a couple of specimens have been reared this delayed moulting could perhaps be the result of vagaries of feeding, particularly as in one of the specimens the moults are not unduly delayed.

The change in the shape of the eye during different stages have already been mentioned. According to Kemp (1913) in the adult condition in this species 'the breadth of the cornea is about equal to the total length (of the eye) and is not more than one-fifth the length of the carapace.' The length of carapace and the dimensions of the eye during some of the early post-larval stages are given in Table XXXVII.

TABLE XXXVII

Squilla quinquedentata: *Dimensions of eye in relation to length of carapace during early post-larval stages*

Post-larval stage	Median length of carapace excl. rostrum (mm.)	Eye		Corneal index
		Total length (mm.)	Width of cornea (mm.)	
I	3·57	..	1·01	3·53
III	3·94	1·37	1·09	3·61
V	5·59	1·74	1·41	3·96
VII	7·05	1·83	1·65	4·27
	8·85	2·47	2·09	4·23

The eye is relatively larger in the early post-larva than in the adult. It gets smaller with each moult and almost adult proportions are attained after the sixth moult. The total length of the eye, however, remains slightly higher than the width of its cornea.

The proportionate size of the important organs during different post-larval stages are given in Table XXXVIII so as to facilitate comparison with related species.

TABLE XXXVIII

Squilla quinquedentata: *Proportionate size of selected parts of the body during early post-larval stages*

Post-larval stage	I	II	III	IV	V	VI	VII
TL/MLC	4·3	..	5·1	5·1	4·7	4·7	4·9
TL/MLT	5·06	6·2	6·0–6·4	7·0	6·6	7·0	6·6–7·3
TL/LRP	4·7	5·7	5·1–5·5	5·5	5·4	5·6	5·5
MLC/LR	5·5	..	..	6·3	5·9–6·7–	6·3	6·9
MLC/AWC	1·9	..	1·6	1·7	1·6–1·7	1·7	1·7
MLC/MWC	1·08	..	1·0	1·09	1·09	1·06	1·06
MLC/LRP	1·1	..	1·0	1·07	1·09–1·15	1–18	1·11
WT/MLT	1·0	1·08	1·0–1·02	1·12	1·14–1·16	1·20	1·24–1·29
LRP/WRP	2·91	3·11	3·28–3·31	3·54	3·31–3·36	3·25	3·77

It is thus seen that the carapace, telson and the raptorial propodus are relatively much larger in the young post-larva than in the later stages and with the succeeding moults these organs gradually attain their adult proportions. The raptorial propodus is invariably shorter than the median length of carapace, and is in the early stage much broader than in the succeeding stages. The telson which is almost as broad as long becomes appreciably broader than long by the seventh stage.

No information is now available on the breeding season of this species. Planktonic larvae, largely in the final pelagic stage, have been caught during almost all the months of the year, though perhaps to a larger extent during March–April and August–September. Though probably a perennial spawner as in the other species discussed in the foregoing pages, it appears to have two peak periods of breeding in the year.

Remarks

S. quinquedentata is not very common in the Indian waters though it has been recorded from Bombay, Kilkarai (Madras) and Balasore Bay (Orissa coast) (Kemp, 1913). Besides the type specimen from the Arafura sea, south of New Guinea, Tweedie (1934) has recorded 6 specimens from Singapore. Adult specimens are occasionally caught along the Madras coast and from the number of larvae caught in the tow-net the species appears to be about half as abundant as *S. wood-masoni* in the Madras waters (Alikunhi, 1952).

The larva, a typical *Alima*, is easily distinguished by its characteristically small carapace (Alikunhi, 1952) and undergoes appreciable reduction in length during the final larval moult and metamorphosis into the post-larva.

The absence of antero-lateral spines on carapace and the presence of a small terminal articulated piece on each of the sub-median spines of telson are characteristics of the first post-larval stage, and as in *S. nepa* and *S. holoschista* both these features disappear with the first post-larval moult. In these latter species the marginal denticles of telson become rounded or blunt following the first post-larval moult but in *S. quinquedentata* all the denticles remain acutely pointed during the second post-larval stage and only by the V-VI stage all of them become smooth-tipped. Though the

final pelagic larva is slightly larger than that of *S. nepa* the early post-larva is of almost identical size as in the latter; post-larval growth and moults in *S. quinquedentata*, however, appear to be definitely slower than in *S. nepa*. The average duration of each of the first four post-larval stages is about 7–8 days but this period increases to 12 days for the fifth and the sixth stages. These are appreciably longer than in *S. nepa* and probably indicate that the adult *S. quinquedentata* is perhaps somewhat smaller or at least not larger than adult *S. nepa*. The largest recorded specimen of *S. quinquedentata* measures 136 mm. in total length, while specimens of *S. nepa* measuring over 150 mm. in length are rather commonly found (Kemp, 1913).

Squilla gonypetes Wood-mason (Figs. 90–100)

Though rather uncommon, pelagic larvae of *S. gonypetes* are occasionally caught in the tow-net hauls off Madras coast (Alikunhi, 1952) and one of the very few larvae that metamorphosed in the laboratory was reared for a period of two months. The following observations are based on this specimen and also on a few early post-larvae which died soon after metamorphosis or after the first post-larval moult.

Post-larval stage I

The carapace is small and devoid of antero-lateral spines (Fig. 90). Median carina of carapace is indicated between the cervical groove and the dorsal pit, beyond which there is no trace of it. The lateral carina is often incipiently formed and discontinuous, while there is no trace of the intermediate carina. The rostrum is conical and almost as long as broad. The cornea of the eye is broader than its stalk and is also somewhat obliquely placed. The raptorial dactylus has 5 teeth including the terminal one and has a small but distinct, external, basal lobe (Fig. 91). The lateral process of the fifth thoracic segment is bilobed with the anterior lobe longer than the posterior, acutely pointed and curved forwards. The corresponding process of the 6th and 7th segments are faintly bilobed, with the posterior lobe much the smaller than the anterior.

On the abdominal segments the following carinae terminate in spines:

Carina ending in spines		On abdominal segments
Sub-median	..	6
Intermediate	..	5, 6
Lateral	..	4, 5, 6
Marginal	..	1, 2, 3, 4, 5

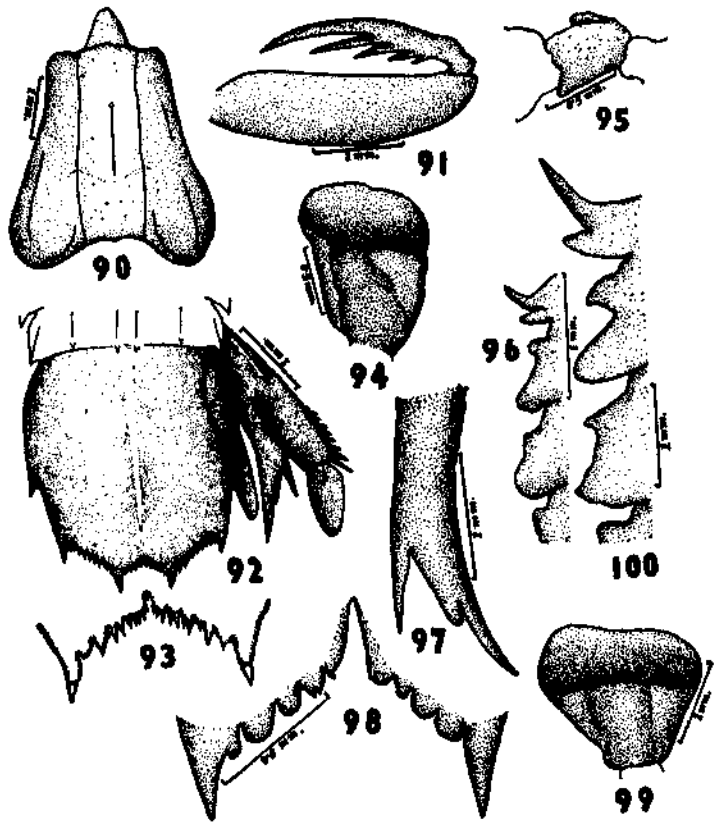
Telson is longer than broad (Fig. 92). Its median dorsal carina stops short of the distal margin and terminates in a small spine. Of the marginal spines the intermediates are the longest. The sub-medians are terminally articulated (Fig. 92). There are 1 lateral and 8 intermediate denticles on each side. Between the two sub-median spines there are 18-20 denticles, all acutely pointed.

In the uropod the basal segment of the exopod carries 8 movable spines. In the ventral prolongation from the base of the uropod the outer spine is about half the length of the inner which has its external margin above the rather inconspicuous lobe almost straight or even very slightly concave (Fig. 92).

Post-larval stage II

With the first post-larval moult rudimentary antero-lateral spines appear on the carapace. The median carina remains very much the same as in the first stage. The intermediate and lateral

carinae are clearly indicated and continuous. The rostrum is more truncate and distinctly broader than long. The cornea of the eye is a little obliquely set and is broader than the stalk (Fig. 94). The corneal index is 3·9. The width of the cornea is less than the length of the eye.



FIGS. 90–100. *Squilla gonypetes*. Figs. 90-93. First post-larval stage: Fig. 90. Carapace and rostrum, dorsal view. Fig. 91. Last two segments of the raptorial limb. Fig. 92. Dorsal view of telson and uropod. Fig. 93. Sub-median spines and denticles of telson, magnified. Figs. 94–97. Second post-larval stage: Fig. 94. Right eye, dorsal view. Fig. 95. Raptorial carpus. Fig. 96. Lateral processes of thoracic segments V–VIII. Fig. 97. Ventral prolongation of the uropod. Fig. 98. Fourth post-larval stage: Sub-median spines and denticles of telson, magnified. Figs. 99 and 100. Seventh post-larval stage: Fig. 99. Left eye, dorsal view. Fig. 100. Lateral processes of thoracic segments V–VIII.

The small external basal lobe on the raptorial dactylus persists. The dorsal keel of the raptorial carpus stops abruptly before reaching its distal end (Fig. 95). The anterior lobe of the lateral process of the fifth thoracic segment is long and acutely pointed, while the posterior one is short, almost straight and rather blunt (Fig. 96). The lateral process of the sixth segment is distinctly bifid, though the anterior lobe is much smaller than the posterior. In the 7th segment the anterior lobe is just a minute prominence. On the abdominal segments the intermediate carinae on the fourth and the lateral carinae on the third also terminate in spines. The sub-median spines of telson may or may not be terminally articulated. The lateral and some of the intermediate denticles are blunt and rounded at tip. Between the sub-median spines there are now only 7 denticles which are all pointed as in the earlier stage. The dorsal spine of telson is at an appreciable distance from its hind margin. The external lobe on the inner spine of the ventral process of the

uropod has become quite prominent and the outer margin of this spine above the lobe is slightly concave (Fig. 97).

Post-larval stage III

Though resembling the earlier stage, the following features are characteristic:

The small outer basal lobe on the raptorial dactylus persists. On the abdominal segments the sub-median carinae on the fifth also terminate in rudimentary spines. Some of the marginal denticles of telson remain acutely pointed.

Post-larval stage IV

On the carapace the anterior bifurcation of the median carina is still wanting. The tips of the antero-lateral spines almost reach the level of the rostral articulation. The sub-median spines on the fifth abdominal segment are well developed. The lateral carina of the second abdominal segment also terminates in spines. Prelateral denticles are visible on telson. Four pairs of sub-median denticles are present, all of them practically rounded and blunt at the tip (Fig. 98).

Post-larval stages V–VII

There is very little change from the earlier stage. The anterior bifurcation of the median carina of carapace is obsolete though there is just a median prominence like the portion immediately in front of the dorsal pit. In most of the features the post-larva now resembles the adult. The cornea of the eye has become wider than in the earlier stages and the corneal index is about 3·3. The width of cornea exceeds the length of eye (Fig. 99). The lateral processes of the fifth thoracic segment are fully developed with the anterior process long, acutely pointed and curved forwards and the posterior one short, sub-actuely pointed and almost straight (Fig. 100). On the sixth and the seventh segments the anterior process is short.

There is nothing characteristic about pigmentation which is similar to that of *S. quinquedentata.*

Frequency of post-larval moults

One specimen which survived for 62 days in the laboratory moulted six times during the period as follows:

TABLE XXXIX

Age at successive moults of a post-larval specimen of Squilla nonypetes *under laboratory conditions*

Age in days after metamorphosis at moult						Remarks
1	2	3	4	5	6	
8	15	23	33	42	55	Died on 62nd day

The duration of the successive post-larval stages up to the seventh in this particular specimen has thus been 8, 7, 8, 10, 9 and 13 days respectively for the first to the sixth stage. Though no conclusions can be drawn from observations on a single specimen the frequency of moulting in the early post-larva appears similar to that in *S. quinquedentata.* The duration of the first three stages is practically the same, while, slightly longer duration is indicated in the subsequent stages.

Post-larval growth

The pelagic larva which measures about 27·0 mm. in length undergoes considerable reduction in length during the final larval moult and metamorphosis, the resulting post-larva measuring only 16·0–16·5 mm. in total length. As in the other species, with regular feeding the post-larva grows quickly with each moult. The growth records of the specimen which survived for 62 days in the laboratory are given in Table XL.

TABLE XL

Total length attained by a specimen of Squilla gonypetes *during early post-larval moults in the laboratory*

Length before moult (mm.)	Length of post-larva in mm. after moult					
	1	2	3	4	5	6
16·0	18·0	20·0	23·0	26·5	30·0	33·0

The actual growth in length during each of the first six post-larval stages in this specimen is thus 2·0, 2·0, 3·0, 3·5, 3·5 and 3·0 mm. respectively. While this growth conforms to the general pattern in the other species, *viz.*, minimum growth during the early stages and gradually increasing growth subsequently it appears to be markedly slower than in the corresponding stages of *S. quinquedentata.*

Though data on the moults and growth of only a single specimen are available, when these are put together the age and possibly the number of moults undergone by juvenile specimens of given size would appear as follows:

TABLE XLI

Age of and probable number of moults undergone by juvenile specimens of S. gonypetes *of given size*

Length of specimen (mm.)	Approximate age in days, after metamorphosis	Probable number of moults undergone after metamorphosis
16·0	1– 8	Nil
18·0	8–16	1
20·0	15–23	2
23·0	23–33	3
26·5	33–42	4
30·0	42–55	5
33·0	55–over 62	6

A comparison of the above data with the corresponding data for *S. quinquedentata* given in Table XXXVI indicates that early post-larval growth is quicker in the latter species. To facilitate similar comparison in respect of other characters the proportionate size of some of the important organs of *S. gonypetes* during the early post-larval stages is given in Table XLII.

TABLE XLII

Proportionate size of selected parts of the body of Squilla gonypetes *during early post-larval stages*

Post-larval stages	..	I	II	III	IV	V	VI	VII
TL/MLC	..	4·7–5·0	4·8	..	4·92	4·82	5·0	5·14
TL/MLT	..	5·4–5·6	5·45	6·23	7·00	6·88	7·0–	..
TL/LRP	..	5·4	6·00	6·23	6·13	..	6·3	..
MLC/LR	..	5·0–5·1	5·80	...	6·40	6·70	7·02	..
MLC/AWC	...	1·59–1·84	1·32–1·85	..	1·70	1·71	1·78	..
MLC/MWC	...	0·97–1·06	0·92–1·00	..	0·98	1·03	0·98	..
MLC/LRP	..	1·08	1·18	..	1·27	..	1·26	..
WT/MLT	..	0·93–1·00	0·94	1·05	1·11	1·19	1·17	..
LRP/WRP	..	3·60	3·02–3·20	3·21	3·44	...	3·47	..

It is seen from Table XLII that the carapace, rostrum, raptorial propodus and telson which are relatively bigger in the early post-larva than in the adult gradually becomes smaller with each post-larval moult. A comparsion of the data given in Table XLII with those in Table XXXVIII where corresponding data relating to *S. quinquedentata* are given shows that the carapace and the raptorial propodus are relatively shorter in *S. gonypetes* and that the telson is wider in *S. quinquedentata.* Detailed studies on more extensive material are likely to indicate more specific features distinguishing the juveniles of these two closely related species.

Remarks

That *S. gonypetes* is closely related to *S. quinquedentata* is well demonstrated in the descriptions of the early post-larvae of the two species given in these pages. That the two are, however, quite distinct species is also seen from the characters of the pelagic larvae described (Alikunhi, 1952). Sunier's view (1918) that *S. gonypetes* is merely based on young individuals of *S. quinquedentata,* because the known specimens of the former are all below 55 mm. in length and since all the known specimens of the latter exceed 100 mm. in length, cannot therefore be accepted. Much smaller specimens of both the species have been examined in detail during the present study and most of the distinguishing characters of *S. gonypetes* listed by Kemp (1913) appear to be dependable specific features.

In *S. gonypetes* the eyes are relatively smaller than in *S. quinquedentata* in the pelagic larval stage (Alikunhi, 1952), and in the first post-larval stage. By the seventh post-larval stage, however, the corneal index in *S. quinquedentata* is about 4·25, while in the corresponding stage of *S. gonypetes* it is only about 3·3 indicating that the eyes are appreciably larger in the latter. As already pointed out, other features in which *S. gonypetes* differs markedly from *S. quinquedentata* are the relatively smaller size of the carapace and raptorial propodus and the relatively longer telson. Though the lateral processes of the last three thoracic segments have not attained their full adult condition by the seventh post-larval stage, they are different from those of *S. quinquedentata* (Compare

Figs. 89 and 100) and show indications of the more even division of the anterior and posterior processes.

As in the preceding species, absence of antero-lateral spines on carapace and the presence of small, terminal articulated pieces on the sub-median spines of telson are characteristic features of the first post-larval stage of *S. gonypetes* also. These features, however, disappear with the first moult. As in *S. quinquedentata* the majority of the denticles of telson remain acutely pointed during the first three post-larval stages and they become rounded and blunt only by the IV–V stage. The differences in the frequency of early moults and growth as compared to *S. quinquedentata* have already been mentioned.

Squilla boops Kemp (Figs. 101–108)

Rather rare in the Madras plankton, only a few specimens metamorphosed in the laboratory and these also did not survive the second post-larval moult. Identification of the species is thus based only on early post-larval characters and must therefore remain tentative for the present.

Post-larval stage I

The 31·0 mm. long pelagic larva metamorphosed into a post-larva measuring only 18·5 mm. in total length. The eyes are large and conspicuous. The carapace is devoid of antero-lateral spines and has the median carina faintly indicated up to the dorsal pit. There is thus no trace of the anterior bifurcation of the carina. The raptorial dactylus has only five teeth including the terminal one. The outer margin of the dactylus is faintly sinuous and has a tubercle basally (Fig. 101). The lateral process of the fifth thoracic segment is bifid with the anterior spine longer than the posterior. The lateral processes of the sixth and seventh segments are hardly bifid. On the abdominal segments the following carinae terminate in spines.

Carinae ending in spines	On abdominal segments
Sub-median ..	6
Intermediate ..	5, 6
Lateral ..	(4), 5, 6
Marginal ..	1, 2, 3, 4, 5

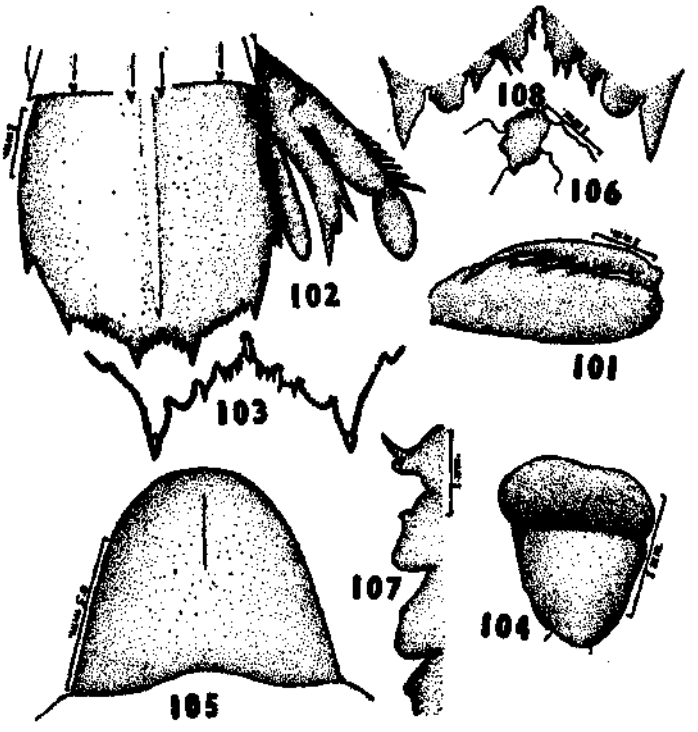
The telson is relatively large with rather short marginal spines. The sub-median spines are terminally articulated (Figs. 102–103). The denticles number 1 lateral, 8 intermediate and 2 sub-median on each side. The lateral and intermediate denticles are all pointed, while the outermost sub-median denticle on each side is bluntly rounded. Each of the other two sub-median denticles bear 1–4 smaller acutely pointed spinules (Fig. 103). In the uropod the basal segment of the exopod carries 8 movable spines. The outer spine of the ventral process of the uropod is about half the length of the inner which has a prominent lobe externally (Fig. 102). The outer margin of this spine above the lobe is almost straight.

Post-larval stage II

Seven days after metamorphosis the post-larva moulted for the first time. Soon after moulting it measured about 22·3 mm. indicating a growth of 3·8 mm. over the earlier stage. The eyes are conspicuous with the cornea broader than the stalk and obliquely set (Fig. 104). The corneal index is about 3·7. The rostrum has distinct median carina at its distal half (Fig. 105). Antero-

lateral spines have appeared on carapace which does not yet have any trace of the anterior bifurcation of the median carina. In the raptorial limb the dorsal keel of the carpus does not reach its distal end, before which it is produced into a small tubercle (Fig. 106). The anterior spine of the lateral process of the fifth thoracic segment is acutely pointed and obliquely directed forwards, while the posterior is short and almost rounded at the tip (Fig. 107). The corresponding process of the sixth segment is just bifid, with the anterior process very small and like a tubercle only. In the seventh segment the process is not bifid, though there is a smooth prominence indicating the position of the anterior spine.

On the abdominal segments the intermediate carinae of the fourth and lateral carinae of the third segments also terminate in rudimentary spines.



FIGS. 101–108. *Squilla boops*. Figs. 101–103. First post-larval stage: Fig. 101. The last two segments of the raptorial limb. Fig. 102. Telson and right uropod, dorsal view. Fig. 103. Sub-median spines and denticles of telson, magnified. Figs. 104–108. Second post-larval stage: Fig. 104. Left eye, dorsal view. Fig. 105. Rostrum, dorsal view. Fig. 106. Raptorial carpus. Fig. 107. Lateral processes of thoracic segments V–VIII. Fig. 108. Sub-median spines and denticles of telson.

In the telson the sub-median spines are not articulated (Fig. 108). A pair of pre-lateral denticles has appeared. Only a few of the marginal denticles of telson have become blunt and rounded, others remaining acutely pointed. In the uropod the outer edge of the inner spine of the ventral process above the lobe has become slightly concave.

The relative size of the important parts of the body during the first two post-larval stages is given in Table XLIII for purposes of comparison with the corresponding stages of allied species detailed in this contribution.

Though only two stages have been available the data offer valuable comparison with the corresponding stages of the closely allied species *S. quinquedentata* and *S. gonypetes*. The eyes

TABLE XLIII

Proportionate size of important parts of the body of early post-larvae of Squilla boops

Post-larval stages	I	II
TL/MLC ...	4·5	4·7
TL/MLT ...	4·9	6·0
TL/LRP ...	5·0	5·5
MLC/LR ...	...	6·2
MLC/AWC ...	1·60	2·1
MLC/MWC ...	0·95	1·1
MLC/LRP ...	1·11	1·15
WT/MLT ...	1·0	1·06
LRP/WRP ..	3·07	3·2

are relatively larger than in *S. gonypetes*. In the size of carapace it is intermediate between *S. gonypetes* and *S. quinquedentata*. The width of carapace between the antero-lateral spines is relatively less than that in the above two species; while the raptorial propodus is slightly larger.

Remarks

As the post-larva did not survive the second stage the specific identification is only tentative. However, such features as the presence of only 5 teeth on the dactylus of the raptorial claw, the median carina of the rostrum, the nature of the median carina of the carapace, the nature of the lateral processes of the last four thoracic segments and the conspicuous eyes assume added significance as distinguishing features in view of the fact that the larval and post-larval stages of the other related species of the '*quinquedentata*' group recorded from the locality have been thoroughly described and are quite different from the species now under consideraton.

The characteristic features of the first post-larval stage of species of the '*nepa*' and '*quinquedentata*' groups, *viz.*, the absence of antero-lateral spines on carapace and the presence of terminally articulated sub-median spines of telson are shared by *S. boops* also. However, the closer relationship of the latter to *S. quinquedentata* and *S. gonypetes* is perhaps indicated in the partial retention of the acutely pointed intermediate and sub-median denticles of telson during the second and perhaps also one or two of the succeeding stages.

The week's duration of the first post-larval stage indicates that the frequency of post-larval moults is perhaps similar to that in *S. gonypetes* and *S. quinquedentata*.

S. boops is rarely found in Indian waters, the type specimen having been obtained from the Gulf of Martaban, Burma (Kemp, 1913). According to Kemp (1913) *S. quadraticauda* described by Fukuda (1911) from Matsuwa, Sigami Province, Japan, is synonymous with *S. boops*. Komai (1938) has recorded *S. boops* from the Kii Peninsula, Japan, and recently the species has been found among stomach contents of Tuna from Hawaiian waters (Townsley, 1953). The species does not appear to have been recorded from the Indian coast so far.

Squilla hieroglyphica Kemp (Figs. 109–113)

Only a single specimen of this rare species was available for study and a brief account of the same has already been given (Alikunhi, 1944). Further details about this specimen which died during the second post-larval stage are as follows:

Post-larval stage I

	mm.
Median length of carapace, excluding rostrum	3·36
Carapace: breadth at antero-lateral corners	2·13
Carapace: maximum breadth	3·50
Length of rostrum	0·63
Width of rostrum (base)	0·77
Eye: length	0 89
Eye: width of corneal portion	0·84
Eye: width of stalk	0·84
Length of raptorial propodus	3·27
Width of raptorial propodus	0·80

The cornea of the eye is a little obliquely placed on the stalk and is of the same width as the stalk (Fig. 110). The corneal index is 4·0. Antero-lateral spines are absent on carapace. Its width at the level of the anterolateral angles is almost $\frac{2}{3}$ its median length excluding rostrum and a little over half the median length including rostrum. The median carina is short and simple without any anterior bifurcation (Fig. 109). The rostrum is conical with smooth tip and has a median carina at the distal half, though not quite extending to the distal border. The lateral process of the fifth thoracic somite is bifid, the anterior process pointed and slightly curved forwards, while the posterior is broader and directed laterally (Fig. 112). The corresponding processes of the 6th–8th segments are broad, foliaceous and undivided. The raptorial dactylus with a small, rather inconspicuous proximal lobe externally, has 5 teeth including the terminal (Fig. 111). The first five abdominal segments have all the four pairs of carinae; while the sixth has three pairs. The following carinae terminate in spines:

Carinae	Abdominal somites
Sub-median	5, 6
Intermediate	5, 6
Lateral	4, 5, 6
Marginal	(1), 2, 3, 4, 5

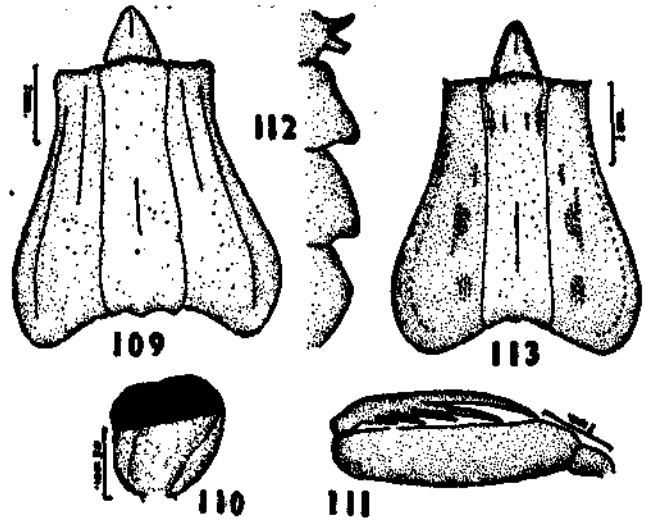
Details about the telson and uropod and the characteristic pigmentation of telson have already been given (Alikunhi, 1944).

Post-larval stage II

On the eighth day after metamorphosis the specimen died undergoing the first post-larval moult. Though the post-larva has not fully moulted and attained the characters of the second stage a partial moult has taken place. Rudimentary antero-lateral spines have appeared on the

carapace (Fig. 113). The rostrum has become less broad than in the first stage. The carapace and rostrum measure as follows:

	mm.
Carapace: median length excluding rostrum ..	3·09
Carapace: width at level of antero-lateral corners ..	1·82
Carapace: maximum width	3·09
Rostrum: length	0·67
Rostrum: width at base	0·70



FIGS. 109–113. *Squilla hieroglyphica*. Figs. 109–112. First post-larval stage: Fig. 109. Carapace and rostrum, dorsal view. Fig. 110. Right eye, dorsal view. Fig. 111. The three terminal segments of the raptorial claw. Fig. 112. Lateral processes of thoracic segments V–VIII. Fig. 113. Second post-larval stage: Carapace and rostrum, dorsal view, showing disposition of chromatophores.

In comparison with the first stage the shape of carapace has considerably changed. Pigment on the carapace is sparse, being distributed in small groups of chromatophores as shown in Fig. 113. The sub-median spines of telson are still terminally articulated and the sub-median denticles also do not show any change from the previous stage.

Remarks

That the species is rare in the Indian waters has already been mentioned (Alikunhi, 1944). Of the four specimens of this species so far recorded the locality of the type specimen is not known (Kemp, 1913); the second was obtained from the Philippines (Kemp, 1915); the third (the present one) from Madras (Bay of Bengal; Alikunhi, 1944) and the fourth from Travancore (Arabian Sea; Kuriyan, 1947). There can thus be no doubt that the species is an Indo-Pacific form and as already pointed out 'it would appear that the species is not altogether so very rare in the Indo-Pacific region' (Alikunhi, 1947).

It is remarkable that the characteristic pigmentation of the telson which is perhaps unlike any other species (Kemp, 1913) is clearly formed even in the first post-larval stage. The carination

of the carapace and rostrum and the nature of the lateral processes of the 5th–8th thoracic segments are also sufficiently characteristic to enable fairly easy identification of the young post-larva with this remarkable species. As is to be expected the carapace and eyes have not attained the adult proportions in the young post-larva.

The remarkable resemblance of this Indo-Pacific species to *S. hildebrandi* from the Panama Canal zone has already been mentioned (Schmitt, 1940; Alikunhi, 1944). But for geographical considerations, the remarkably close similarity of *S. hildebrandi* particularly in the colouration of telson, carination of carapace and rostrum, pigmentation of the eyes, the nature of the lateral processes of the 5th thoracic segment and the structure of the raptorial limb, with *S. hieroglyphica* would not appear to justify the creation of a new species for the American specimens.

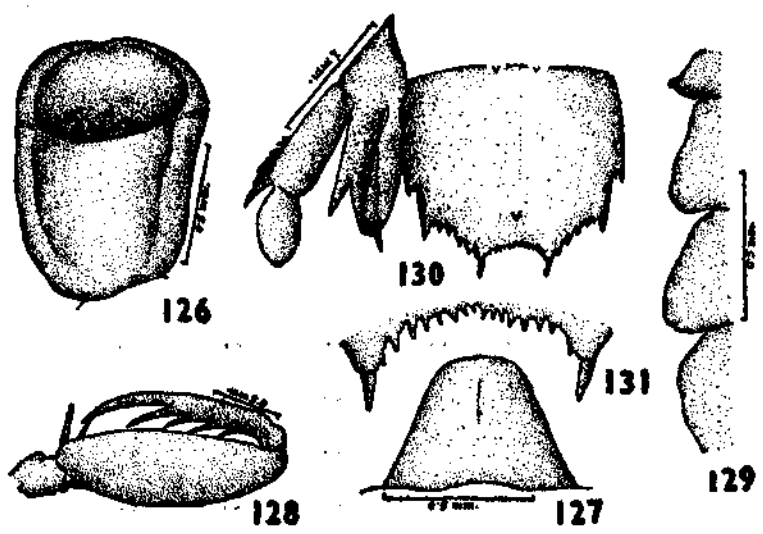
Squilla scorpio Latreille (Figs.126–131)

No post-larval specimens of this species were available for study in the Madras material. However, a small post-larva, 9·4 mm. long, collected from the Barbalong Estuary, Chandipur Coast, Orissa, on the 16th May 1950, is described here for purposes of comparison with other species. The specimen measures as follows:

	mm.
Total length	9·43
Carapace: median length	2·24
Carapace; anterior width	1·37
Carapace: maximum width	1·83
Rostrum; length	0·45
Rostrum: width	0·61
Eye; length	0·93
Eye: width of cornea	0·64
Telson; length	1·37
Telson: width	1·65
Raptorial propodus: length	1·65
Raptorial propodus: width	0·49

The small slender specimen is opaque white in colour and has the eyes fairly conspicuous. The cornea is slightly obliquely placed and is a litle wider than the stalk (Fig. 126). The carapace, shorter than a fourth of the total length, carries rudimentary antero-lateral spines. The median carina is rudimentary and does not extend anterior to the dorsal pit. The rostrum is smoothly tapering and near its anterior edge is only about half as broad as it is at the base. It bears a faint median carina over the distal half (Fig. 127). In the raptorial limb the dorsal keel of the carpus stops short of its distal end. The propodus is fairly stout and the dactylus has five teeth including the terminal (Fig. 128). The external basal lobe of the dactylus is small and inconspicuous. The lateral process of the fifth thoracic segment seen from above is a single, laterally directed, subacute process, with its posterior margin showing a tendency to curve forwards (Fig. 129). The corresponding processes of the sixth and seventh segments are simple, flat and rounded. On the abdominal

segments the submedian, intermediate and lateral carinae of the sixth and the marginal carinae of the fifth segments alone terminate in spines. The postero lateral corners of the first four abdominal segments are smooth, the marginal carinae not ending in spines. The telson is broader than long, with the marginal spines moderately long. The submedian spines have long, slender terminal articulations (Figs. 130, 131). The denticles are all pointed and they number 1 lateral, 5 intermediate and 8 submedian on each side. There is a distinct median dorsal carina on the telson, terminating in a small spine distally.



FIGS. 126–131. *Squilla scorpio* (?). Second post-larval stage (?): Fig. 126. Left eye, dorsal view. Fig. 127. Rostrum, dorsal view. Fig. 128. The three terminal segments of the raptorial limb. Fig. 129. Lateral processes of thoracic segments V–VIII. Fig. 130. Telson and left uropod, dorsal view. Fig. 131. Sub-median spines and denticles of telson, magnified.

The basal segment of the exopod of the uropod carries seven movable spines. The inner margin of the ventral prolongation is not serrated. The terminal inner spine of the ventral process has a conspicuous lobe, above which its outer margin is almost straight (Fig. 130).

To facilitate useful comparison with related species the proportionate size of the various parts of the body are given below:

Median length of carapace in total length ..	4·2
Length of telson in total length	6·8
Length of raptorial propodus in total length ..	5·7
Length of rostrum in median length of carapace ..	5·0
Carapace: anterior width in median length ..	1·6
Carapace: maximum width in median length ..	1·2
Length of raptorial propodus in median length of carapace ..	1·3
Telson: length in width	1·2
Raptorial propodus: width in length	3·3

Remarks

In view of the presence of rudimentary spines at the antero-lateral corners of carapace the specimen appears to be in the second post-larval stage. The retention of the articulated nature of the submedian spines of telson even after the first post-larval stage probably indicates its affinity to species of the *chloridella* and *raphidea* groups.

There is no direct evidence that the specimen described above belongs to *S. scorpio*. Size and features would place it either as *S. scorpio* or as *S. gibba*. However, features like the cornea of the eye being wider than the stalk and the relatively few abdominal segments on which carinae (particularly the marginals) terminate in spines indicate that it very probably belongs to *S. scorpio*. Though the absence of the characteristic dark spot on the lateral process of the fifth thoracic segment would indicate that it belongs to the variety *immaculata* it is possible that as the lateral process itself is not yet fully formed the pigment spot might appear at a subsequent stage.

Kemp (1920) has figured a 8·0 mm. long post-larval specimen of *S. scorpio* var. *immaculata* from the Chilka lake. Though small this specimen does not appear to be in the first post-larval stage. It is, however, largely similar to the specimen described here. Kemp's identification of the post-larva as the variety *immaculata* is not final and he mentions the possibility that the two are inseparable until they have reached a length of about 2 cm. Of the typical *S. scorpio* a post-larva 21·0 mm. long was found to have the characteristic features of the adult (Kemp, 1920). It is possible that distinguishing features between the typical form and the variety are not so marked in the early stages.

Squilla latreillei (Eydoux and Souleyet)* (Figs. 132–145)

Several larve metamorphosed into post-larvae in the laboratory but most of them died after two or three moults and only one specimen survived up to the fifth moult.

Post-larval stage I

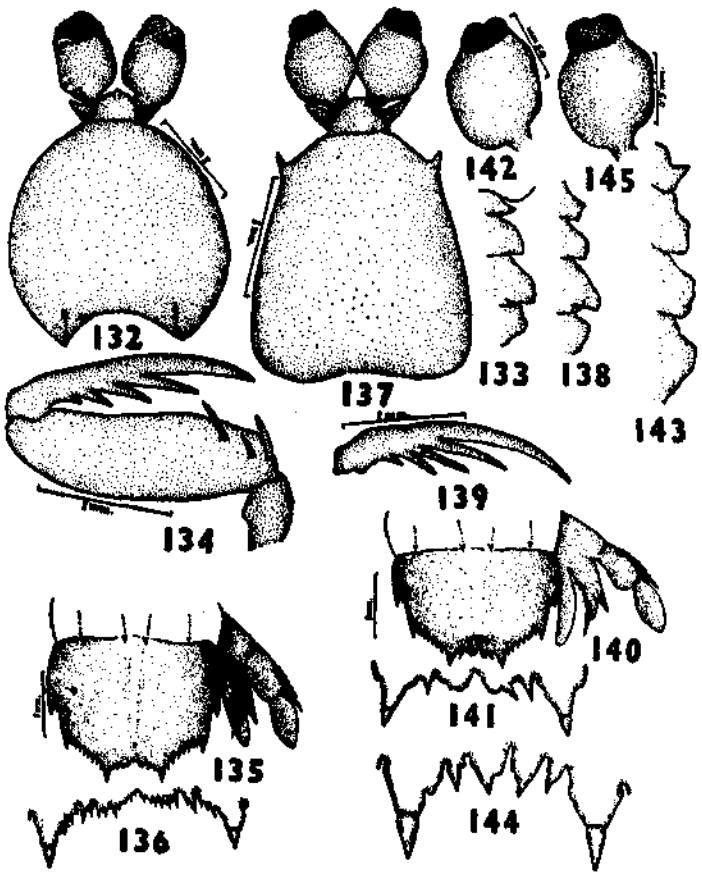
A very small, pale-white *Squilla*, it hardly resembles the adult. The carapace is roughly round without anterolateral angles. The anterior margin is markedly convex, with the small rostrum having a short terminal point (Fig. 132). The shape of the eye is far different from that in the adult. The basal portion of the stalk is swollen, the cornea is not distinctly bilobed and is relatively broad, the maximum breadth being ¾ the width of the stalk. The basal segments of the antennular peduncle are longer than the terminal one. The raptorial propodus is fairly stout and has three spines proximally, the middle one being smaller than the other two. The dactylus has five distinct teeth (Fig. 134); while, rarely in some specimens only four teeth are found, including the terminal one. The lateral process of the fifth thoracic segment is short and conical; while, those of the sixth to eighth segments are broad and lobose (Fig. 133). Of the abdominal segments submedian carinae are present only on the sixth, the intermediate carinae on the fifth and sixth, the laterals on all segments and marginals on the first five. The following carinae terminate in spines:

Carina ending in spines	On abdominal segments
Submedian ..	6
Intermediate ..	5, 6
Lateral ..	5, 6
Marginal ..	1, 2, 3, 4, 5

* This species was wrongly identified as *S. microphthalma* by Alikunhi & Aiyar, vide *Curr. Sci.* **11** (2), 56–68, 1942 and *Ibid.*, **12** (3): 80–82, 1943.

The telson is small and broader than long, with a median dorsal ridge terminating distally in spine. The submedian spines have movable tips (Fig. 135). The submedian denticles are irregularly arranged, some being very small and rudimentary (Fig. 136). There are 1 lateral and 6–8 intermediate denticles on each side. There are 29–30 denticles between the two submedian spines. The distal dorsal aspect of the peduncular segment of the uropod is provided with a small spine. The basal segment of the exopod carries seven free spines. The ventral prolongation of the uropod has the outer spine half as long as the inner which has a conspicuous smooth prominence basally. The inner margin of this ventral prolongation is provided with five small teeth or spinules.

Colouration.—Soon after metamorphosis pigment is scarce on the body which is opaque-white in colour. Within the next two days chromatophores appear all over the body and group



FIGS. 132–145. *Squilla latreillei*. Figs. 132–136. First post-larval stage: Fig. 132. Carapace, rostrum and eyes, dorsal view. Fig. 133. Lateral processes of thoracic segments V–VIII, magnified. Fig. 134. Terminal segments of the raptorial limb. Fig. 135. Telson and uropod, dorsal view. Fig. 136. Sub-median spines and denticles of telson, magnified. Figs. 137–141. Second post-larval stage: Fig. 137. Carapace, rostrum and eyes, dorsal view. Fig. 138. Lateral processes of thoracic segments V–VIII. Fig. 139. Raptorial dactylus. Fig. 140. Telson and uropod, dorsal view. Fig. 141. Sub-median spines and denticles of telson, magnified. Figs. 142–144. Third post-larval stage: Fig. 142. Left eye, dorsal view. Fig. 143. Lateral processes of thoracic segments V–VIII. Fig. 144. Sub-median spines and denticles of telson, magnified. Fig. 145. Fourth post-larval stage: Left eye, dorsal view.

themselves into a transverse, dark-brown band at the posterior border of each of the abdominal segments and the exposed thoracic segments.

Post-larval stage II

With the first moult the carapace assumes a more regular shape, with a pair of rudimentary antero-lateral spines and a smooth-tipped rostrum. The anterior margin of the carapace is still markedly convex with the result that the tips of the short antero-lateral spines do not reach the level of the rostral base. No trace of the median carina is seen on the carapace (Fig. 137). The cornea of the eye is small and bilobed, its width being only about half the width of the swollen middle portion of the stalk. The inner margin of the stalk is not fully straight but the two eyes touch each other along the inner margin basally. The terminal tooth of the raptorial dactylus has become longer and more slender than in the previous stage (Fig. 139). The lateral process of the fifth thoracic segment is broader, with a short spine (Fig. 138). The corresponding processes of the sixth-eighth segments are smooth and flat.

The telson has become shorter and relatively broader than in the earlier stage (Fig. 140). The submedian spines have terminal articulations. The number of submedian denticles is very much reduced, only a single pair being present on either side of the median line (Fig. 141). The uropod, though a trifle longer, is similar to that in the first post-larval stage. The carination and their spines on the abdominal segments remain unchanged.

The colouration becomes fairly well defined towards the later part of the second post-larval stage. On the hind border of each abdominal segment and also on the last three thoracic segments there is a continuous narrow band of dark brown pigment in the form of a line. From this line small pigment spots extend forwards. On the carapace there is a more or less continuous, narrow band of dark pigment along its margin, more prominent at the sides and anteriorly, including the rostrum and less so at the hind border. Further, on either side of the median line of the carapace there is a row of chromatophores extending from the anterior to the posterior end and appearing as a pair of parallel narrow lines.

Post-larval stage III

Though there is not much increase in length the specimen has grown appreciably stout. The eyes have become more like those of the adult though the inner margin of the swollen portion of the stalk is not as straight as in the adult (Fig. 142). In the raptorial dactylus the fifth tooth, though small, is quite distinct. The lateral process of the fifth thoracic segment is produced into a short, acute spine which is antero-laterally directed (Fig. 143). Corresponding processes of the sixth-eighth segments are broad and truncate. The telson is nearly one and a half time as broad as long; has the lateral and intermediate spines pointed and the submedians with terminal joints (Fig. 144). The intermediate and submedian denticles (5–6 and 2 respectively on either side) are pointed. The spinules along the inner margin of the ventral prolongaion of the uropod are well developed.

The pigmentation of body, though better developed and more defined, is more or less similar to that in the previous stage. A patch of chromatophores has appeared in the middle region of the carapace, in between the two parallel bands of pigment. In the abdominal segments also the forward extension of pigment band at the hind margin is getting more prominent. The general body surface has a distinct yellowish tinge.

Post-larval stage IV

After the third moult the specimen has grown markedly stout though there is no corresponding increase in length. T submedian spines of telson have terminal joints the denticles are also pointed.

The ground colour of the body is yellow. On the anterior border of all the abdominal segments there is a yellow band which near the lateral margin becomes broader and more conspicuous. Telson has a dark-yellow or reddish-yellow colour. The dark-brown pigment has the same arrangement as in the earlier stage.

Post-larval stage V

The eyes have assumed the characteristic adult shape (Fig. 145). The anterior margin of carapace remains markedly convex, with the antero-lateral spines not reaching the level of articulation of the small rostrum. As in the earlier stages the raptorial dactylus has a small basal prominence externally. The terminal tooth of the dactylus is very much longer than the penultimate; while the proximal or the fifth tooth is small, distinct and situated close to the fourth. The submedian spines are terminally articulated and the submedian and intermediate denticles are pointed. Submedian carinae have not yet appeared on the first five abdominal segments. Colouration remains the same as in the earlier stage.

Frequency of post-larval moults

Out of the 14 larvae that metamorphosed in the laboratory only four survived up to or beyond the fourth post-larval stage. The frequency of moulting in respect of these four specimens is shown in Table XLIV.

TABLE XLIV

Frequency of moulting of Squilla latreillei *after metamorphosis into post-larva*

No.	Age in days after metamorphosis at moult				
	1	2	3	4	5
1	4·5	11·5	18·0	30·0	41·0
2	10·0	16·0	23·0	31·0	..
3	5·5	12·5	18·5	..	..
4	6·5	13·5	19·5	..	..

From the data given in Table XLIV and similar observations on other post-larvae which died after the first or second moult the duration of each of the first few post-larval stages is found as in Table XLV.

TABLE XLV

Duration in days of successive post-larval stages of S. latreillei

Post-larval stages	..	I	II	III	IV	V
Duration in days:						
Range	..	4–10	6–7	6–7	8–12	11
Average	..	6·5	6·75	6·5	10·0	..

The duration of each of the first three post-larval stages is almost the same, but it is longer for the next two stages. This is in general agreement with the pattern of post-larval moults in the foregoing species.

Post-larval growth

Early post-larvae of *S. latreillei* range from 10·0–11·0 mm. in total length. As the total length of the final pelagic larva including rostrum is only 12·6–13·0 mm. practically no shrinkage in the length of body seems to take place during the final larval moult. Details of the growth in length of the post-larva following successive early moults are given in Table XLVI.

TABLE XLVI

Squilla latreillei: *Total length attained after successive early post-larval moults*

Specimen No.	Length of pelagic larva	Length of post-larva in mm.					
		Before moult	After moult				
			1	2	3	4	5
1	13·0	11·0	12·0	14·0	16·0	19·0	21·2
2	12·6	10·0	11·0	12·0	14·5	18·0	..
3	13·0	11·0	12·5	14·0	16·0	..	..
4	12·4	10·0	11·0	12·0	14·0	..	..

It is seen from the data given in Table XLVI that the actual growth in length is only 1·0–1·5; 1·0–2·0; 2·0–2·5; 3·0–3·5 and 2·2 mm. respectively following the first, second, third and fourth post-larval moults. Compared to the species discussed earlier in this report the growth is rather slow, though gradually increasing with each moult.

Considering the growth under laboratory conditions akin to normal, natural growth the available information on the size, age and moulting of post-larvae may be put together as shown in Table XLVII.

TABLE XLVII

Squilla latreillei: *Age of and number of moults undergone by specimens of particular size*

Length of specimen (mm.)	Approximate age after metamorphosis (days)	Probable number of moults undergone after metamorphosis
10·0–11·0	4–10	Nil
11·0–12·5	11–16	1
12·0–14·0	18–23	2
14·0–16·0	30–31	3
18·0–19·0	41	4
21·0–22·0	..	5

As *S. latreillei* is closely related to other species of the '*Chloridella*' group and as early post-larval stages of some of the related species are to be described in the subsequent sections of this report measurements of selected parts of the body of post-larvae of different stages are given in Table XLVIII to facilitate identification.

TABLE XLVIII

Squilla latreillei—*Measurements, in millimetres, of selected parts of the body of post-larvae of different stages*

Specimen No.	..	1	2	3	4
Age in days	..	2·5	6·5	13·5	..
Total length	..	11·0	12·0	13·0	..
Carapace:					
Median length	..	2·03	1·95	2·25	..
Anterior width	..	..	1·35	1·50	..
Maximum width	..	2·31	1·84	2·66	..
Rostrum:					
Length	..	0·42	0·33	..	..
Width at base	..	0·56	0·56	..	..
Telson:					
Width	..	..	2·34	2·69	..
Length	..	..	1·53	1·88	..
Raptorial propodus:					
Length	..	1·95	1·80	2·27	..
Width	..	0·64	..	0·85	..
Eye:					
Length	..	0·93	0·86	0·90	0·95
Width of stalk	..	0·69	0·62	0·65	0·68
Width of cornea	..	0·56	0·33	0·33	0·42
Corneal index	..	4·25	5·90	6·88	..

It is seen from these measurements that during the first two stages the carapace, eyes and other structures continue to shrink but begin to grow only from the third post-larval stage. The eyes are comparatively large in the first stage but the width of the corneal portion steadily decreases making the corneal index correspondingly higher. In the raptorial limb the propodus is almost one-third as broad as long.

Remarks

S. latreillei is commonly found in the Bay of Bengal. Outside this region it has been recorded from Singapore and the Persian Gulf (Kemp, 1913). From the occurrence of planktonic larvae in the townet catches it comes fifth in abundance, preceded by *S. nepa*, *S. holoschista*, *S. woodmasoni* and *S. quinquedentata* respectively in the Madras waters (Alikunhi, 1952). The size of the pelagic larva and the early post-larva and also the relatively slow post-larval growth seem to indicate that *S. latreillei* is perhaps one of the smaller species of the genus. The largest specimen recorded by Kemp (1913, p. 27) measures only 73 mm. (specimen from the Persian Gulf).

Unlike species of the '*nepa*' group the pelagic larva (*Alimerichthus* with stout abdomen and short antenna-labral region) does not undergo any appreciable reduction in length during the final larval moult and the length of the early post-larva is almost the same as that of the final pelagic larva excluding the rostrum.

From the account of the early post-larval stages it is seen that the carapace assumes its adult shape only from the second post-larval stage; while, in the case of the eyes the adult condition is attained only after the first four post-larval moults. In the raptorial limb the dactylus has an inconspicuous prominence at the base externally even in the first post-larval stage. The number of teeth

on the dactylus may be four or five and when five are present the fifth or the proximal one is small but quite distinct. The submedian denticles of telson undergo marked reduction in number after the first post-larval stage. The submedian spines are terminally articulated right from the first post-larval stage and these terminal pieces are broken off only in well-grown adult specimens (Kemp, 1913, p. 26). In this fetaure *S. latreillei* differs from species of the '*nepa*' group in which the terminal articulations of the submedian spines have only a transitory existence, usually only during the first post-larval stage. *H. raphidea*, however, resembles *S. latreillei* in this feature to a certain extent.

The submedian carinae on the first five abdominal segments which form a distinguishing feature of this species as compared to *S. microphthalma* have not made their appearance even after the fourth moult. In spite of the absence of this important feature, the shape of the eyes is so characteristic that there is no doubt that the specimens dealt with here belong to *S. latreillei*. That the formation of the weak submedian carinae may be delayed has already been shown in the case of *H. raphidea*.

Squilla fasciata De Haan (Figs. 146–153)

A single larva which metamorphosed in the laboratory was reared to the second post-larval stage when it died.

Post-larval stage I

	mm.
Total length	11·0
Length of telson	2·2
Width of telson	2·2

Hardly shorter than the final pelagic larva (excluding its rostrum) the young post-larva has a more slender appearance than the corresponding stage of *S. latreillei*. The eyes are conspicuous, with the cornea of almost the same width as the stalk and reach beyond the first peduncular joint of the antennule. The rostrum is fairly large and almost triangular, with a blunt anterior extremity. The carapace is more elongated than in *S. latreillei*, has a smooth dorsal surface and is devoid of any distinct carina. The antero-lateral spines are absent. The raptorial dactylus has six teeth including the terminal one. The lateral processes of the fifth thoracic segment, seen from the dorsal aspect, are single, short and sub-acutely pointed. In the sixth-eighth segments the lateral processes are rounded. Among the abdominal segments, sub-median carinae are present only on the sixth and these end in spines. The marginal, lateral and intermediate carinae are present on the first five abdominal segments. These are thin and poorly developed and in none of these five segments the intermediate and lateral carinae terminate in spines. The telson is almost as broad as long (Fig. 146). The marginal spines, particularly the intermediate and submedian, are long and pointed. The submedian spines are not terminally articulated. There is a median dorsal carina which posteriorly terminates in a spine. There are 1 lateral, 6–7 intermediate and 16–17 submedian denticles on each side. All the denticles are acutely pointed. The submedians are arranged roughly in 10 groups of three each, besides three small ones medially (Fig. 147). The uropod is fairly long; the basal segment of the exopod has eight spinules externally; the ventral prolongation has its inner margin provided with eight spinules and of its two terminal processes the outer one is only about half the length of the inner which has a very conspicuous smooth prominence externally.

Colouration.—To the unaided eye the young post-larva appears as an opaque, light brown little *Squilla*. Under the binoculars several stellate chromatophores are seen on the eye stalk and the dorsal aspect of the ophthalmic somite; at the base of the rostrum on either side as a small

group; over the carapace, particularly at the middle; in the form of a transverse, inconspicuous band on the mid-dorsal aspect of each of the last four thoracic somites and on the first five abdominals in the form of a broad patch, each incipiently divided into two halves. On the sixth abdominal segment this median patch of chromatophores is very inconspicuous. However, a distinct narrow, transverse band of chromatophores extends across the hind border of the segment. Less conspicuous groups of chromatophores are present on the dorsal aspect of the merus of the raptorial limb, near the postero-lateral corners of abdominal segments, on the distal half of the basal segment of uropod, on the exopod and ventral prolongation of the latter and also on either side of the median carina of telson.

Post-larval stage II

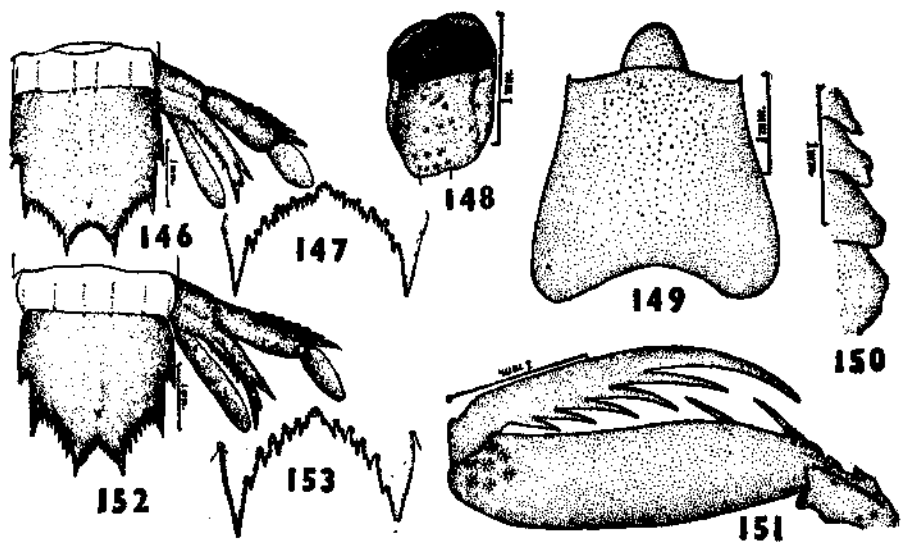
The early post-larva moulted for the first time, 6·5 days after metamorphosis (final larval moult) and entered the second post-larval stage.

	mm.
Total length after moult	12·4
Carapace: median length excluding rostrum ..	2·05
Carapace: anterior width	1·81
Carapace; maximum width	2·52
Telson: length	2·10
Telson: width	2·30
Raptorial propodus; length	2·58
Raptorial propodus: width	0·70
Eye; total length	1·21
Eye: width of stalk	0·82
Eye; width of corneal portion	0·82
Eye: corneal index	2·49

The eyes resemble those of *S. nepa* but the cornea is a little obliquely placed (Fig. 148). The cornea is of the same width as the stalk and the corneal index is only about 2·5. Rudimentary antero-lateral spines have appeared on the carapace (Fig. 149). The width of carapace at the level of its antero-lateral angles is a little over two-thirds its maximum widh and is almost 9/10th its median length, excluding rostrum. The lateral processes of the fifth thoracic segment are short but distinctly pointed (Fig. 150). Corresponding processes on the sixth–eighth segments are rounded. The dorsal carina of the raptorial carpus terminates in a short spine (Fig. 151). The middle one of the three movable spines of the propodus is the smallest. The propodus is broader than in the corresponding stage of *S. latreillei*. The dactylus has a small basal tubercle externally. As in the adult, submedian carinae are absent in the first five abdominal segments. The following carinae terminate in spines:

Carina ending in spines		On abdominal segments
Submedian	...	5
Intermediate	...	5, 6
Lateral	...	4, 5, 6
Marginal	...	(1), 2, 3, 4, 5

The telson has become shorter than in the previous stage and is now definitely broader than long. The marginal spines also appear a little longer; the denticles are all pointed, the lateral and intermediate denticles have become prominent and there are 1 lateral, 6–7 intermediate and 10–11 submedians on each side. Unlike the previous stage the submedian denticles are now arranged in groups of two each, except one near the submedian spine and one or two medially (Figs. 152, 153). This progressive reduction in the number of submedian denticles indicates that probably with the next moult their number might be reduced to 4–5 on each side as in the adult. The spinules along the inner margin of the ventral prolongation of the uropod are prominent, as also the tubercle on the outer aspect of its terminal inner spine.



FIGS. 146–153. *Squilla fasciata*. Figs. 146 and 147. First post-larval stage: Fig. 146. Telson and uropod, dorsal view. Fig. 147. Sub-median spines and denticles of telson, magnified. Figs. 148–153. Second post-larval stage: Fig. 148. Left eye, dorsal view. Fig. 149. Carapace and rostrum, dorsal view. Fig. 150. Lateral processes of thoracic segments V–VIII. Fig. 151. The three terminal segments of the raptorial limb. Fig. 152. Telson and uropod, dorsal view. Fig. 153. Sub-median spines and denticles of telson, magnified.

Colouration.—On the pale whitish body the chromatophores appear quite prominent and brighter than in the previous stage. The pigment pattern is more or less the same as in the first stage.

Two days after the first post-larval moult the specimen died and further observations on the completion of metamorphosis could not be made.

Remarks

Though still a juvenile specimen in the second post-larval stage, features like the nature of the eyes, number of teeth on the raptorial dactylus, nature of the lateral processes of the last four thoracic somites, carination of the abdominal segments and the structure of the telson and uropods unmistakably indicate its identity with *S. fasciata*.

The first post-larval stage of *S. fasciata* is remarkable in not having the submedian spines of telson articulated and by this feature alone it could be distinguished from the corresponding stage of the other species of the genus described in this report.

As in *S. latreillei* there is very little reduction in length accompanying the final larval moult and metamorphosis into the post-larva. The frequency of moulting probably does not differ markedly from that in the allied species like *S. latreillei.*

Besides the number of teeth on the raptorial dactylus, features like the shape of the eyes, the lateral processes of the fifth thoracic segment, the nature and spinulation of telson and colouration facilitate in easily distinguishing the young post-larva from the corresponding stages of *S. latreillei.*

So far as known *S. fasciata* is a rather rare species in Indian waters. The nearest locality to Madras from where it has been recorded is Port Blair in the Andamans (Kemp, 1913). A dredge collection made on 17th July 1939 from the sandy level sea bottom (10–15 fathoms) off the Madras coast contained a specimen of *Squilla* (Samuel, 1944). This specimen belongs to *S. fasciata* and measures about 35 mm. in length. The somewhat rare occurrence of its larvae in the coastal plankton (Alikunhi, 1962), supplemented by the record of only this single specimen from Madras indicates that the species though definitely available, is perhaps not so very abundant in the Bay of Bengal. That the species is a new addition to the stomatopod fauna of Indian waters has already been indicated (Alikunhi, 1952).

Squilla lata Brooks (Figs. 154–157)

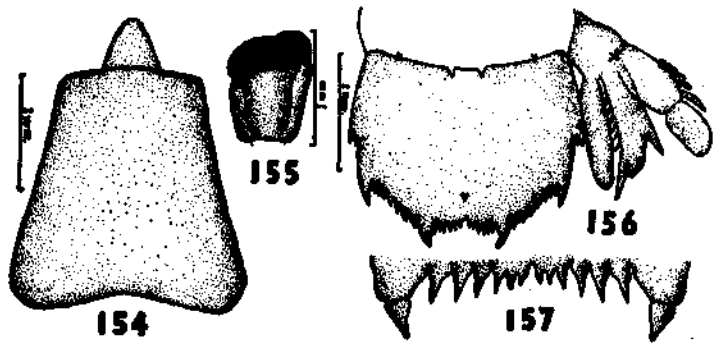
As only a single larva metamorphosed into the post-larva in the laboratory and as it died before undergoing any post-larval moult only the first post-larval stage of the species has been available for study.

Post-larval stage I

The small, slender, pale-white post-larva measured as follows:

	mm.
Total length	10·87
Carapace: median length	1·96
Carapace: anterior width	1·26
Carapace: maximum width	2·06
Rosturm: length	0·43
Rostrum; width	0·50
Eye; length	0·97
Eye: width of cornea	0·73
Eye; width of stalk	0·70
Raptorial propodus: length	1·71
Raptorial propodus; width	0·54
Telson; length	1·35
Telson: width	2·03

The eyes are rather conspicuous, almost as in the corrpondesing stage of *S. fasciata* and has the cornea a little broader than the stalk (Fig. 155). The carapace is very small; the antero-lateral angles are devoid of spines; and carinae are indistinct (Fig. 154). The rostrum, conical with smooth-tip, is broader than long. The raptorial dactylus has six teeth including the terminal one and has a distinct basal tubercle externally. The lateral process of the fifth thoracic segment seen from above is single and subacutely pointed; the corresponding processes of the sixth and seventh segments are rounded. The telson is very small and distinctly broader than long, the median length being only two-thirds its maximum width. Of the marginal spines, the laterals are the smallest and the intermediates the largest (Fig. 156). The submedians are terminally articulated (Fig. 157) and between them there are six pairs of pointed denticles of which the two innermost pairs are very much smaller than the rest. There are 7 intermediate denticles and one lateral on each side. Near the distal margin of telson there is a short median dorsal spine. The basal segment of the uropod carries a terminal spine dorsally; while, there are 6 movable spines on the outer aspect of the basal segment of the exopod. The inner margin of the ventral prolongation of the uropod is provided with a series of 6–7 small spinules (Fig. 156). The basal lobe on the inner terminal spine of the ventral prolongation is also very conspicuous.



FIGS. 154–157. *Squilla lata*. First post-larval stage: Fig. 154. Carapace and rostrum, dorsal view. Fig. 155. Left eye, dorsal view. Fig. 156. Telson and right uropod, dorsal view. Fig. 157. Sub-median spines and denticles of telson, magnified.

No characteristic pigmentation had developed when the specimen died before the first post-larval moult.

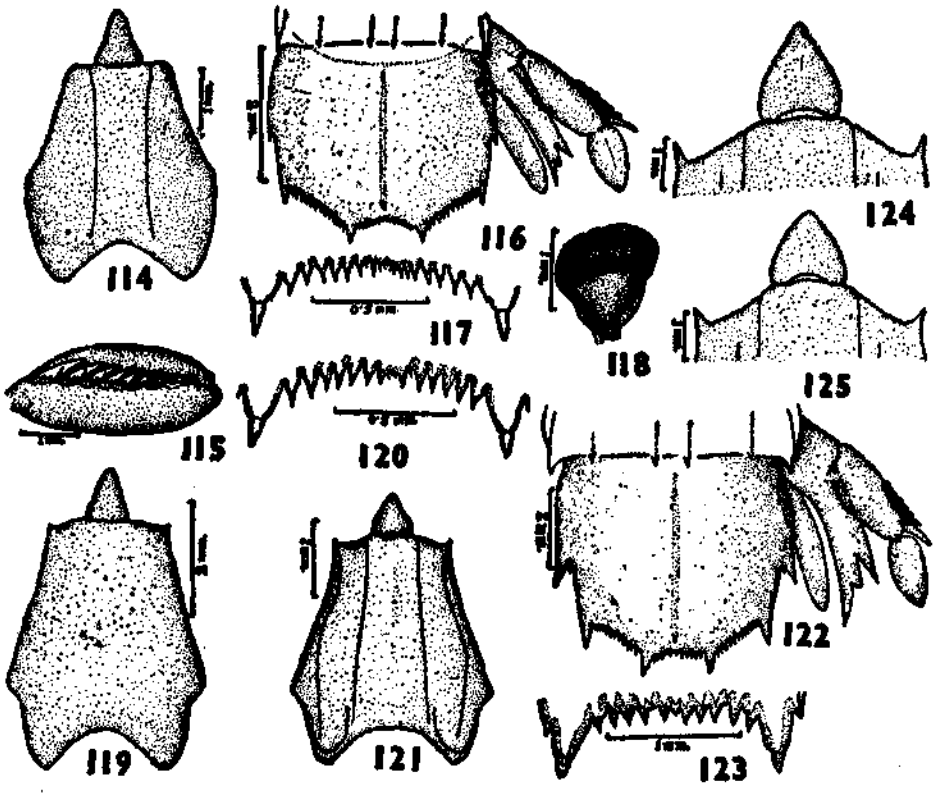
Remarks

A comparison of the measurements of the final pelagic larva (Alikunhi, 1952) with those of the early post-larva shows that hardly any reduction in the length of body has taken place during the final larval moult, though the carapace has become very much smaller than in the larva. In this feature it agrees with the other typical *Alimerichthus* larvae (e.g., *S. latreillei, S. fasciata*) which have the antenna-labral region short and the thoracic and abdominal segments relatively stouter than in the larger *Alima* larvae.

The species appears to be rather rare in the Madras waters (Alikunhi, 1952). The specific identification based on the characters of only the first post-larval stage is necessarily tentative, particularly since *S. lata* is very closely related to *S. gilesi* which has been recorded off the Madras coast (Kemp, 1913). The rather conspicuous outer basal lobe on the inner spine of the ventral prolongation of the uropod and the prominent series of spinules on the inner margin of the latter are features in which the post-larva differs from *S. gilesi* and which have weighed in favour of tentatively assigning it to *S. lata*.

Harpiosquilla raphidea (Fabricius) (Figs. 114–125)

One of the largest stomatopod known, *H. raphidea* is a common, fairly widely distributed Indo-Pacific species occurring from Japan to Zanzibar (Kemp, 1913). Pelagic larvae of this species are rarely found in the Madras plankton though a few larvae obtained in the live condition were successfully reared in the laboratory, enabling specific identification. One of these specimens was reared for 284 days after metamorphosis and during this period it moulted 15 times. Observations on these specimens are given below:



FIGS. 114–125. *Harpiosquilla raphidea*. Figs. 114–117. First post-larval stage: Fig. 114. Carapace and rostrum, dorsal view. Fig. 115. The two terminal segments of the raptorial claw. Fig. 116. Telson and right uropod, dorsal view. Fig. 117. Sub-median spines and denticles of telson, magnified. Figs. 118–120. Second post-larval stage: Fig. 118. Left eye, dorsal view. Fig. 119. Carapace and rostrum, dorsal view. Fig. 120. Sub-median spines and denticles of telson, magnified. Figs. 121–123. Third post-larval stage: Fig. 121. Carapace and rostrum, dorsal view. Fig. 122. Telson and right uropod, dorsal view. Fig. 123. Sub-median spines and denticles of telson, magnified. Fig. 124. Sixth post-larval stage: Rostrum and anterior margin of carapace. Fig. 125. Seventh post-larval stage: Rostrum and anterior margin of carapace.

Post-larval stage I

The slender, opaque, pale white early post-larva has the eyes larger and more conspicuous than in most other species. The rostrum is long and conical with a blunt tip and the lateral margins almost straight or slightly concave (Fig. 114). The anterolateral corners of carapace are perfectly smooth and devoid of spines and but for a smooth angulation there is also no trace of the lateral spinous prolongation along the margin on either side. There is no trace of the submedian carina;

only the intermediate carinae are clearly seen. The raptorial propodus is a little longer than the median length of carapace. The inner margin of the propodus carries a row of 7 spines, with 2–4 smaller spines in between adjacent larger spines. The dactylus in the majority of specimens has 8-teeth (rarely 9) including the terminal and has a small inconspicuous basal lobe externally (Fig. 115). The lateral margins of the last four thoracic segments are not produced into characteristic processes.

The submedian carinae are absent on the first five abdominal segments. The following carinae terminate in spines:

Carinae ending in spines		On abdominal somites
Submedian	...	6
Intermediate	...	5, 6
Lateral	..	2, 3, 4, 5, 6
Marginal	...	1, 2, 3, 4, 5

The telson is broader than long and has the marginal spines relatively short; the intermediates being the longest of the three pairs (Fig. 116). The submedian spines are terminally articulated and fairly wide apart. The margin of telson between the two submedian spines is neither deeply concave nor notched at the middle and hence not separated into two distinct halves (Fig. 117). There are 18–20 pointed denticles between the two submedian spines and of these a few towards the middle are very small. Besides, there are 12–13 intermediate and 1 lateral denticles on each side of telson. Its dorsal carina terminates in a spine a little in front of the distal margin. The basal segment of the exopod of the uropod has 9 movable spines. The outer spine on the ventral process of the uropod is almost half the length of the inner which has a prominent lobe externally (Fig. 116).

The early post-larva has no characteristic pigmentation. Chromatophores however, gradually appear and towards the end of the first post-larval stage they are concentrated in conspicuous transverse narrow dark-brown bands at the hind margin of each of the first five abdominal segments. The distal portion of the uropod is also tinged dark brown.

Post-larval stage II

The eyes are still conspicuous, with the cornea much wider than the stalk on which it is almost transversely placed (Fig. 118). The rostrum is long and conical with a smooth tip but the sides are straight and not concave as in the earlier stage (Fig. 119). Rudimentary spines may or may not be present at the antero-lateral corners of the carapace which has its anterior margin not as straight as in the foregoing stage. On either side, towards the end of the middle third of the lateral margin there is a smooth prominence—the rudiment of the spinous processes in the adult.

The inner margin of the raptorial propodus has 7–8 long spines but the smaller spines are less numerous (17–18) than in the previous stage. The dactylus has 8–9 teeth including the terminal.

The submedian carinae are absent on the first five abdominal segments. The intermediate carinae on the fourth abdominal segment also end in spines.

The marginal spines of telson have grown longer and stouter than in the previous stage (Fig. 120). Each of the submedian spines has a movably articulated, small terminal piece. The width of telson between the submedian spines is relatively less than in the previous stage. The denticles are all acutely pointed. Between the two submedian spines there are now only 13 normal size denticles, though medially there are 3–4 very small rudimentary ones also (Fig. 120).

The pigment bands on the hind border of the abdominal segments are more distinct than in the previous stage.

Post-larval stage III

The rostrum has become almost heart shaped with the tip more pointed than in the earlier stage (Fig. 121). Antero-lateral spines on carapace are short and pointed. The anterior margin has become distinctly convex and the tip of the antero-lateral spines hardly reach the level of the basal articulation of the rostrum. The median carina of carapace is indicated as a thin inconspicuous ridge. On either side, the lateral margin of carapace at the commencement of its distal third is produced into a subacute spinous process. All the carinae, excepting the median are, well developed.

The raptorial propodus is characteristically longer than the median length of carapace, excluding rostrum. Submedian carinae are still absent on the first five abdominal segments. The following carinae terminate in spines:

Carinae ending in spines		On abdominal somites
Submedian	..	6
Intermediate	..	3, 4, 5, 6
Lateral	..	1, 2, 3, 4, 5, 6
Marginal	..	1, 2, 3, 4, 5

The spines and denticles of telson are similar to those in the earlier stage, except that the number of submedian denticles has been further reduced to 12.

Post-larval stage IV

The rostrum, of almost the same shape as in the previous stage, is longer than broad; with the distal half of the lateral margin almost straight or imperceptibly concave. Antero-lateral spines, now well developed, have their tips inferior to the level of the basal articulation of rostrum. The lateral spinous projections are prominent.

In most other features the specimen resembles the previous stage. In the telson the distance between the submedian marginal spines has become relatively shorter, resulting in a greater approximation of its shape to the adult telson (Fig. 122). The marginal spines are quite prominent; the submedians remaining terminally articulated though the terminal piece is smaller than in the previous stage. All the denticles are acutely pointed and between the two submedian spines there are now only 5–6 pairs of denticles (Fig. 123). The basal lobe on the outer aspect of the inner spine of the ventral prolongation of uropod is quite conspicuous.

Pigmentation remains almost unchanged as compared to the earlier stage.

Post-larval stages V and VI

Rostrum continues to be of the same shape as in the fourth stage. The anterior margin of carapace is distinctly convex (Fig. 124). The median carina is thin, continuous and ridge-like. Rudimentary submedian carinae are present on the fifth abdominal segment during the sixth stage. The intermediate carinae of the second abdominal segment also end in spines. In the telson the submedian spines still have minute terminal joints. Marginal denticles are all pointed and their number remains unchanged. The median dorsal spine of telson has its tip almost reaching the distal margin. No pre-lateral denticle is present on the telson.

Post-larval stage VII

The shape of rostrum is appreciably changed; it is now typically heart-shaped and is broader than long unlike the earlier stages (Fig. 125). The anterior margin of carapace appears more conspicuously vaulted or convex so that the tips of the antero-lateral spines are markedly inferior to the level of rostral articulation. In other features the specimen closely resembles the previous stage.

Late post-larval stages

While most of the adult characters have been attained even at the seventh post-larval stage the submedian spines of telson retain their terminal articulations even after the ninth post-larval moult (10th post-larval stage). They are dropped off with the 10th moult; but the marginal denticles of telson become blunt as in the adult only after the 12th or 13th moult. Though the submedian carinae are indicated on the fifth abdominal segment during the sixth post-larval stage the submedian carinae on the first five abdominal segments are fairly fully formed only after the 12th post-larval moult. By this time the intermediate carinae on the first and the second abdominal segments are also produced into spines. The dorsal carina of telson has grown into a thick ridge with its distal spine overhanging the submedian denticles.

Pigmentation remains much the same as in the earlier stages, with a distinct, narrow, transverse band of dark pigment at the hind border of the last three thoracic and the first five abdominal segments. A diffused transverse streak of dark pigment is seen at the middle of the second abdominal segment; while, at the base of the median crest of telson there is a conspicuous patch of reddish-brown pigment.

Frequency of post-larval moults

As in other species, when fed regularly the young post-larva undergoes moults in quick succession and grows steadily. Though only three specimens could be successfully reared in the laboratory for 32, 80 and 284 days respectively, quite a few larvae were reared up to the second or third post-larval stage. In all these cases the first post-larval moult took place 4·5 to 7 days after the final larval moult and the interval between successive moults after the first gradually increased with age. Details of post-larval moults of three specimens in relation to their age after metamorphosis are given in Table XLIX.

TABLE XLIX

Frequency of moulting of H. raphidea *after metamorphosis into post-larva*

No.	Age in days after metamorphosis at moult														
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV
1	6·0	11·0	19·0	25·0	32·0	..	..	..	..	..	..	..	..	..	..
2	4·5	9·5	14·5	19·5	26·5	36·5	45·5	57·5	71·0	..	..	..	..	..	..
3	6·0	14·0	21·0	28·0	36·0	52·0	71·0	85·0	99·0	114·0	135·0	159·0	181·0	232·0	282·0

From Table XLIX and from observations on a few other specimens reared through the first 2–3 post-larval stages the duration of the successive stages is given in Table L.

Though the data given in Table L relate only to a few specimens and might not perhaps warrant inferences thereon, they are in striking resemblance to the condition observed in other species under similar conditions. The average duration of each of the first five post-larval stages is 6–7 days; during the sixth to the tenth stage the duration of each stage is about 14

TABLE L

Duration in days of successive post-larval stages of H. raphidea *under laboratory conditions*

Post-larval stages	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV
Duration in days:															
Range	4·5–7·0	5·0–8·0	5·0–8·0	5·0–7·0	6·0–8·0	10·0–16·0	9·0–19·0	12·0–14·0	13·5–14·0	15·0	21·0	24·0	22·0	52·0	50·0
Average	5·7	6·0	6·7	6·0	7·0	13·0	14·0	13·0	14·0	..	..	..	..	..	..

days; from the eleventh to the thirteenth stage it increases to about three weeks, after which during the next two stages the duration is about 50 days. It is probable that the interval between subsequent moults also might not normally exceed 50 days.

Post-larval growth

The early post-larva of *H. raphidea* is 15·0–16·0 mm. long. The final pelagic larva being only about 18·2 mm. in length including the rostrum, there is hardly any reduction in length during the final larval moult and metamorphosis. As in the other species growth is rapid immediately following each moult when the chitinous exoskeletion is soft (Pl. II B). The length attained after successive moults in aquaria in respect of three specimens are given in Table LI:

TABLE LI

H. raphidea: *Total length attained after successive post-larval moults*

No.	Length of pelagic larva (mm.)	Length of post-larva in mm.							
		Before moult	After moult						
			1	2	3	4	5	6	
1	18·2	16·0	21·0	26·0	31·0	43·0	55·0*	..	
2	18·2	15·5	19·5	24·0	29·0	34·0	42·0	46·0	
3	18·1	15·0	19·0	23·5	28·0	35·0	41·0	48·0	

No.	Length of post-larva in mm.								
	After moult								
	7	8	9	10	11	12	13	14	15
1	..	..	..	..	..	..	..	..	..
2	55·0	65·0	76·0	..	..	..	..	..	..
3	51·0	54·0	62·0	71·0	79·0	88·0	94·0	100·0	115·0

* Abnormal specimen which became blind after second moult.

While the growth of the first specimen is commented upon elsewhere (*cf.* Regeneration of limbs) individual variations and possibly variations in the availability of food are perhaps reflected somewhat in the growth of the other two specimens. The actual increase in length following successive moults in these specimens is as follows:

TABLE LII

H. raphidea: *Growth in length after successive post-larval moults*

No.	Growth in length in mm. after moult														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	5·0	5·0	5·0	12·0	12·0	..	..	..	..	..	..	..	..	..	..
2	4·0	4·6	5·0	5·0	8·0	4·0	9·0	10·0	11·0	..	..	..	..	..	..
3	4·0	4·5	4·5	7·0	6·0	7·0	3·0	3·0	8·5	8·5	8·0	9·0	6·0	6·0	15·0

From Table LII it is seen that except for certain anomalies in growth after the sixth moult in the second specimen and after the seventh and eighth moults in the third specimen actual growth following each moult steadily increases with age. It is the minimum after the first moult, being only about 4·0 mm., but increases to 8·5–11·0 mm. by the ninth moult. An increase of 15·0 mm. following the 16th moult is the maximum so far observed under aquarium conditions.

Though it might perhaps be presumptuous to generalise on the meagre data on the early growth of just two or three specimens of the species, in the absence of any information at all on these aspects it is tempting to consider the growth under aquarium conditions at least akin to normal and attempt an assessment of the age and possibly the number of moults undergone by specimens of given size. The available data reviewed from this aspect may be tabulated as shown in Table LIII.

TABLE LIII

H. raphidea: *Age of and number of moults undergone by specimens of particular size*

Length of specimen (mm.)	Approximate age after metamorphosis (days)	Probable number of moults undergone after metamorphosis
15·0–16·0	0– 7	Nil
19·0–21·0	5– 14	1
23–5–26·0	10– 21	2
28·0–31·0	15– 28	3
34·0–35·0	20– 36	4
41·0–42·0	27– 52	5
46·0–48·0	37– 71	6
51·0–55·0	46– 85	7
54·0–65·0	58– 99	8
62·5–76·0	71–114	9
71·0	115–135	10
79·0	136–159	11
88·0	160–181	12
94·0	182–232	13
100·0	233–282	14

Though the above tabulation is based on far too inadequate data, in the absence of any other information it serves to give an approximate idea of the age of juvenile specimens up to 100·0 mm. in total length.

That the post-larva assumes most of the distinguishing features of the adult during the first three or four moults has already been shown. The different organs of the body, however, assume their proportionate adult size only gradually (Pl. II A). The eyes are quite characteristic in *H. raphidea* but as only a very limited number of specimens were available for study and as these had to be carefully reared to the adult stage, they could not be risked for measurements of the eyes to be taken at every stage. In specimens after the first moult (second post-larval stage) the width of cornea ranges from 1·25–1·55 mm. which works out the corneal index as 2·1–2·5. A specimen, about 81·0 mm. long, after the ninth moult, has the cornea 5·40 mm. broad; the corneal index still being only 2·54.

The relative size and progressive growth of some of the important organs are clearly seen from measurements taken during the successive post-larval stages of the single specimen reared up to the fifteenth moult.

TABLE LIV

H. raphidea: *Measurements of selected parts of the body of a specimen during its first 14 post-larval stages*

Post-larval stage	Total length	Carapace			Rostrum		Telson		Rapt. Propodus	
		Median length	Anterior width	Maximum width	Length	Width	Length	Width	Length	Width
I	15·0	3·21	2·02	3·48	0·73	0·69	2·66	3·11	3·48	0·73
II	19·0	3·62	2·17	3·74	0·77	0·73	2·84	3·30	4·16	0·81
III	23·5	4·05	2·29	4·03	0·82	0·78	3·02	3·66	4·95	0·92
IV	28·0	4·85	2·75	4·49	1·01	0·85	3·57	4·58	6·23	1·10
V	35·0	6·15	3·30	6·00	1·22	1·05	4·67	5·62	7·99	1·32
VI	41·0	7·42	3·94	7·69	1·47	1·28	5·77	6·60	9·89	1·56
VII	48·0	8·24	4·21	8·61	1·37	1·42	6·41	7·51	10·90	1·74
VIII	51·0	8·79	4·49	8·79	1·37	1·51	6·78	7·79	11·45	1·92
IX	54·0	9·89	5·22	9·89	1·60	1·65	7·33	8·70	12·82	2·20
X	62·5	10·99	5·40	10·99	1·83	1·83	8·70	10·08	14·84	2·56
XI	71·0	12·82	6·23	13·28	2·11	2·20	9·89	11·36	17·04	2·93
XII	79·0	14·20	6·96	14·83	2·38	2·38	10·99	12·46	18·75	3·30
XIII	88·0	15·50	7·80	16·45	2·65	2·66	12·36	14·11	21·52	3·76
XIV	94·0	16·76	8·70	18·14	2·93	2·93	13·74	16·21	22·35	4·12

From the measurements given in Table LIV and similar data in respect of other specimens reared in the laboratory the proportionate size of the different structures is seen to be as in the Table LV.

From Tables LIV and LV it is seen that in the early post-larva the carapace and telson are relatively much bigger than in the later stages, but it is remarkable that after the second post-larval stage the proportionate size of carapace remains fairly constant. The telson steadily gets smaller, up to the seventh or eighth stage after which it maintains a constant proportionate size. The length-width ratio of telson remains remarkably constant throughout.

TABLE LV

H. raphidea: *Relative size of selected parts of the body during successive post-larval stages*

Post-larval stage	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV
TL/MLC ..	4·67–5·14	5·24	5·80	5·77	5·45–5·69	5·52	5·82	5·80	5·46–5·91	5·68–5·89	5·53	5·56	5·67	5·60
TL/MLT ..	5·63	6·69	7·78	7·84	7·28–7·49	7·10	7·48	7·52–7·80	7·09–7·36	7·18	7·17	7·18	7·12	6·84
TL/LRP ..	4·31–4·41	4·56	4·74	4·49	4·07–4·38	4·14	4·40	4·32–4·45	4·07–4·21	4·21	4·16	4·20	4·08	4·20
MLC/AWC ..	1·58	1·66	1·76	1·76	1·83–1·86	1·88	1·95	1·95	1·84–1·89	2·03	2·05	2·04	1·98	1·92
MLC/MWC ..	0·92	0·96	1·00	1·08	1·02	0·96	0·95	1·00	0·92–1·00	1·00	0·96	0·95	0·94	0·92
MLC/LRP ..	0·92	0·87	0·81	0·77	0·74–0·77	0·75	0·75	0·76	0·69–0·77	0·74	0·75	0·75	0·72	0·75
MLC/LR ..	4·40	4·70	4·94	4·80	5·04–5·93	5·04	6·01	6·41	6·18	6·00	6·07	5·98	5·85	5·72
WR/LR ..	0·94	0·94	0·95	0·84	0·86	0·87	1·03	1·10	1·00	1·00	1·04	1·00	1·00	1·00
WT/MLT ..	1·17	1·16	1·21	1·28	1·20–1·25	1·14	1·17	1·14	1·18	1·15	1·14	1·13	1·14	1·17
LRP/WRP ..	4·76	5·13	5·38	5·66	6·05–6·08	6·34	5·26	6·00	5·82–6·22	5·80	5·81	5·69	5·72	5·42

The raptorial dactylus up to the eighth stage remains proportionately smaller than in the subsequent stages; but its width which is more in the early stages, gets steadily reduced till the eighth or ninth stage after which it shows a gradual relative increase in width. The relative length of the rostrum also steadily decreases up to the ninth or tenth stage after which it shows slight increase. The width of carapace between the antero-lateral angles steadily decreases, becoming only about half the median length of the same, by the tenth stage. During the thirteenth and fourteenth stages the anterior width shows a slight increase. The length of the raptorial propodus which was 0·92 in the median length of carapace in the first stage increases to 0·77 by the fourth stage and thereafter maintains that proportion. The median length of carapace is thus only about $\frac{3}{4}$ the length of the raptorial propodus.

The above comments based on the measurements of stages of two or three specimens can only be very general, though the proportionate size of the various parts is not likely to be far different from what is arrived at from this meagre data.

Regeneration of limbs

That one or more of the appendages may be lost during moults, either due to predation by other specimens or due to some other causes, has already been mentioned (cf. *Squilla nepa*). Certain observations on this aspect made on a specimen of *H. raphidea* are detailed below:

A pelagic larva of *H. raphidea* when picked out from plankton had the uropod on one side absent. It metamorphosed in the laboratory and after the first post-larval moult the missing uropod was found developing afresh. This specimen (Specimen No. 1 in Tables XLIX and LI), 11 days, old after metamorphosis, moulted for the second time, five days after the first moult. The regenerating rudiment of the uropod was then appreciably larger than in the previous stage, though still markedly smaller than the normal uropod. Two days after the second moult its body developed a whitish opaque colour. The eyes had lost their lustre, the stalks had become whitish and the corneal portion black. The specimen, however, was active and feeding normally. On moulting for the third time on the 19th day (8 days after the second moult) the opacity of the body became quite prominent. Both the eyes were missing, having fallen off from their bases. The raptorial claws were also likewise missing, having fallen off from the ischio-meral joint. The regenerating uropod had, however, attained normal size and was fully differentiated. Within 19 days the entire appendage was, thus, fully regenerated.

The specimen continued to be active and moulted for the fourth time six days after the third moult. There was a remarkable increase in length of about 12·0 mm. following this moult. The specimen was characteristically whitish resembling an albino. Pigment on the body was extremely reduced and the few chromatophores visible were small and dot-like. In the place of the eyes a pair of minute feeler-like processes, each about 1·0 mm. long, had appeared. On the stumps of the dropped off raptorial claws two minute but complete claws had appeared.

Though blind the specimen was quite healthy and active and was feeding readily and regularly. Seven days after the fourth moult it moulted again (fifth moult, 32 days after metamorphosis). Here also the increase in length following the moult was about 12·0 mm. The opacity of the body continued; the feeler-like processes in the place of the eyes had reached almost half the length of the antennal flagellum and the regenerating raptorial claws were fully formed and normal. The specimen died before the sixth moult.

In this instance therefore the claws were lost with the third moult on the 19th day but were fully regenerated within two weeks, by the fifth moult on the 32nd day.

Remarks

Though one of the largest stomatopods known, the pelagic larva of *H. raphidea* is relatively small indicating that the size of the larva is perhaps not a dependable criterion to the size of the

adult. Its resemblance to the *Alimerichthus* type of larvae and differences from the typical *Alima*-type of larvae have been pointed out (Alikunhi, 1952). Unlike the larvae of *S. holoschista* or *S. wood-masoni* it has the antenna-labral region relatively short and stout and consequently during the final larval moult and metamorphosis into the post-larva it hardly undergoes any reduction in length. In this feature it clearly resembles the *Alimerichthus* larvae of *S. latreillei* and allied species.

As in the species earlier described in this report the early post-larva is characterised by the absence of antero-lateral spines on the carapace and the presence of terminally articulated sub-median spines on telson. Though rudimentary spines appear on the antero-lateral corners of carapace during the second or the third post-larval stage, the terminal articulation of the submedian spines of telson continues to be present even after the ninth post-larval moult. In the species of the *nepa* group the terminal articulation of the submedian spines disappears with the first post-larval moult; *i.e.*, it is present only during the first post-larval stage. In this feature also *H. raphidea* differs from *S. nepa* or *S. wood-masoni* but resembles *S. latreillei* (*Chloridella* group). The marginal denticles of telson remain acutely pointed even after the tenth or eleventh post-larval moult but in the species of the *nepa* group the denticles are acutely pointed only during the first post-larval stage, all of them becoming blunt and smooth-tipped with the first moult. In this feature also *H. raphidea* resembles *S. latreillei* and allied species. The relatively slow and poor development of the submedian carinae on the anterior abdominal segments and the relatively vaulted or convex anterior margin of the carapace resulting in the level of the rostral articulation being anterior to the level of the tip of the antero-lateral spines are also features in which *H. raphidea* resembles *S. latreillei.*

It is thus clear that the somewhat intermediate position which the pelagic larva of *H. raphidea* was found to occupy between the *Alima* and the *Alimerichthus* types of larvae is again well reflected in the characters of the post-larva, which as discussed above, perhaps shows a greater resemblance to *S. latreillei* and allied species. The conspicuously large eyes of *H. raphidea* are, however, an outstanding difference and the possession of fixed spines on the inner aspect of the raptorial propodus, as mentioned by Kemp (1913) at once places it in a separate section of the genus. The absence of pre-lateral denticles on telson is another feature in which *H. raphidea* differs from species of both *Chloridella* and the *nepa* groups.

The frequency of post-larval moults appears to be somewhat quicker than in *S. nepa* and *S. holoschista*, and though the duration of the successive post-larval stages gradually increases with age as in the latter species, it is interesting to observe that while a specimen of *S. nepa* took 215 days after metamorphosis to undergo the 12th moult, a specimen of *H. raphidea*, reared under similar conditions, required only 157 days to undergo a similar number of moults. Likewise, while the duration of the 8th–10th stages in *S. nepa* has been about 28–29 days each, in *H. raphidea* the duration of corresponding stages was only 13–15 days each. The size of the post-larva during the early stages is almost the same as in *S. nepa* but in the later stages *S. nepa* appears to grow quicker than *H. raphidea*. This, however, could not be confirmed as only a single specimen of the latter species has been reared to over 10 post-larval stages.

Measurements and the proportions of the various parts of the body of stages reared in the laboratory were compared with similar measurements of adult specimens collected from elsewhere It is seen from this that the different structures attain adult proportions by the 10th–11th stage.

Sexual maturity is not attained even after the 15th moult after metamorphosis. Other specimens upto 137·0 mm. in length were also found immature in March.

That blinded larvae also undergo metamorphosis and grow in the laboratory have been mentioned (Alikunhi, 1950). It is also well known that pigmentation in crustacea is remarkably arrested when the eyes are lost. A specimen of *H. raphidea* which was growing normally became blind after the third moult. The growth in length of this specimen during the two subsequent moults was remarkably higher than in normal specimens. Though the blind specimen would

naturally be at a disadvantage in food procurement and should therefore grow less rapidly as compared to the normal specimens the very much enhanced growth following the loss of eyes would seem to indicate that some growth inhibiting centre was also probably lost or disorganised with the loss of the eyes and the associated pigment regulating centres.

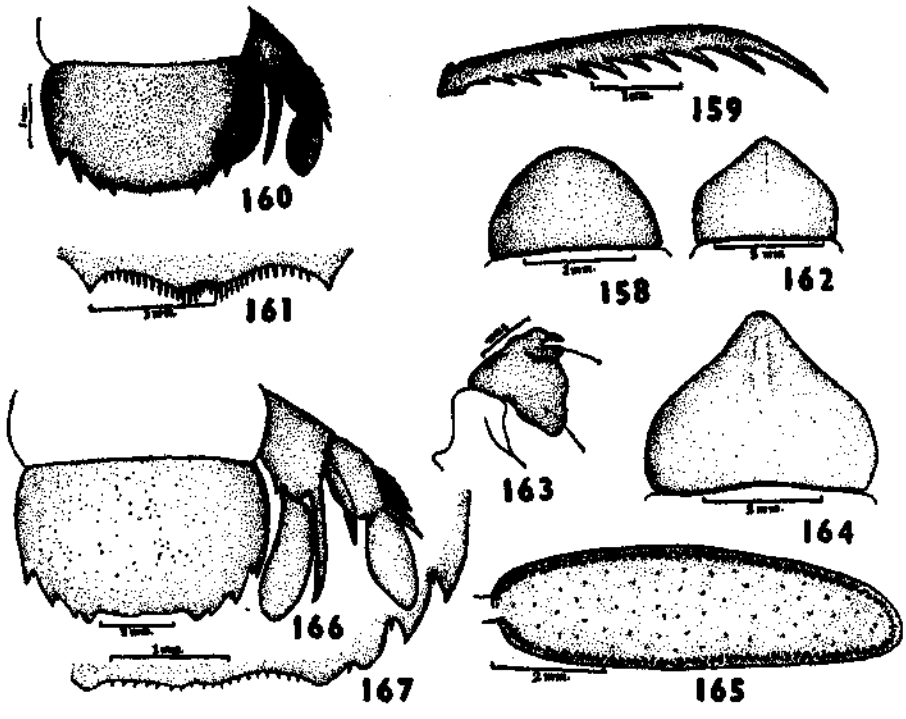
In a recent contribution Tiwari and Biswas (1952) have dealt with *H. raphidea* and have shown that the specimens hitherto ascribed to this species are actually a mixture of two distinct species one of which they have designated *H. raphidea* itself and for the other the name *H. harpax* has been revived. According to the diagnostic characters of the two species given by these authors the present material reared in the laboratory, should really belong to *H. harpax*.

Lysiosquilla maculata (Fabricius) (Figs. 158–167)

Several larvae successfully metamorphosed in the laboratory and were thereafter reared to distinguishable stages.

Post-larval stage I

One of the largest stomatopods in the Madras waters, the early post-larvae, soon after metamorphosis, are opaque-white, with the least indication of the characteristic colour pattern of the adult. The rostrum is almost semi-circular (Fig. 158). The raptorial dactylus has 11–12 teeth



FIGS. 158–167. *Lysiosquilla maculata*. Figs. 158–161. First post-larval stage: Fig. 158. Rostrum, dorsal view. Fig. 159. Raptorial dactylus. Fig. 160. Telson and right uropod, dorsal view. Fig. 161. Sub-median area of telson, magnified. Fig. 162. Fourth post-larval stage: Rostrum, dorsal view. Fig. 163. Fifth post-larval stage: Carpus of the raptorial limb. Figs. 164 and 165. Seventh post-larval stage: Fig. 164. Rostrum, dorsal view. Fig. 165. Antennal scale showing the marginal row of chromatophores. Figs. 166 and 167. Third post-larval stage: Fig. 166. Telson and right uropod, dorsal view. Fig. 167. Marginal spines and sub-median area of telson, magnified.

including the terminal one. The outer margin of the dactylus is nearly straight and has a small inconspicuous basal tubercle (Fig. 159). The shorter ramus of the sixth thoracic appendage is more or less oval. The abdomen is flat and depressed, with the postero-lateral corners of the first five pointed. The telson is broad and flat, considerably broader than long and has the three pairs of marginal spines short, stout and pointed. The submedian spines are not movable (Fig. 160). The sub-median area which is notched at the middle is rather narrow occupying only about $\frac{1}{5}$th the total width of telson. There are 15–18 pairs of pointed denticles between the two submedian spines (Fig. 161). Excepting one or two pairs at the median notch the denticles near the middle are the longest. Between the submedian and intermediate spines there are three denticles, the second one of which is much shorter than the other two and may or may not have a pointed tip. There is a lateral denticle at the base of the lateral spine also. The uropod is much longer than in the pelagic larva and has nine movable spines on the basal segment of the exopod and a small spine ventrally near the inner basal aspect of the articulation of the uropod. The inner spine of the ventral prolongation is distinctly longer than the outer one.

Pigment is gradually developed. On the second day after metamorphosis chromatophores are arranged in certain definite regions, though not conspicuously. They are distributed at regular intervals on the antennules which consequently present a faint, transversely banded appearance. The eye stalks are largely brownish in colour. On the carapace chromatophores are arranged in three distinct transverse bands. On the last three thoracic and on all the abdominal segments a pair of light brown transverse bands could be seen, the anterior band in each segment being rather inconspicuous. On the distal third of telson there are 3 distinct, triangular, light-brown patches in a row. By the fourth or the fifth day after metamorphosis the colour patterns become prominent by the formation of more chromatophores. The anterior band in each of the abdominal segments has become broader and more conspicuous than the posterior one which, situated closely along the hind border of the segment, is narrow but darker than the other.

Post-larval stage II.—Pigment has become brighter. The antennal scales have a row of dark chromatophores all round the margin; while, none is present in the middle. The small outer basal lobe on the raptorial dactylus has disappeared. Postero-lateral corners of the first four abdominal segments are pointed. The lateral and intermediate spines of telson have become longer and stouter but the submedians are more inconspicuous than in the previous stage. The second intermediate denticle has become stout and blunt. The submedian denticles are rudimentary and smaller than in the previous stage.

Post-larval stage III

The rostrum is short and somewhat heart-shaped, with a faint median ridge near the tip. The marginal row of chromatophores on the antennal scales has become prominent. The spine on the dorsal carina of carpus of the raptorial limb is well developed though short. The marginal spines (lateral and intermediate) of telson may be blunt or subacutely pointed (Fig. 166). The submedian spine is a smooth prominence only. The submedian denticles are absent or when present, rudimentary and small (Fig. 167).

Post-larval stage IV

The median ridge near the blunt tip of rostrum is better developed than in the previous stage (Fig. 162). The submedian denticles of telson have disappeared.

Subsequent stages

With the next moult (stage V) the dorsal spine on the carpus of the raptorial limb becomes large, stout, pointed and curved (Fig. 163). The submedian spine may be just a smooth elevation or a small blunt process. A smooth median dorsal ridge appears on the distal half of the telson. The intermediate and lateral denticles also disappear. The tip of rostrum remains smooth though

the anterior median ridge becomes fairly prominent (Fig. 164). The marginal row of chromatophores on the antennal scale is quite characteristic (Fig. 165). With the sixth-seventh moult the specimen shows all the adult characters.

Frequency of post-larval moults and growth

Though several larvae metamorphosed in the laboratory most of them died after the third or fourth moult and only one specimen survived up to the seventh moult. Available details of the periodicity of moulting in respect of five specimens are given in Table LVI.

TABLE LVI

Lysiosquilla maculata: *Frequency of early post-larval* moults

Specimen No.	Age in days after metamorphosis at the time of moult						
	1	2	3	4	5	6	7
1	6	13	21	30	39	52	81
2	10	22	34	45	..	..	..
3	10	19	29	..	..	..	..
4	6	14	22	..	...	...	...
5	8	18	30	..	...	...	...

The size attained by these specimens after the respective moults is given in Table LVII.

TABLE LVII

Lysiosquilla maculata: *Size attained after successive early post-larval moults*

Specimen No.	Length in mm.							
	Before moult	After moult						
		1	2	3	4	5	6	7
1	23·0	28·0	34·0	44·0	54·0	62·0	70·0	77·0
2	22·0	26·0	33·0	40·0	48·0	..	..	..
3	23·0	29·0	35·0	42·0	..	..	..	..
4	22·0	26·0	32·0	40·5	..	..	..	..
5	23·0	28·0	35·0	43·0	..	..	..	..

From Tables LVI and LVII the duration of and growth during successive post-larval stages are seen as in Table LVIII.

The duration of the first post-larval stage is shorter than the succeeding stages. From the second to the fifth stage the duration of each is about 10 days. It increases to about two weeks during the sixth stage and to about a month during the seventh. Increase in length following the first moult is appreciably less than that following subsequent moults. From the third to the seventh moult the growth is practically the same, ranging from 7·0-9·0 mm.

TABLE LVIII

Lysiosquilla maculata: *Duration of and growth during successive early post-larval stages*

Post-larval stage	Duration in days		Growth in mm.	
	Range	Average	Range	Average
I	6–10	8	..	..
II	7–12	9	3·5– 6·0	4·7
III	8–12	10	6·0– 7·0	6·4
IV	9–11	10	7·0–10·0	8·1
V	..	9	8·0–10·0	9·0
VI	..	13	..	8·0
VII	..	29	..	8·0
VIII	..	..	..	7·0

When the age and size data relating to the reared material are considered together some idea of the age of and moults undergone by specimens of known size becomes available as in Table LIX.

TABLE LIX

Lysiosquilla maculata: *Age of and number of moults undergone by specimens of given size*

Length of specimen (mm.)	Approximate age after metamorphosis (days)	Probable number of moults undergone after meta-morphosis
22·0–23·0	1–10	Nil
26·0–29·0	7–22	1
32·0–35·0	13–34	2
40·0–44·0	21–45	3
48·0–54·0	30–39	4
62·0	39–52	5
70·0	52–81	6

As the actual and proportionate size of the various parts of the body differ considerably during the early post-larval stages measurements of selected parts of the body of specimens reared in the laboratory are given in Table LX to facilitate identification of post-larval and juvenile specimens of this common species which is closely related to *L. sulcirostris* and *L. glabriuscula.*

With growth in length the different parts of the body also grow and gradually assume adult proportions which will thus differ from those in the earlier stages. The proportionate size of certain parts of the body during successive post-larval stages, as seen from the Table LX, is given in Table LXI.

TABLE LX

Lysiosquilla maculata: *Measurements of selected parts of the body of post-larval specimens of different size*

(All measurements in millimetres)

Total length	Carapace			Rostrum		Telson		Submedian area	Raptorial propodus		Corneal index
	Median length	Anterior width	Maximum width	Length	Width	Length	Width		Length	Width	
22·0	..	..	..	..	..	3·36	4·72	1·82	4·63	0·70	..
21·0	4·50	..	..	..	..	3·00	4·46	...	4·73	0·79	..
22·0	4·20	..	..	1·00	1·54	..	..	..	..	..	2·73
24·0	4·72	..	..	..	..	3·10	5·00	1·73	5·20	0·75	2·60
32·0	6·00	..	..	..	..	..	..	..	7·54	1·54	2·72
34·0	6·27	..	..	1·36	2·10	4·00	6·45	2·10	7·70	1·63	..
39·0	7·00	..	..	..	..	..	..	..	9·50	1·90	2·56
38·5	7·00	..	..	1·63	3·10	..	..	..	10·00	1·80	2·33
38·5	..	..	..	..	..	4·36	7·27	2·61	10·10	1·82	2·66
44·0	7·45	7·20	9·00	1·63	2·54	5·20	8·10	2·45	9·60	2·20	..
54·0	9·50	10·40	12·70	2·20	3·00	6·00	10·20	3·27	12·30	2·82	..
70·0	11·30	9·50	14·00	2·20	3·20	8·40	12·30	4·20	14·30	3·40	..
77·0	13·30	10·60	15·50	2·89	3·90	10·00	14·50	4·50	17·10	3·60	3·50

TABLE LXI

Lysiosquilla maculata: *Proportionate size of selected darts of the body of post-larval specimens of different size*

Post-larval stages	.. I	II	III	IV	V	VI	VII	VIII
Total length (mm.)	.. 22·0	24·0	34·0	38·5	44·0	54·0	70·0	77·0
TL/MLC	4·6	5·1	5·4	5·5	5·9	5·7	6·2	5·8
TL/LR	22·0	..	25·0	..	27·0	24·5	31·8	26·6
TL/MLT	6·54	7·74	8·50	8·80	8·46	9·00	8·33	7·70
TL/LRP	4·75	4·61	4·41	3·81	4·58	4·39	4·89	4·50
WR/LR	1.54	..	1.54	..	1·55	1.36	1.45	1.35
WT/MLT	1·40	1·61	1·61	1·66	1·55	1·70	1·46	1·45
WT/Submedian area	0·38	0·34	0·32	0·35	0·30	0·32	0·34	0·31
LRP/WRP	6·60	9·93	4·72	5·54	4·36	4·36	4·80	4·75

It is thus seen that the carapace which is proportionately very large in the early post-larva is very much smaller in the 77·0 mm. long specimen. From measurements of some adult specimens given by Kemp (1913, p. 114) the adult proportion of carapace is seen as follows:

Total length in mm.	60·0	80·0	95·0	100·0	107·0	112·0	133·0	136·0	144·0	182·0	186·0	208·0	283·0
Length of carapace in total length	4·6	5·5	5·4	5·4	5·6	5·4	5·9	5·6	5·3	5·6	6·2	5·3	5·3

The carapace in the 60·0 mm. long specimen appears to be somewhat larger in comparison with the present series; the largest of which has the carapace of almost adult proportions. The breadth of telson steadily decreases up to the 54·0 mm. stage, after which there is appreciable increase in length also. The submedian area of telson also steadily decreases in relation to the total width of telson. The raptorial propodus which was nearly 1/7th the total length in the early post-larva grows to almost a fifth of the total length. As is generally the case in stomatopods the relative size of the eyes diminishes with growth (Kemp, 1913, p. 114). The corneal index starting from about 2·73 in the first post-larval stage, is 3·4 in the young adult, 77·0 mm. long. In fully grown specimens, the corneal index varies from 4·4 to 4·9 (Kemp, 1913).

Remarks

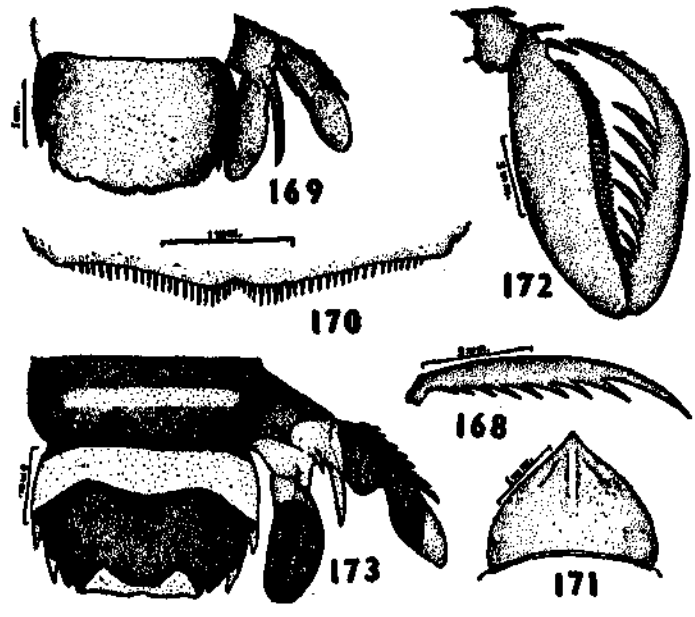
One of the largest and perhaps the most conspicuous post-larval stomatopod metamorphosed in the laboratory, it resembles the adult closely even towards the end of the first post-larval stage so that identification is not very difficult. Compared to *A. multifasciata* and *A. tigrina* (*vide infra*) pigment is developed rather early in *L. maculata*; in the former species even in the third or fourth post-larval stage the young one having only just an indication of the adult pigment patterns. In size, appearance and formation of pigment it closely resembles the corresponding stage or stages of *L. sulcirostris* (*vide infra*) but is easily distinguished from it by the characteristically narrow submedian area of telson. The various features—larval, post-larval and adult, that distinguish *L. maculata* from *L. sulcirostris* have been detailed and discussed under the latter species.

L. maculata is widely distributed in the Indo-Pacific region and has been recorded from the east and the west coasts of India. In the Atlantic this species has been recorded from Antigua, West Indies (Stebbing, 1902) and from Florida (Boone, 1930). Kemp (1913) has stated that the West Indies specimens differ from the Indo-Pacific examples in having the fifth pleon segment denticulate along the hind margin, the sixth denticulate in an arched proximal band and round the distal margin and the telson with three spines on each side and the truncate portion cut into five square teeth on one side and six on the other side of a small median emargination. Boone's (*op. cit.*) specimens from Florida also appear identical with the West Indian specimens, having the characteristic spinulation on the fifth and sixth abdominal segments. The specimen figured by Boone has the rostrum more acutely pointed than in *L. maculata* and the basal segment of the uropod is also shown as having a row of three spines. In these features, particularly in the spinulation of the fifth and sixth abdominal segments and telson, the Atlantic specimens markedly differ from the typical Indo-Pacific examples and should, in all probability, be separated from them as a distinct species. Boone further states that the younger West Indian specimens of *L. maculata* he examined had only 5–8 teeth on the dactylus of the raptorial claw and as the principal distinguishing character between *L. maculata* and *L. glabriuscula* is the different dentition of the retrochela (9–10 in *L. maculata* and 5–8 in *L. glabriuscula*) it becomes necessary to unite the two species under the older name *L. maculata* (Boone, *op. cit.*, p. 31). The present study has, however, shown that not only the full number of dactylar teeth are seen through the transparent shell in the final pelagic larva, but in the first post-larval stage itself these teeth are in most cases fully developed. Such wide variations as 5–7 or 8 in the young specimens and 9–10 in the adult cannot normally be expected in a species and the present study in respect of several species of *Lysiosquilla* and *Squilla* does not

support such a presumption. In the Indo-Pacific specimens of *L. maculata* such variations in the number of teeth on the dactylus do not occur in young individuals. In view of these the suggestion to consider *L. glabriuscula* as a synonym of *L. maculata* cannot be accepted unless more convincing reasons are forthcoming.

Lysiosquilla sulcirostris (Kemp) (Figs. 168–173)

A single larva obtained from plankton collected on 17-9-1942 metamorphosed into the post-larva on the 17th–18th night in the laboratory and was subsequently reared for 80 days. The following description is based on this material.



FIGS. 168–173. *Lysiosquilla sulcirostris.* Figs. 168–170. First post-larval stage: Fig. 168. Raptorial dactylus. Fig. 169. Telson and uropod, dorsal view. Fig. 170. Sub-median spines and denticles of telson, magnified. Figs. 171–173. Seventh post-larval stage: Fig. 171. Rostrum, dorsal view. Fig. 172. The three terminal segments of the raptorial limb. Fig. 173. The sixth abdominal segment, telson and right uropod, dorsal view.

Post-larval Stage I

The young post-larva, soon after metamorphosis, is pale white in colour, 21·5 mm. long and comparatively stout in appearance. The eyes are conspicuous, the rostrum is conical and the raptorial dactylus is long and slender and has 9 teeth including the terminal one (Fig. 168). A small tubercle-like prominence is seen at the base of the dactylus externally. Telson is very much broader than long and has only two pairs of marginal spines, the lateral and intermediate. The submedian spines are totally wanting (Fig. 169). The submedian area is, however, characteristically wide, occupying more than half the width of telson. There is a shallow median notch in the submedian area which is provided with 26 pairs of denticles. From the sides towards the median notch the denticles progressively increase in size, though a few of the very median ones are small (Fig. 170). There are one lateral and two intermediate denticles on either side. The surface of the telson is smooth and devoid of spines. The exopod of the uropod has eight movable spines on the outer aspect of the basal segment, at the base of which there is another spine. The endopod is large, oval and flat. The outer spine of the ventral prolongation is smaller than the inner.

Twenty-four hours after metamorphosis numerous chromatophores appear on the body and though no characteristic pigment pattern is laid yet, inconspicuous, light-brown pigment bands could be seen on all the abdominal segments. On the third day after metamorphosis the colouration becomes characteristic. The eye stalks are brownish. The antennules have a brown banded appearance. The carapace has three, transverse, brown bands, one at the anterior end, one across the middle and the third across the hind end. The pigment bands on the carapace extend on to the raptorial limb on either side. Each of the last three thoracic segments has a transverse band across the hind margin. Each of the abdominal segments has a pair of brown bands at either margin. The distal half of the telson has a transverse band which is insipiently cut up into three patches. The basal segment of the uropod, the endopod and the distal portion of the exopodite are also brownish in colour.

By the fifth day after metamorphosis the above pigment pattern becomes well defined and the colour darker. The third band on the carapace is particularly dark and conspicuous at the sides. Pigment on the telson is darker. The lighter coloured areas have a yellowish tinge and at a casual glance the colour scheme is one of alternating transverse bands of dark-brown or dark and yellow.

Post-larval stage II

With the moult the colour has become brighter. In the abdominal segments the anterior band in each is broader than the posterior one. The antennules, including the flagellum, have a distinct, transversely banded appearance of brown and white. Yellow tinge predominates on the antennal scales which have a few large stellate chromatophores appearing as minute dark dots. The basal segments of the walking legs and the tip of the terminal segment of the exopod of the uropod are coloured light yellow.

In the telson in the place of the submedian spines a minute denticle has appeared. The lateral and intermediate spines have become stouter. The submedian denticles are unchanged. The tubercle-like prominence seen on the outer basal aspect of the raptorial dactylus has disappeared.

During subsequent growth, up to the seventh post-larval stage when the specimen (a female) died, very few structural changes take place. The rostrum is conical with the tip ending in a sub-acute point (Fig. 171). It is broader than long and is terminally raised into a blunt ridge from the tip backwards, aggravated by the deep grooves running almost parallel to the sides at the anterior third. The eyes are prominent; the cornea is just over 3·00 mm. in width and the corneal index is 3·24. The raptorial carpus has a dorsal carina ending in a spine (Fig. 172). The dactylus has 9 teeth, the terminal one of which is much longer than the penultimate. The outer margin of the dactylus is weakly convex. Telson is broader than long and has the lateral and intermediate marginal spines stout and pointed (Fig. 173). Submedian spines are wanting. The wide submedian space is provided with 40-42 pointed denticles. There are one lateral and two intermediate denticles, one of which is large and blunt.

The pigment pattern is the same as in the earlier stages. The fifth thoracic segment has only a transverse streak of pigment; while, the sixth is almost fully covered with dark brown pigment. The remaining segments up to the fifth abdominal have two transverse bands each; the anterior one almost double the width of the posterior. The sixth abdominal segment has a border of brown pigment on all the four sides, leaving a central strip of yellow (Fig. 173). The distal two-thirds of the telson excepting the tip, the basal portion of the uropod, the distal half of the basal segment of the exopod including the movable spines, the proximal two-thirds of the terminal segment of the same and the endopod are pigmented dark brown.

Moulting and Growth

The periodicity of moulting and the size attained after each moult are given in Table LXII.

TABLE LXII

Lysiosquilla sulcirostris: *Periodicity of early post-larval moults and size attained after each*

	Before moult	After moult						
		1	2	3	4	5	6	7
Age in days		6·5	16·5	31·5	42·5	51·5	64·0	80·0
Total length (mm.) ..	21·5	26·0	29·0	35·0	41·5	48·0	54·0	63·0

The duration of the successive post-larval stages and the growth in length during each, as seen from Table LXII, are furnished in Table LXIII.

TABLE LXIII

Lysiosquilla sulcirostris: *Duration of and growth during successive post-larval stages*

	Post-larval stages							
	I	II	III	IV	V	VI	VII	VIII
Duration in days ..	6·5	10	15	11	9	13	16	?
Growth in length (mm.) ..		4·5	3·0	6·0	6·5	6·5	6·0	9·0

The somewhat longer duration of the second and the third post-larval stages could in all probability be due to fluctuations in feeding, as even the first moult would be considerably delayed than normal if the post-larva is not regularly fed. The rate of growth steadily increases and is fairly rapid, though perhaps lower than in *L. maculata*.

Though there has been only a single specimen available for study, when the age, size and moulting data are considered together some useful comparison with the closely related *L. maculata* can be made.

TABLE LXIV

Lysiosquilla sulcirostris: *Age of and number of moults undergone by specimens of known size*

Length of specimen (mm.)	Approximate age after metamorphosis (days)	Probable number of moults undergone after metamorphosis
21·5	1 – 6	Nil
26·0	6·5–16	1
29·0	16·5–31	2
35·0	31·5–42	3
41·5	42·5–51	4
48·0	51·5–64	5
54·0	64·0–80	6
63·0	Over 80	7

A comparison of the data given in Table LXIV with those given in Table LVI for *L. maculata* shows that at least up to the fifth moult the frequency of moulting in the latter is perhaps a little more rapid than in *L. sulciostris*. Though the early post-larva is of almost identical size in both the species early post-larval growth appears to be more rapid in *L. maculata* than in *L. sulcirostris* (Pl. III). For purposes of comparison with *L. maculata* measurements of various parts of the body made from a few of the post-larval moults which could be retrieved are also given below:

TABLE LXV

Lysiosquilla sulcirostris: *Measurements of selected parts of the body of post-larvae of different stages*

Total length	..	21·5	26·0	48·0	63·0
Carapace:					
Median length	..	..	..	..	10·0
Anterior width	..	..	..	..	10·0
Maximum width	..	..	..	..	11·0
Rostrum:					
Length	..	..	..	..	1·67
Width	..	..	..	..	2·33
Telson					
Length	..	3·30	3·44	..	6·80
Width	..	4·42	4·81	..	9·5
Raptorial propodus:					
Length	..	4·77	..	8·17	11·0
Width	..	1·00	..	2·30	2·82
Sub-median area of telson:					
Width	..	3·00	2·85	..	4·70

Remarks

For a specimen of *Lysiosquilla* (116 mm. long, from the Andaman Islands) close to *L. maculata* but differing from it in the structure of the rostrum, the raptorial dactylus and the nature of the sixth abdominal segment Kemp (1913) created a new variety *sulcirostris* under the speices *maculata*, remarking that *L. sulcirostris* is perhaps specifically distinct from '*L. maculata*, but its resemblance to the latter form is so great that I hesitate to adopt such a course on the evidence of a single specimen.' Monod (1925) and Bigelow (1931) suggested that this variety probably represents only an abnormal individual of the type form of *L. maculata*. Chopra (1934) found the characters of the variety given by Kemp variable but the rostrum in the *forma typica* and the variety always distinct. According to him the association of the *sulcirostris* type of rostrum with the smaller number of teeth on the raptorial dactylus is noteworthy and sufficient to distinguish between the two. Komai (1938) recorded the var. *sulcirostris* from Kii waters in Japan. Serene (1952) also considers the var. *sulcirostris* distinct from the type form of *L. maculata*.

Owing to certain important differences from *L. maculata* in the characters of the carapace and the telson of the final pelagic larvae the present author (Alikunhi, 1952) raised the variety to specific rank under the same name—*sulcirostris*. These main differences between the advanced pelagic larvae of the two forms are given in Table LXVI.

These differences between the pelagic larvae which at a casual glance resemble each other so strikingly, are far too great for mere varietal significance. Careful study of grown-up adult

TABLE LXVI

Distinguishing characters of the larvae of Lysiosquilla maculata *and* L. sulcirostris

Distinguishing features	Final pelagic larvae of	
	L. maculata	*L. sulcirostris*
Rostrum	Short, stout	Longer, more slender
Postero-lateral spines of carapace	Very short, with a stout spinule at the base	Appreciably longer, with a slender spinule at the base
Antero-lateral spines of carapace	Absent	Present, short
Dorsal spine of carapace	Present, often blunt	Wanting
Carapace: Lateral downward extension	Ends in a stout spine	Ordinarily not spinous
Marginal spines of telson	Laterals most conspicuous; then the submedians	Submedians most conspicuous; then the intermediates
Submedian space of telson	About 2/5 the width of telson; denticles 14–18 pairs only	A little under 2/3 the width of telson; denticles 26–27 pairs

specimens confirms the above view. A comparison of two specimens, one of each species and both of the same age after metamorphosis, is instructive in this connection and tends to confirm that *L. sulcirostris* is specifically distinct from *L. maculata*.

TABLE LXVII

Distinguishing features of two comparable specimens of Lysiosquilla sulcirostris *and* Lysiosquilla maculata

Salient features	*L. maculata*	*L. sulcirostris*
Age after metamorphosis	81 days	80 days
No. of moults undergone	6 (7)	6
Total length	77·0 mm.	63·0 mm.
General appearance	Stoutly built	Long and slender
Colour pattern	Dull black bands, alternating with light yellow ones which in some has an ashy tinge. 6th abdominal segment completely dark dorsally, only proximal half of the terminal segment of exopod of uropod pigmented	Bright, dark-brown bands alternating with yellowish-pink ones; 6th abdominal segment with dark pigment on the four sides only, leaving the central region yellowish; distal third of the terminal segment of the exopod of uropod without pigment
Antennal scale	Ordinarily with chromatophores all round giving the appearance of a dark border. Very few chromatophores on the body of the scale	No such dark border. Several dark chromatophores on the body of the scale
Rostrum	With blunt tip	Tip more pointed
Raptorial claw	10–12 teeth; carpus with a dorsal carina ending in a conspicuous curved spine	Only 9 teeth: dorsal carina of carpus ending in a short spine
Telson	Post-larva: 3 pairs of marginal spines present. Submedian area narrow; denticles 15–18 pairs	Post-larva: Submedian spines absent; submedian area wide; denticles 22–27 pairs
	Adult: Submedian spines stout, stumpy, smooth-tipped; submedian area narrow; no denticles	Adult: Submedian spines absent. Submedian area wide; 20–21 pairs of denticles present
Corneal index	3·34	3·24

Besides distinguishing larval characters, Table LXVI, as also the descriptive account of the different post-larval stages of the two forms, clearly indicate that *L. sulcirostris* is specifically quite distinct from *L. maculata* with which, however, it closely resembles and is undoubtedly closely related.

In Madras waters the species appears to be rather very rare if the relative abundance of planktonic larvae gives any idea of the abundance of the adult in the locality (Alikunhi, 1952).

Acanthosquilla multifasciata Wood-Mason (Figs. 174–185)

A single larva, in the final pelagic stage, obtained alive on 23–11–1942 metamorphosed in the laboratory on the 23–24th night into a post-larva which was then reared in aquaria for 202 days during which period it moulted 13 times. The following account is based on the various stages of this specimen.

Post-larval stage I

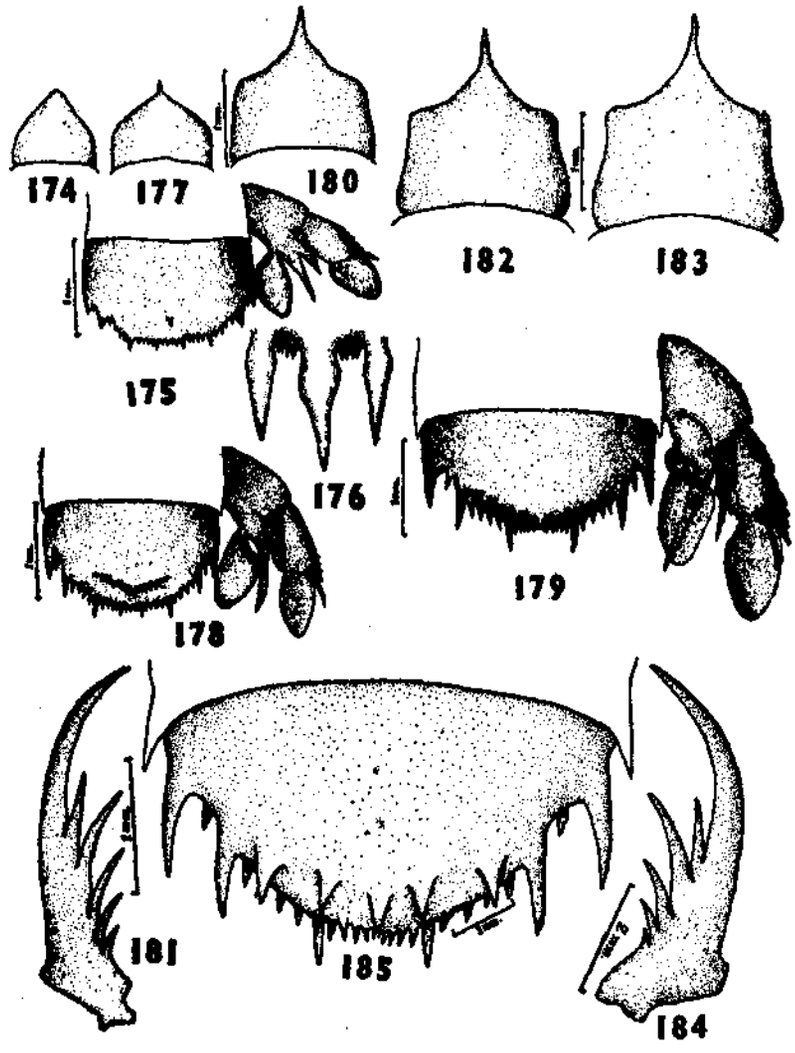
The young post-larva is a small, active semi-transparent stomatopod, with rather prominent eyes. Pigment is almost absent on the body. The rostrum which is conical and broader than long, has a smooth tip (Fig. 174). The raptorial dactylus has six teeth on the right limb and five on the left. The external proximal part of the dactylus is cut up into two lobes which are unequal even at this stage. The shorter ramus of the seventh thoracic limb is roughly oblong or rounded. The postero-lateral corners of the sixth abdominal segment are sub-acutely pointed. The telson is broader than long and has a median dorsal spine distally (Fig. 175). The marginal spines are prominent though short. The submedian spines are not movably articulated. There are one lateral and four intermediate denticles on each side. The second and fourth intermediate denticles are smaller than the other two. The submedian space which occupies more than one-third the total width of telson is marked into three sections as in the pelagic larva and the denticles number 4–1–4–1–4; *i.e.*, the fifth denticle from either side is longer than the rest. The space between adjacent denticles is also finely serrated with 3–4 minute spinous processes (Fig. 176). The uropod is much longer and more conspicuous than in the larva and has six movable spines on the basal segment of the exopod. The endopod is roughly oval. The ventral prolongation has the inner spine definitely longer than the outer.

Post-larval stage II

After the first moult the rostrum develops a slender terminal spine (Fig. 177), but it is still broader than long. The postero-lateral corners of the sixth abdominal segment remains sub-acutely pointed. On either side of the median dorsal spine of telson rudiments of two more have appeared (Fig. 178). The marginal spines of telson have become longer than in the earlier stage. The submedian spines are long and basally articulated or movable. The submedian space has become shorter, but the number and arrangement of denticles remains unchanged, though the marginal serrations in between adjacent denticles have disappeared. In the raptorial dactylus the penultimate tooth is smaller than the ante-penultimate.

Chromatophores have appeared on the body, laying the foundation of the characteristic adult pattern of pigment. On the tenth day after metamorphosis the general body colour of the post-larva still remained pale or yellowish. The eye stalks are brown. On the carapace chromatophores are crowded to form three diffuse transverse bands, the first two of which being very inconspicuous. The third band at the hind border of the carapace is broad and patch-like laterally and narrow and inconspicuous medially. The last three thoracic segments have each a transverse dark band. The abdominal segments have a pair of transverse bands each—a distinct dark band at the hind border of the segment and a thin dark-brown streak in front forming the second band. The telson has a pair of transverse bands which are cut up into four patches, the anterior two farther

apart than the hind pair. The merus of the raptorial claw and the tip of the uropod are also brown in colour.



FIGS. 174–185. *Acanthosquilla multifasciata*. Figs. 174–176. First post-larval stage: Fig. 174. Rostrum, dorsal view. Fig. 175. Telson and uropod, dorsal view. Fig. 176. Three sub-median denticles, highly magnified to show the serrations in between. Figs. 177 and 178. Second post-larval stage: Fig. 177. Rostrum, dorsal view. Fig. 178. Telson and uropod, dorsal view. Fig. 179. Fourth post-larval stage: Telson and uropod, dorsal view. Figs. 180 and 181. Fifth post-larval stage: Fig. 180. Rostrum, dorsal view. Fig. 181. Raptorial dactylus. Fig. 182. Seventh post-larval stage: Rostrum, dorsal view. Fig. 183. Eighth post-larval stage: Rostrum, dorsal view. Figs. 184 and 185. Thirteenth post-larval stage: Fig. 184. Raptorial dactylus. Fig. 185. Telson, dorsal view.

Post-larval stage III

The pigment pattern as a whole is better defined than in stage II. The terminal spine of rostrum is shorter. In the telson the dorsal row of spines is fully formed. The fifth submedian

denticle of telson is not so conspicuous as in the previous stage; while the seventh or the median pair is small and slender.

Post-larval stage IV

The shape of rostrum approximates more to that of the adult. Postero-lateral corners of the sixth abdominal segment are produced into short though acute spines (Fig. 179). Telson is twice as broad as long and but for the spines is semi-circular in shape. All the five dorsal spines are equal in size. The four intermediate denticles are also of uniform size. The submedian space is only about one-fourth the width of telson and is not divided into sections. Only six pairs of submedian denticles are present and these gradually decrease in size from the outermost to the median pair.

Post-larval stage V

The rostrum is now almost as broad as long but the antero-lateral corners are smooth (Fig. 180). The teeth on the raptorial dactylus have assumed the adult condition (Fig. 181). The sixth pair of submedian denticles are very small. The pigment pattern has become well defined and resembles that of the adult.

With subsequent moults the specimen steadily grows in length. The antero-lateral angulation of the rostrum is ony gradually assumed (Figs. 182 and 183). The adult condition of the telson and the raptorial dactylus as seen after the 12th post-larval moult is shown in Figs. 184 and 185.

The specimen, a male, after the 13th post-larval moult, has the typical pigment pattern of the adult specimen described by Kemp (1915) from the Philippines. The anterior and middle portions of the carapace are lightly pigmented. At the hind border of carapace there is a transverse dark band which is broad and patch-like at the sides, but narrower and less dark at the middle. On each of the exposed thoracic segments there is a single transverse band, leaving a narrow posterior strip and a broader anterior strip of the tergum pigmented light yellow. Each of the first five abdominal segments has a pair of transverse dark bands, the anterior thin, narrow and brownish not extending to the sides, and the posterior along the hind margin of the tergum broader and darker than the anterior and tending to become patch-like at the sides. The sixth abdominal segment and the telson have a single band each, that on the latter being semi-circular and reaching upto the base of the dorsal spine. The basal segment of the exopod and the endoped of the uropod, are also pigmented dark or dark-brown.

Growth and moults

The growth of the post-larva under laboratary conditions and the frequency of moulting during the 202 days period of rearing are given in Table LXVIII.

TABLE LXVIII

A. multifasciata: *Periodicity of early post-larval moults and size attained after successive moults*

	Before moult	After moult												
		1	2	3	4	5	6	7	8	9	10	11	12	13
Age in days	..	5	13	21	29	43	56	73	90	106	123	147	168	198
Total length (mm.)	9·0	11·0	13·0	17·0	20·0	23·0	27·0	30·5	33·5	37·0	42·0	45·0	47·0	49·0

Duration of the successive post-larval stages and the growth in length following each moult as seen from Table LXVIII are given in Table LXIX.

TABLE LXIX

A. multifasciata: *Duration of and-growth during successive early post-larval stages*

	Post-larval stage												
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII
Duration in days ..	5	8	8	8	14	13	17	17	16	17	24	21	30
Growth in length (mm.)		2·0	2·0	4·0	3·0	3·0	4·0	3·5	3·0	3·5	5·0	3·0	2·0

Excluding the rostrum the length of the final pelagic larva of the species is only about 10 mm. (Alikunhi, 1952). During the final larval moult and metamorphosis into the post-larva there is thus a slight reduction in length. Thereafter, following successive moults growth is steady though slow. After the first three stages the growth increases to 3·0–5·0 mm., but shows a tendency to come down again after the 12th moult when the specimen has attained adult size.

Though only a single specimen could be reared the available data relating to its size, growth and moults are considered together in Table LXX so that besides getting some idea of the age of specimens of particular size, the data could be compared with those for related species also.

TABLE LXX

A. multifasciata: *Age of and number of moults undergone by specimens of known size*

Length of specimen (mm.)	Approximate age after metamorphosis (days)	Probable number of moults undergone after metamorphosis
9·0	1– 5	Nil
11·0	5– 13	1
13·0	13– 21	2
17·0	21– 29	3
20·0	29– 43	4
23·0	43– 56	5
27·0	56– 73	6
30·5	73– 90	7
33·5	90–106	8
37·0	106–123	9
42·0	123–147	10
45·0	147–168	11
47·0	168–198	12
49·0	Over 200 days	13

Compared to the two foregoing species, *L. maculata* and *L. sulcirostris*, the present one is obviously a much smaller species and the post-larval growth is also very slow. At a size equal to the first post-larval stage of *L. maculata* the young post-larva of *A. multifasciata* would be at least a month old after the final larval moult and would have undergone at least four post-larval moults.

The progressive growth of important organs of the body during successive post-larval stages could be seen from Table LXXI of measurements made from the various post-larval moults recovered.

TABLE LXXI

A. multifasciata: *Measurements of selected parts of the body during different post-larval stages*

Total length	Carapace			Rostrum		Telson		Raptorial propodus: length
	Median length	Anterior width	Maximum width	Length	Width	Length	Width	
11·0	..	..	..	..	..	0·99	1·81	..
17·0	..	..	..	..	..	1·21	2·23	..
20·0	..	..	..	..	..	1·21	2·97	2·55
23·0	..	..	..	..	..	1·50	3·30	2·85
27·0	4·60	4·80	6·48	1·80	1·77	1·80	3·73	3·34
30·5	5·05	5·21	7·14	2·01	1·87	1·98	4·05	3·60
33·5	5·53	5·71	7·80	2·07	1·93	2·16	4·50	4·03
37·0	6·52	6·63	8·94	2·40	2·26	2·55	5·10	4·83
42·0	..	..	..	2·59	2·47	2·76	5·58	5·29
45·0	..	..	..	..	..	3·00	6·37	5·47
47·0	8·40	8·55	11·49	3·01	2·79	3·52	6·64	5·89

(All measurements in millimetres)

It is seen from Table LXXI of that in specimens 27·0–33·5 mm. long the median length of carapace is almost exactly one-sixth the total length. In larger specimens (37·0–47·0 mm.) however, the carapace is a little larger proportionately (1 in 5·6). The rostrum continues to be longer than broad in specimens 27·0–47·0 mm. in total length. In the early post-larva upto 17·0 mm. long, the median length of telson is a little over half its greatest width, though in the later stages the width becomes more than double the length. In the 47·0 mm. long adult, however, the length of telson is again a little over half its maximum width.

Remarks

A. multifasciata, though not a rare stomatopod, is not very common in the Indian waters. It was originally recorded from the Arabian sea. It is, no doubt, available in the Bay of Bengal also, but appears to be rather rare off Madras and during a period of 7½ years from 1936–43 only 11 final pelagic larvae of this species were encountered out of over 14,000 stomatopod larvae collected (Alikunhi, 1952). In a recent contribution Tiwari and Biswas (1952) have recorded a specimen of *A. multifasciata* from Cox's Bazaar, Chittagong.

The size of the final pelagic larva and the early post-larva and also the rate of growth of the latter probably indicate that it is of almost similar size as *A. tigrina* and *A. acanthocarpus* (*vide*

infra). The majority of specimens of *A. multifasciata* recorded range from 28–44 mm. in length. The specimen from Chittagong measures 50 mm. long (Tiwari and Biswas, *op. cit.*). The present specimen, measuring 49 mm. in length, is 202 days old after metamorphosis and is perhaps the average size of the adult. If growth under laboratory conditions is akin to normal none of the specimens of this species so far recorded could be older than the present specimen. *A. acanthocarpus* is perhaps a slightly larger species and specimens 85–86 mm. long have been recorded from the Madras coast (Kemp, 1913). Post-larval growth under laboratory conditions is almost similar in *A. multifasciata* and *A. tigrina*, though starting from same size the former took 90 days to undergo the eighth moult (then attaining a length of 33·5 mm.), while the latter underwent the eighth moult on the 81st day but attained only a length of 29·7 mm.

It is interesting that in the first post-larval stage, unlike that of *A. tigrina* and *A. acanthocarpus*, the submedian spines of telson are not basally articulated. In the second stage, however, they become articulated and as prominent as the lateral and intermediate spines. Compared to the above two species the intermediate denticles of telson are also earlier developed in *A. multifasciata* and unlike them, more of those denticles grow into short spines. The submedian denticles get progressively reduced in number. The arrangement of these denticles in three sections is lost with the third post-larval moult; while, in *A. tigrina* (*vide infra*) even after the fourth moult the seventh submedian denticle from either side remains larger than the rest. The dorsal row of spines on the telson is almost uniform, though the outermost pair is a shade larger than the rest. Of the corresponding spines of *A. tigrina* the median one is markedly larger than the outer ones.

The number of teeth on the raptorial dactylus varies from 5–6 on the two limbs of the same individual. The characteristic unequal lobes on the outer proximal aspect of the dactylus are clearly formed even in the first post-larval stage.

L. valdiviensis described by Jurich (1904) from a specimen 14·6 mm. long, has been included by Kemp (1913) as a synonym of *A. multifasciata*. From the growth of the specimen reared in the laboratory Jurich's specimen should be in the third post-larval stage. In *A. multifasciata* all the five dorsal spines of telson are indicated in the second post-larval stage and by the third stage they are clearly formed. After the first stage when only one spine is present, the other four appear simultaneously with the first post-larval moult. In Jurich's specimen, however, only three spines are present on the telson and though, as stated by Kemp, description of new species from only larval or juvenile specimens is greatly to be deprecated, in this particular case there is a possibility that the Valdivia specimen belongs to a species different from but closely related to *A. multifasciata*.

Acanthosquilla tigrina Nobili (Figs. 186–188)

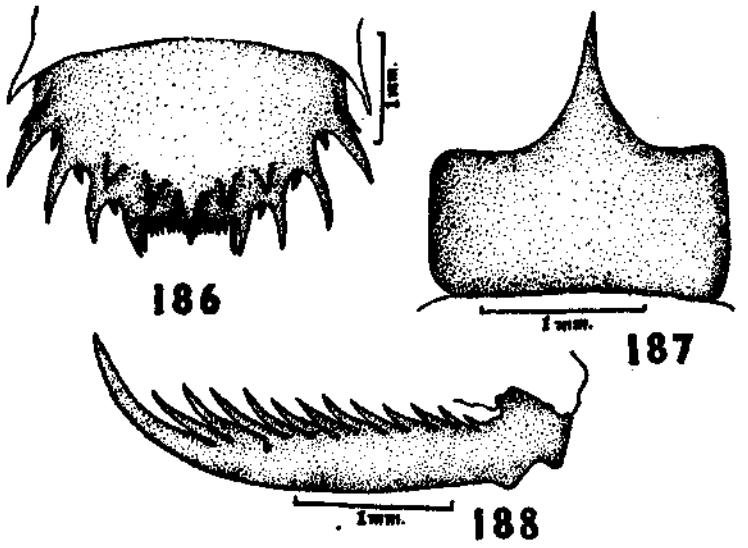
During the present study only a single larva was obtained alive and this metamorphosed in the laboratory and lived for 81 days in aquaria, undergoing eight moults during the period. A brief description of the final pelagic larva and some of the post-larval stages has already been given (Alikunhi, 1944*a*). Detailed notes on the post-larval stages are now furnished so as to facilitate identification of the species even in its juvenile stages.

Post-larval stage 1

The eyes are prominent and the rostrum blunt anteriorly. Raptorial dactylus has 10–12 teeth including the terminal one. The shorter ramus of the seventh thoracic appendage is almost rounded or oblong and is about double the size of the corresponding ramus of the sixth appendage. The postero-lateral corners of the sixth abdominal segment are sub-acutely spinous. Telson is appreciably shorter than in the larva and the marginal spines are long and pointed. The submedian spines are basally articulated, the outer aspect of the base of articulation being slightly produced. The submedian denticles number 6–1–5–1–6 as in the final pelagic larva. There are

one lateral and three intermediate denticles. Near the distal margin of telson there is a single median dorsal spine. The uropod, much longer than in the larva, has six spines on the outer aspect of the basal segment of the exopod and the outer spine of the ventral prolongation is only a trifle shorter than the inner.

Pigment is sparsely developed and the body appears opaque, pale white.



FIGS. 186–188. *Acanthosquilla tigrina.* Fig. 186. Sixth post-larval stage: Dorsal view of telson. Figs. 187 and 188. Seventh post-larval stage: Fig. 187. Rostrum, dorsal view. Fig. 188. Raptorial dactylus.

Post-larval stage II

Tip of rostrum is spinous. Postero-lateral corner spines of the last abdominal segment are longer. Telson is further shortened, with the marginal spines more prominent. The second intermediate denticle has become stout. The outer aspect of the base of articulation of the movable submedian spine is produced to form the fourth intermediate denticle. The submedian denticles are shorter. At the base of the lateral marginal spine, ventrally, a small spinule has appeared. On the dorsal aspect of telson on either side of the median spine two more have appeared, making a row of five spines. The inner spine of the ventral prolongation of the uropod is now distinctly longer than the outer and has a small spinule at the base. The distal end of the basal segment of the exopod has a small setose lobe ventrally.

No characteristic colouration is developed yet. Owing to chromatophores crowded at places on the antennules and the eye stalks these have a faint, transversely striped appearance, against a white background.

Post-larval stage III

The hind border of the last abdominal segment has a ventral row of four simple spines—a feature characteristic of *A. tigrina* (Kemp, 1913). The ventral spinule at the base of the lateral spine of telson is long and pointed. The second intermediate denticle has outgrown the rest and appears like a spine. The fourth denticle at the base of the movable submedian spine is also long and pointed. The median one of the submedian denticles has disappeared. The dorsal row of spines of telson is better developed, with the spines stouter. The inner setose lobe of the exopod reaches the level of the articulation between the basal and terminal segments of the appendage.

On the carapace chromatophores are arranged in three transverse bands, the hindmost of which being the best defined and most conspicuous. The rostrum is brown in colour. Each of the last four thoracic segments has a small, transversely disposed dorsal band of pigment medially. The first two abdominal segments are sparsely pigmented; while on the last four rudiments of a transverse band near the hind margin of each are visible. The area near the base of the dorsal spine of telson is deep brown; while a little ahead of this two small spots are seen on either side of the median line.

Post-larval stage IV

The fourth intermediate denticle of telson, just external to the movable submedian spine, is long and stout like one of the marginal spines. This, the second intermediate denticle which has already grown into a spine and the intermediate and lateral spines proper, together form the four pairs of marginal spines of the telson in the adult. The raptorial dactylus has 10 (right) to 12 (left) teeth including the terminal one. The proximal end of the dactylus externally is divided into two sub-equal lobes, the distal one of which is more prominent than the other.

The pigment band on each of the exposed thoracic segments is divided into three areas, the central trapezoidal area being of a deeper brown shade than the lateral areas. Pigment bands on the abdominal segments are more distinct. The sixth abdominal segment is more or less completely pigmented brown dorsally. These bands show a tendency of fuse at the middle.

Post-larval stage V

The rostrum is slightly broader than long, with acutely spinous tip and smooth antero-lateral corners. The marginal spines of telson have become very conspicuous. These, as already shown, are the lateral and intermediate spines and the second and fourth intermediate denticles outgrown into stout spines on either side. The movable submedian spines, long and slender, form the fifth pair of marginal spines. The submedian denticles are of almost uniform size though the seventh from either side is still a shade longer than the rest. The two median pairs of submedian denticles have become smaller than in the previous stage. The dorsal spines have become quite prominent.

Pigment is better defined though the patterns remain as in the previous stage.

Post-larval stage VI

The right raptorial dactylus has 11 teeth including the terminal one. Rudiments of three more spines have appeared on the hind inferior margin of the last abdominal segment. The submedian denticles of telson are all of almost uniform size (Fig. 186).

The pale yellow areas on the body have acquired an ashy tinge.

Post-larval stage VII

The rudimentary spines on the hind inferior margin of the sixth abdominal segment have grown; while a fresh spine has also appeared making a series of eight. The rostrum is still broader than long and has the anterolateral corners smooth (Fig. 187). The left raptorial dactylus has now 13 teeth including the terminal; the penultimate tooth of these is not appreciably smaller than the next in the series (Fig. 188).

Post-larval stage VIII

In all important aspects it is very similar to the preceding stage.

Post-larval stage IX

The specimen died in the act of moulting. The pigmentation is characteristic. The two anterior pigment bands on the carapace are more or less completely coalesced. The band on the

fifth thoracic segment is very slender. Excepting the anterior and posterior margins the dorsum of the last three thoracic segments is dark brown. On the first five abdominal segments the pigment bands are somewhat fused, the intervening lightly pigmented areas being more or less invaded by chromatophores. On the telson the spots on either side of the base of the median dorsal spine are distinct.

Growth and moults

Growth of the post-larva and the frequency of moults it has undergone in the laboratory aquarium during the 81 days period of rearing are summarised in Table LXXII.

TABLE LXXII

A. tigrina: *Periodicity of early post-larval moults and the size attained after each moult*

	Before moult	After moult							
		1	2	3	4	5	6	7	8
Age in days		8	16	23	30	40	50	62	81
Total length (mm.) ..	9·0	11·0	13·0	15·0	18·5	22·0	25·0	28·5	29·7

From Table LXXII it is seen that the duration of successive post-larval stages and growth in length during each stage are as follows:

TABLE LXXIII

A. tigrina: *Duration of and growth during successive early post-larval stages*

	Post-larval stage							
	I	II	III	IV	V	VI	VII	VIII
Duration in days ..	8	8	7	7	10	10	12	19
Growth in length (mm.) ..	2·0	2·0	2·0	3·5	3·5	3·0	3·5	1·2*

* Moult was incomplete and the specimen died before it could grow fully after moult.

For purposes of comparion with related species like *A. multifasciata*, the age, length and moults data in respect of the present specimen during its early post-larval stages may be summarised as follows:

A comparison of the above figures with those given in Table LXX shows that the size of the post-larva during the first three stages is identical with that of the corresponding stages of *A. multifasciata*. However, from the fourth stage onwards the latter grows a little more rapidly than *A. tigrina*. The periodicity of moulting is also practically identical in the two species.

Measurements of important organs taken from some of the post-larval moults which could be retrieved from the aquarium are given in Table LXXV for purposes of comparison with related species.

A comparison of these measurements with those of comparable stages of *A. multifasciata* given in Table LXXI shows that the carapace, raptorial propodus and telson are relatively shorter in *A. tigrina* than in the former species.

TABLE LXXIV

A. tigrina: *Age of and number of moults undergone by specimens of known size*

Length of specimen (mm.)	Approximate age after metamorphosis (days)	Probable number of moults undergone after metamorphosis
9·0	1–8	Nil
11·0	8–16	1
13·0	16–23	2
15·0	23–30	3
18·5	30–40	4
22·0	40–50	5
25·0	50–62	6
28·5	62–81	7
29·7	Over 81	8

TABLE LXXV

A. tigrina: *Measurements of selected parts of the body during successive post-larval stages*

Total length ..	11·0	15·0	18·5	22·0	25·0
Carapace:					
Median length ..	..	..	2·89	3·51	3·90
Anterior width ..	..	..	3·22	3·33	3·82
Maximum width ..	..	..	3·67	4·77	5·55
Rostrum:					
Length ..	..	..	1·29	1·54	1·68
Telson:					
Length ..	0·90	1·08	1·29	1·66	1·78
Width ..	1·53	1·87	2·47	2·88	3·40
Raptorial propodus:					
Length ..	..	1·90	2·30	2·71	3·31

(All measurements in millimetres)

Remarks

A. tigrina appears to be a rare stomatopod which is known from a single male specimen, 45 mm. long, found at Santuborg, Borneo, and preserved in the Sarawak Museum. Kemp (1913) re-examined this specimen and supplemented Nobili's original account (Nobili, 1903) with additional notes and figures. The present specimen is the second one known representing the species and is a female. That it is a rare stomatopod, at least in the Madras waters, is proved by the fact that out of over 14,000 stomatopod larvae collected from the Madras coast during the years 1936–43 only *two* belonged to *A. tigrina* (Alikunhi, 1952). Though rare it is now certain that this species occurs in the Bay of Bengal.

The present specimen, 29·7 mm. long, has undergone 8 moults within a period of 81 days after metamorphosis into the post-larva. The colour scheme of its body, already discussed, agrees with the one described by Kemp (1913, p. 126). In all other important features also it agrees with the type specimen.

The post-larval characters are such that until after the second moult (third post-larval stage) it is difficult to refer the specimen to the particular species. The adult pattern of pigment is also laid somewhat slowly. The number of spines on the raptorial dactylus shows limited variation even on the two limbs of the same individual. In the present case, starting with 10 and 11 teeth in the early post-larva, the number increased to 11 and 13 respectively by the sixth moult. Kemp found only 11 teeth in the specimen from Borneo.

The study of the differentiation of structures during successive post-larval moults has revealed the exact nature of the four marginal spines of telson which according to Kemp (1913, p. 125), are a pair of submedians, two pairs of intermediates and one pair of laterals. It is now shown that of these four pairs only a pair each of laterals and intermediates are actual spines and the pair of so-called sub-medians and the second pair of intermediates are actually modified fourth and second intermediate denticles respectively. It is also seen that the movable spines close to the fourth (so-called submedian) pair of spines, described by Kemp as the outermost submedian denticles, are actually the submedian spines of telson, which unlike other marginal spines become less conspicuous as the specimen grows. The submedian denticles in the early post-larva are 19 in number but with growth this number gets gradually reduced. In the 45 mm. long specimen Kemp found only 5 pairs (excluding the movable spines) of submedian denticles; but in the 29·7 mm. long specimen there are still 9 pairs of them. The rostrum has also not attained the full adult shape.

From the size of the final pelagic larva and the early post-larva and also from the relatively slow post-larval growth *A. tigrina* may be considered as one of the smaller species of the genus, akin to *A. multifasciata* and *A. acanthocarpus*. Though no conclusions are warranted from observations on a single specimen, and that too, under laboratory conditions, it is clear that the frequency of moulting and post-larval growth are favourably comparable with those of *A. multifasciata*.

Acanthosquilla acanthocarpus Miers (*var. Septemspinosa*) (Figs. 189–194)

A single larva which metamorphosed in the laboratory was reared to the second post-larval stage when it died.

Post-larval stage I (Figs. 189–190)

	mm.
Total length	10·0
Length of telson	1·2
Width of telson	1·8

A small, slender, active creature with a light pink shade on the opaque white body, the early post-larva has not developed any characteristic pigment pattern. The rostrum is conical in shape (Fig. 189) and the eyes are rather elongated. The raptorial dactylus, with two small, inconspicuous outer lobes basally, bears seven teeth including the terminal one. The postero-lateral corners of the sixth abdominal segment are sub-actuely pointed. The telson is broader than long and has the marginal spines quite conspicuous. The intermediate spines are stouter than the laterals, while the submedians have long terminal articulations. There are, one lateral and two intermediate

denticles on each side. The submedian space is still marked out into three sections as in the final pelagic larva (Fig. 190), and has the same arrangement of denticles as in the latter (6–1–6–1–6). There is a single median dorsal spine at the distal third of telson. The uropod when fully laid back reaches the tip of the submedian spines of telson. The exopod of the uropod has seven spinules on the basal joint. The outer spine of the ventral prolongation is a little over half the length of the inner.

Post-larval stage II (Figs. 191–194)

With regular feeding and renewal of water the early post-larva lived for six days and moulted into the second stage on the seventh day.

	mm.
Total length	11·4
Median length of carapace, including rostrum ..	3·8
Maximum width of carapace ...	2·0
Length of telson	1·0
Width of telson	2·0

Unlike the first stage the rostrum is acutely pointed, the tip reaching just below the corneal level of the eye. It is broader than long and has no spines or angularities laterally (Fig. 191). The eyes are elongated and the cornea, though conspicuous, is not wider than the stalk (Fig. 192). The lobes on the outer basal aspect of the raptorial dactylus are more or less equal in size (Fig. 193). There is a short spine on the raptorial carpus. The penultimate tooth on the raptorial dactylus is as long as the ante-penultimate. Telson is markedly broader than long. The lateral spines of telson have become larger and stouter than the other marginal spines. The submedian spines, shorter than in the first stage, are still terminally articulated (Fig. 194). The lateral denticle on either side has become prominent. Between the two intermediate denticles on each side a smaller third one has appeared close to the base of the second. The basal portion of the articulation of the submedian spine is produced into a short denticle extrernally, with the result that the proximal half of the articulated spine has become very inconspicuous. In the submedian space while the three sections are still noticeable the denticles in the middle section have become reduced to four (6–1–4–1–6). On either side of the median dorsal spine of telson two more smaller ones have appeared, making a total of five spines. Uropod shows no marked change from the first stage except that it now projects distinctly beyond the hind margin of telson.

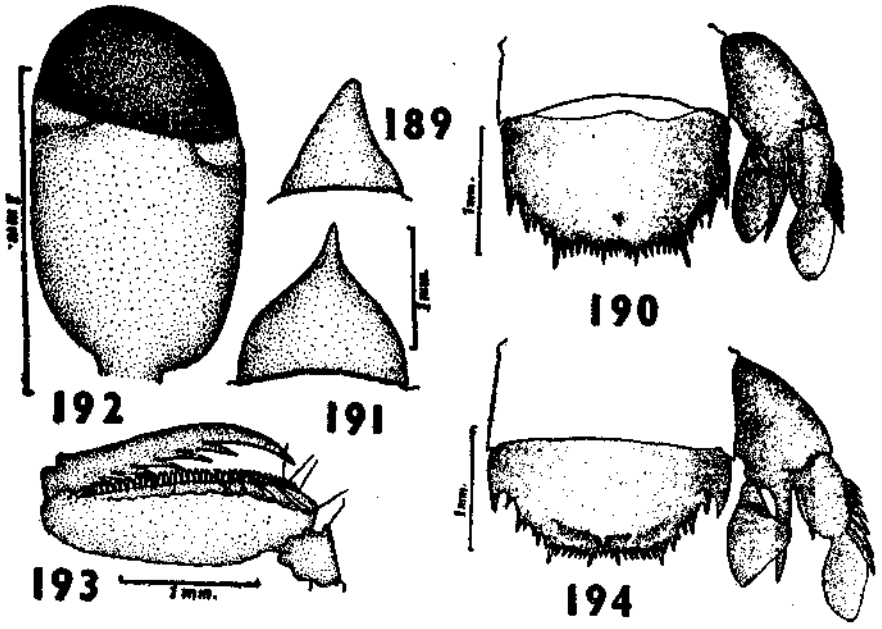
Colouration.—Though no characteristic pigment pattern has yet developed, chromatophores are more numerous and brighter than in the first stage. Brown chromatophores are conspicuous on the antennular peduncles, the eye stalks and the base of the rostrum. On the carapace chromatophores are concentrated anteriorly just behind the rostrum, a few at the middle region and also in a transverse now near the hind border. Chromatophores are very few on the exposed thoracic segments. At the distal third of the telson three fairly conspicuous groups of chromatophores have appeared.

The specimen died a day after the first post-larval moult.

Remarks

With only a single post-larval specimen available, its identification as *A. acanthocarpus* can only be regarded as tentative. In the possession of seven teeth on the raptorial dactylus and in the

almost equal size of the penultimate and the ante-penultimate teeth of the same the present specimen agrees with *A. acanthocarpus* var. *septemspinosa*, described by Miers from Senegambia. It is however quite possible that these features might change during subsequent stages; and in the absence of further material the identification cannot now be confirmed.



FIGS. 189–194. *Acanthosquilla acanthocarpus* (?). Figs. 189 and 190. First post-larval stage: Fig. 189. Rostrum, dorsal view. Fig. 190. Telson and uropod, dorsal view. Figs. 191–194. Second post-larval stage: Fig. 191. Rostrum, dorsal view. Fig. 192. Right eye, dorsal view. Fig. 193. The three terminal segments of the raptorial limb. Fig. 194. Telson and uropod, dorsal view.

The early post-larva is distinguished from the corresponding stages of *A. multifasciata* and *A. tigrina* as given in Table LXXVI.

TABLE LXXVI

Distinguishing features of early post-larva of three species of Acanthosquilla

Post-larval stage	Species	Teeth on raptorial dactylus	Dorsal spines on telson	Inter-mediate denticles	Submedian denticles	Uropod: spines on exopod
I	*A. multifasciata*	6	1	1	4-1-4-1-4	6
	A. tigrina	10–12	1	3	6-1-5-1-6	6
	A. acanthocarpus	7	1	2	6-1-6-1-6	7
II	*A. multifasciata*	6	5	4	4-1-4-1-4	6
	A. tigrina	10–12	5	4	6-1-5-1-6	6
	A. acanthocarpus	7	5	4	6-1-4-1-6	7

In the telson though only two intermediate denticles are seen in the first post-larval stage, after the first moult two more rudimentary ones are seen developing much in the same manner as

in *A. tigrina*. The median ones of the submedian denticles are also getting reduced. Though the adult condition of the marginal spines of telson is not yet distinct in the second post-larval stage it is clearly indicated that as in *A. tigrina*, the three pairs of marginal spines are not all primary spines. Kemp (1913) states that 'close beneath each submedian there is a conspicuous movable spine...' However, as in *A. tigrina* the movable spines are the submedian spines and the spine just external to each movable submedian (designated by Kemp as submedian) is actually a denticle outgrown from the articulated base of the movable submedian spine.

Discussion and Conclusions

Like many other crustaceans the pelagic larvae of stomatopods, particularly in their early stages, bear very little resemblance to their adult forms and correct identification of the larva with the particular adult species is practically impossible unless the pelagic larvae are observed to metamorphoseinto post-larvae and grow into the adult, or by observing eggs, collected from known adult species, hatch out into pelagic larvae. The early post-larval forms resemble the adults much more closely than the pelagic larvae but correct specific identification of the post-larvae is far from easy as several of the distinguishing specific characters do not appear during the early post-larval stages. As in the case of the larval forms, considerable confusion has therefore been caused in the identification of young post-larval stages also. Detailed descriptions of the various post-larval stages included in this contribution supplement similar descriptions of pelagic larvae (Alikunhi, 1952) and should be of value in facilitating their future identification.

Till the year 1942 when the present investigations commenced our knowledge of the habits of stomatopods was extremely meagre. Certain observations on the mechanism of post-larval moults and the feeding habits of larval and post-larval specimens under laboratory conditions have subsequently been given (Alikunhi, 1950). The detailed data on the frequency of post-larval moults, growth and age at different sizes relating to several species furnished in the present paper are of considerable interest, being the first and so far probably the only set of such observations in the history of this interesting group, which even now forms an object of fishery in certain parts of the Indo-Pacific region. It is also interesting to observe that except for the present series of observations there does not appear to be any other record of either a post-larval or an adult stomatopod moulting under laboratory conditions.

Metamorphosis and shrinkage in length

It has already been shown that when the larva is in the final pelagic stage it will have the outlines of the post-larval carapace and telson clearly marked out underneath the transparent chitinous shell and that such larvae when picked out and kept in aquaria of fresh sea-water metamorphose into post-larvae, almost invariably during the night, in the course of 6–10 hours (Alikunhi, 1950). The details of this remarkable metamorphosis which transforms the transparent, frail, pelagic larva into an opaque-white, stout, non-pelagic post-larva have also been discussed in detail. One of the important changes during this metamorphosis is a reduction in the length of the larva. The extent of this reduction in the species dealt with in this paper is given in Table LXXVII.

[redacted] when the total length of the larva including the rostrum is taken into account there is

TABLE LXXVII

Change in length of the final pelagic larva during metamorphosis into post-larva, in several species of stomatopods of the Madras coast

Type of larvae	Species	Average length at final pelagic stage		Average length of post-larvae
		Including rostrum	Excluding rostrum	
Alimerichthus	*S. latreillii*	12·6	10·0	10·5
	S. fasciata	14·5	11·2	11·0
	S. scorpio	..	9·2	..
	H. raphidea	18·1	15·9	15·5
Alima	*S. nepa*	22·8	20·0	16·5
	S. holoschista	34·5	30·2	19·0
	S. wood-masoni	35·5	31·0	20·5
	S. interrupta	29·5	25·0	18·2
	S. quinquedentata	27·4	24·0	16·5
	S. gonypetus	27·0	23·8	16·0
	S. boops	31·0	27·0	18·5
	S. hieroglyphica	30·0	26·0	17·0
Lysioerichthus	*L. maculata*	23·5	23·3	22·7
	L. sulcirostris	..	..	21·5
	A. multifasciata	15·0	10·0	11·0
	A. tigrina	13·5	9·2	9·0
	A. acanthocarpus	14·0	9·5	10·0

Alimerichthus type: Ordinarily reduction in length to the extent of 0·3–2·5% only, occasionally gain in length to the extent of 5%.

Alima type: Invariably reduction to the extent of 17·5–37·0% (Average 30·7%). No gain in length.

Lysioerichthus type: Ordinarily gain in length to the extent of 1·8–10·0%. Occasionally reduction in length to the extent of 2·2%.

The rostrum in the larva is generally very long compared to that in the post-larva or in the adult. In the *Alimerichthus* and *Lysioerichthus* types of larvae the loss of rostrum generally accounts for the almost entire reduction in length that takes place during metamorphosis. Hence, in these larvae when the length of rostrum is excluded the reduction in length during metamorphosis becomes insignificant. This shows that there is no appreciable reduction in the length of the body proper. In the case of the *Alima* larva, however, the reduction in length due to loss of the long larval rostrum is only about a fourth of the total reduction. This shows that unlike the other two types of larvae the body proper undergoes considerable shortening during the final larval moult. As has already been pointed out (Alikunhi, 1950) shortening of the highly telescoped region between the antenna and the labrum accounts for the major part of this reduction; while, the

relatively long and slender thoracic and abdominal segments also get shortened and become stouter.

Larval and Adult characters

As the habits and habitat of the larvae are very much different from those of the adults structural dissimilarities are naturally to be expected between them. The larvae which lead a pelagic existence are essentially modified for that life and consequently most of the characters on which identification of the adults is based are absent in them. Even in advanced larvae the carinae and spinulation on the carapace and abdominal segments, so helpful in identifying even the most closely related adult species, are not indicated. Only in the final pelagic stage we see some of the post-larval characters indicated in the larva, but as these are also often different from adult characters, are of limited value in specific identification.

The identification of several larvae with their adults after rearing them in laboratory aquaria has shown that several of the larval features are specific, though hitherto considered of little significance and could be relied upon for easily distinguishing them from one another. It has already been pointed out that differences between larvae of two closely related species might often be trivial but constant (Alikunhi, 1952). However, the striking general similarity of structure and appearance brought about by their pelagic existence, necessitates careful description of even minor larval characters so as to facilitate their easy identification and avoid confusion caused by mixing up of larvae of different species.

Size of the larva and the adult

From the data furnished in this paper it would appear that the relative length of the larva at the final pelagic stage gives no reliable indication of the relative size of the adult. While our knowledge of the adult forms is by no means complete and the maximum size attained by several of even the common species may not now be exactly known, the available records do indicate in a measure the relative size, of at least the common species. On this basis *H. harpax* and *L. maculata* are two of the largest of the stomatopods known. The final pelagic stage larvae of these species measure about 18·5 and 23·5 mm. respectively in total length and are much smaller than some of the larvae recorded from the Indo-Pacific region (*Alima*, 45–60 mm. long and *Lysioerichthus* 45 mm. long from Hawaiian waters, Townsley, 1953). *Alima hyalina* is also known to attain a length of about 60 mm. If the length of the pelagic larva has any direct relation to the size of the adult then the large larvae mentioned above should belong to adult species much larger than either *H. harpax* or *L. maculata*. This, however, is extremely unlikely for if such species existed they would have been collected and recorded long before, particularly by virtue of their large size. Available information and circumstantial evidence thus tend to show that the size of the final pelagic larva is merely a specific character which however, does not give a true indication of the relative size of the adult.

Post-larval characters

The early post-larvae show characters resembling more the adult than the larvae. As has been shown in the species described in this paper the shrinkage in length commencing with the final larval moult continues during the subsequent two or three stages, when, even though there is no further reduction in total length, the various parts of the body continue to shrink and gradually assume adult proportions. In the early post-larvae therefore, the proportionate size of the various parts of the body is far different from that in the adult. The adult proportions of such important distinguishing features as the shape and size of the eyes, the shape of the lateral processes of the last four thoracic segments and spinulation of abdominal somites are, in the majority of cases, attained only after the first few post-larval moults. As in the case of the larvae it is therefore necessary to have detailed descriptions of the early post-larval stages also if we are to identify them correctly. Supplementing the earlier contribution on the larvae (Alikunhi, 1952) an attempt has been made

in this paper to furnish this information with reference to species commonly occurring along the Madras coast.

It is a remarkable feature that in all the species dealt with in this paper the full adult complement of teeth on the raptorial dactylus is formed even in the first post-larval stage. As has been mentioned earlier in the final pelagic larva also these teeth are fairly clearly indicated through the larval shell. Variation in the number of teeth on the dactylus in the first or second post-larval stage is extremely limited if not exceptional and always the number present is well within the range found in the adult. In the light of this observation it is tempting to generalise that the number of teeth on the raptorial dactylus in the first or second post-larval stage is normally the number that is characteristic of the particular species.

During the present study a total number of 607 larvae, representing 11 species of the genus *Squilla* one of *Harpiosquilla*, two species of the genus *Lysiosquilla* and three species of *Acanthosquilla* metamorphosed in the laboratory aquaria into early post-larvae (*vide* Table LXXVIII).

TABLE LXXVIII

Showing the number of larvae of Squilla, Harpiosquilla, Lysiosquilla and Acanthosquilla *that metamorphosed and the maximum period for which they were reared in the laboratory*

Species	No. of larvae that metamorphosed into the first post-larval stage	Maximum period for which the post-larva was reared in laboratory	
		No. of days	No. of moults undergone
S. nepa ..	298	215	12
S. holoschista ..	137	120	9
S. woodmasoni ..	12	136	9
S. interrupta ..	13	37	4
S. quinquedentata ..	21	76	6
S. gonypetes ..	9	62	6
S. boops ..	1	12	1
S. hieroglyphica ..	1	8	1
S. latreillei ..	14	41	5
S. fasciata ..	1	9	1
S. lata ..	1	Died after moulting	
H. raphidea ..	14	284	15
L. maculata ..	21	81	6
L. sulcirostris ..	1	80	6
A. multifasciata ..	1	202	13
A. tigrina ..	1	81	8
A. acanthocarpus ..	1	8	1

In all these specimens the number of teeth on the raptorial dactylus during the first and succeeding post-larval stages was either exactly the same as in the respective adult species or within the range known for the species. Dealing with *L. maculata* Boone (1930) has stated that "the

largest West Indian specimen taken by the *Ara* has 10 teeth on the retrochela, while, younger West Indian specimens I have examined have only 5–8." As detailed above twenty-one larvae of *L. maculata* metamorphosed into post-larvae in the laboratory during the present study. The number of teeth on the raptorial dactylus in these specimens varied from 10 to 12 only; none had less than 10. This and similar observations in respect of other species given above do not permit acceptance of the assumption that the number of teeth on the dactylus might increase with age. On the contrary it is perhaps the one feature in which the young post-larva resembles the adult fully and is often of considerable help in attempting identification of early post-larval stages.

It is remarkable that in all the species of *Squilla* dealt with in this paper the first post-larval stage is characterised by the absence of the antero-lateral spines on carapace. These spines, however, make their appearance after the first or second post-larval moult. Similarly, during the first post-larval stage the telson is characterised by the possession of a pair of submedian spines with movably articulated terminal joints. These latter also have only a transitory existence and are lost during the succeeding stages. These and similar features might possibly have some bearing on the relationships between the various genera and species and are discussed in further detail in a subsequent section.

Moulting and growth

The mechanism of moulting has already been described in detail (Alikunhi, 1950). The frequency of moulting in the different species has also been discussed. With regular feeding post-larval moults were also regular. On the other hand when feeding was irregular the interval between moultings became long. A young post-larva of *S. nepa* was kept in an aquarium for 37 days with only regular renewal of water but no feeding. The specimen did not undergo a single moult during this period but when regular feeding was started it began moulting within 5 days. The slight differences in the duration of some of the post-larval stages in certain species detailed in this report could therefore be ascribed to fluctuations in feeding intensity.

As a rule, the duration of the earlier post-larval stages is shorter than that of the later stages. Once the adult condition is reached then the interval between successive moultings is of the order of about a month.

As in other crustacea visible growth is in 'pulses' being immediately following moults and before the new shell hardens. The size given for a particular post-larval stage is, therefore, actually attained during the first one or two days of that stage, after which there is hardly any increase in length till the next moult or commencement of the next stage.

From the data relating to the various species dealt with in this report it may be generalised that the actual growth in length is the minimum following the first post-larval moult, and that it steadily increases with the subsequent moults. The increase in length following each moult varies in the different species and has, perhaps, a direct relation to the maximum size attained by the particular species. In other words, the rate of growth is relatively more rapid in the larger species than in the smaller ones.

Under the conditions described above post-larval growth in the laboratory aquaria is quite rapid. In the total absence of any data on the natural growth of stomatopods it is difficult to assess the growth under aquarium conditions in terms of their natural growth. Ordinarily in most animals growth under laboratory conditions will be appreciably slower than the natural growth. In the present instance the rapid growth may be accounted to the regularity of feeding, the abundance of food that was generally available and perhaps also the peculiar habits of the species.

Duration of larval life

Giesbrecht (1910) has shown that there are 9 distinct stages in the larval life of *Squilla* and *Lysiosquilla*. These stages are distinguished by changes caused during progressive differentia-

tion of parts. As in other crustacea, in the stomatopods also structural changes like growth take place only during and immediately following moults. The nine stages in the larval life would therefore mean at least 8 or 9 moults during the period. There is at present no information regarding the duration of each or any of these larval stages. Gurney (1937) kept the egg ball of a specimen of *Gonodactylus glabrous* under circulation of water for some days and a few of the larvae obtained lived through the first moult a week later. It has also been shown that the pelagic larva can be kept in aquaria for days and regularly fed (Alikunhi, 1950). Various stages of larvae of *S. nepa, S. quinquedentata* and *S. latreillei* have been observed to moult into later stages in the laboratory during the present studies. In all these cases the moult took place within 24–72 hours after collection from the sea.

The above observations do not give any clear idea of the duration of larval life. However, from the frequency of post-larval moults, rate of growth and age after metamorphosis in respect of the species dealt with in this report an attempt may be made to assess the duration of the larval period. In all these species the early post-larva undergoes the first moult within 5–8 days after metamorphosis. The interval between successive moults gradually lengthens with age. The time taken to undergo the first 6–9 post-larval moults in some of the species dealt with here is given in Table LXXIX.

TABLE LXXIX

Time taken to complete specified number of early post-larval moults in selected species of stomatopods

Species	No. of days required after metamorphosis to complete		
	6 moults	8 moults	9 moults
S. nepa ..	34–46	77–81	102–114
S. holoschista ..	48–56	82	120
S. woodmasoni ..	38–49	65	99
S. quinquedentata ..	47–67	..	..
S. gonypetus ..	55	..	..
H. raphidea ..	37–52	58–85	71–99
L. maculata ..	52	..	..
L. sulcirostris ..	64	..	..
A. multifasciata ..	56	90	106
A. tigrina ..	50	81	..

Thus, in the ten species listed in Table LXXIX, the first six post-larval moults are completed within a maximum period of 8 or 9 weeks after metamorphosis. The minimum period taken for the same is only 5 weeks. Likewise the 8th moult is completed within a period of 9–12 weeks. On this basis it may be reasonably stated that the duration of the various larval stages may not be longer than that of the early post-larval stages. If this is the case the larval life which is supposed to comprise of only 9 stages (8 moults only) cannot be longer than the maximum period of 3 months required to complete the first 8 post-larval stages. As the duration of the earlier post-larval stages, is shorter than that of the later stages and as all the larval stages are earlier to the first post-larval stage it is even possible that the duration of at least the early larval stages may be shorter than that of the early post-larval stages. If such is the case the duration of larval life can be appreciably shorter than even three months. It is relevant to note in this connection that the minimum period taken to complete 8 post-larval moults was only 58 days. In the light of these observations

it seems probable that larval life in these stomatopods is not only not very prolonged but is, on the other hand, rather short. According to Townsley (1953), however, "the larval life is longer and they pass through many moults before reaching the adult stage, "and their long planktonic existence easily accounts for the world-wide distribution of the genera and the presence of species such as *Pseudosquilla ciliata* in the Pacific Ocean, Indian Ocean, Red Sea and Atlantic Ocean." The present observations, as already shown, do not support such a supposition.

Intra-generic and Inter-generic Relationships

Based on certain larval characters the relationship between various groups of species in the genus *Squilla* was discussed at some length in an earlier contribution by the author (Alikunhi, 1952). The characteristic post-larval features of these species are now examined in this light.

According to Brooks (1886) the species which he included under the genus *Protosquilla* and which are regarded by Kemp (1913) merely as a section of *Gonodactylus* are the most primitive that persist. Kemp (1913), however, concludes that it is among species of the genus *Squilla* that the most primitive forms are to be sought. While it is not proposed to critically examine the relationship of the various genera and species in this report, some of the outstanding post-larval features which might prove to be of help in determining the relationship between the various forms are discussed here.

In the first post-larval stage the important features which are likely to be of phylogenetic significance are:

(*a*) the absence of antero-lateral spines on carapace.

(*b*) the extremely poorly developed carination of carapace.

(*c*) the presence of terminal articulations on the submedian spines of telson, and

(*d*) the acutely pointed nature of the marginal denticles of telson.

With the first post-larval moult, however, the antero-lateral spines appear on the carapace in most species. But, in some, even in the second post-larval stage these spines may be either absent or rudimentary (cf. *H. raphidea, S. latreillei*). Kemp (1913) records *S. miles* and *S. rotundicauda* as having no antero-lateral spines on the carapace in the adult condition. Generalising from these it may be stated that those species of *Squilla* having antero-lateral spines on carapace in the adult condition pass through a stage, though of short duration, when those spines are absent. When this is seen to be the case in the majority of species some phylogenetic significance has to be attributed to the same. It is of interest to mention in this connection that the antero-lateral corners of the carapace ordinarily remain rounded (without spines) in the species of the genera *Pseudosquilla, Lysiosquilla, Coronida, Odontodactylus* and *Gonodactylus.*

Well-developed carination of the carapace and abdominal segments is a characteristic feature of the species of the genus *Squilla.* Invariably these carinae are poorly developed in the early post-larva. In species of the '*nepa*' and '*quinquedentata*' groups the carinae are developed perhaps a little more rapidly than in species of the '*Chloridella*' or '*raphidea*' groups. Thus, as in the case with the antero-lateral spines of the carapace, in all the species of *Squilla,* probably irrespective of their adult condition, there is a stage when the carniation of the carapace and body segments is temporarily suppressed or very poorly developed. In none of the other genera of stomatopods there are longitudinal carinae on the carapace; only *Pseudosquilla* has longitudinal carinae on the abdominal segments and in the other genera such carinae on the majority of the abdominal segments are entirely suppressed.

The terminal articulated piece on the submedian spines of telson is characteristic of the first post-larvae of species of the genus *Squilla.* In *S. nepa, S. holoschista, S. wood-masoni* and *S. interrupta,* the terminal articulation of the submedian spine is lost with the first post-larval moult.

In *H. raphidea* and *S. latreillei* this terminal articulation is retained even after the first 4–5 post-larval moults. In the adult condition, however, in the majority of species the submedian spines are not articulated. Thus, before reaching the non-articulated condition of the submedian spines of telson the specimen passes through a stage when the spine has a distinctly articulated terminal piece. Here again it is interesting to point out that the submedian marginal spines of telson in all the other genera of stomatopods remain articulated in the adult condition.

In almost all cases studied the marginal denticles of telson are acutely pointed in the first post-larval stage. In *S. nepa* and related species, with the first post-larval moult these denticles beomc smooth or round-tipped. In species like *H. raphidea*, *S. latreillei*, etc., these denticles continue to be acutely pointed even after 4–5 post-larval moults. In several species of the *Chloridella* group the denticles remain acutely pointed in the adult stage also. In most species of the other genera of stomatopods also these marginal denticles remain pointed in the adult stage. The round, smooth, marginal denticles on the telson in at least some of the species of the genus *Squilla* are thus evolved probably from pointed denticles which continue to be retained in their original form partially in *Squilla* and fully in the other allied genera.

It is to be pointed out here that all the four *post-larval* characters of *Squilla* discussed above have only a transitory existence in its life-history, while in the other genera these are permanent adult characters. If these characters have any phylogenetic significance it would appear that the species included under the genus *Squilla* are more specialised or evolved than those included under the other stomatopod genera. Kemp (1913), however, states that "*Squilla*··· is the oldest established genus of stomatopoda at present living and probably contains the most primitive species of the order." The post-larval characters discussed above do not seem to be in accord with Kemp's assumption.

The set of characters discussed above further indicates that within the genus *Squilla* species of the '*Chloridella*' group are perhaps more primitive than those of '*nepa*' or "*quinquedentata*" groups. Similarly the belated appearance of the antero-lateral spines on carapace and the continued retention of the terminal articulations of the submedian spines of telson in *H. raphidea* indicate its closer affinity to species of the *Chloridella* group than to any other group in the genus. It is interesting that this relationship which was suggested on the basis of larval characters of *S. latreillei* and *H. raphidea* (Alikunhi, 1952) is now again indicated on the strength of post-larval characters of the two species. On the basis of information furnished in this report it is difficult to go into details about the relationship between the other species of the genus. It would, however, appear that species of the "*quinquedentata*" group are more closely related to the '*Chloridella*' and '*raphidea*' groups than species of the '*nepa*' group are to the latter.

Key for Identification of Early Post-larvae

A simple key for easy identification of the first post-larval stage of the species dealt with in this report is given below:

Genus *Squilla* Fabricius and *Harpiosquilla* Holthuis.

First post-larval stage

Carapace without antero-lateral spines; submedian spines of tel · terminally articulated; marginal denticles of telson all pointed.

Genus *Harpiosquilla* Holthuis

1. Upper margin of propodus of raptorial claw with a series of stiff, large and small, alternating spines.

Lateral margin of carapace with a smooth angulation, almost halfway along, on either side; raptorial dactylus with 8–9 teeth; submedian denticles of telson 18–20; total length 15–16 mm.

.....*H. raphidea.**

Genus *Squilla* Fabricius

II. Upper margin of propodus of raptorial claw with a series of even pactinations, in addition to a few movable spines proximally.

A. Lateral process of fifth thoracic segment single, sub-acute or pointed; inner margin of ventral prolongation of uropod with spinules.

(*a*) Width of cornea of eye less than width of stalk.

Raptorial dactylus with 4–5 teeth; ventral prolongation of uropod with 5 spinules; total length 10–11 mm.

.....*S. latreillei.*

(*b*) Cornea of eye of equal width as or broader than stalk; raptorial dactylus with 6 teeth.

(1) Cornea of equal width as stalk; ventral prolongation of uropod with 6–7 spinules; total length 11 mm.

.....*S. lata.*

(2) Cornea wider than stalk; ventral prolongation of uropod with 8 spinules; total length 11 mm.

.....*S. fasciata*

B. Lateral process of fifth thoracic segment bifid; inner margin of ventral prolongation of uropod without spinules.

(*a*) Raptorial dactylus with 5-teeth; no anterior bifurcation on median carina of carapace.

(i) Lateral process of the sixth thoracic segment not bifid.

(1) Cornea hardly wider than width of stalk; rostrum with a median dorsal carina distally; total length 17 mm.

.....*S. hieroglyphica.*

(2) Cornea distinctly wider than stalk, no dorsal carina on rostrum, total length 18·5 mm.

.....*S. boops.*

(ii) Lateral process of sixth thoracic segment bifid; cornea obliquely placed and wider than stalk.

(1) Telson quadrate; with 6 large submedian denticles, each with one or more spinous processes; total length 16·5 mm.

.....*S. quinquedentata.*

(2) Telson longer than broad; with 18–20 submedian denticles; total length 16 mm.

.....*S. gonypetes.*

* *H. harpax*, according to Tiwari and Biswas (1952). Holthuis (*Crustaceana*, Vol. 7, Part II: 140–41, 1964) has referred *S. raphidea*, *S. harpax* and *S. annandalei* to a new genus *Harpiosquilla*. This has been adopted here.

(*b*) Raptorial dactylus with 6 teeth; lateral process of 6th thoracic segment bifid and that of the 7th insipiently so.

(i) Anterior bifurcation of median carina of carapace wanting; cornea of eye markedly wider than stalk.

(1) Submedian denticles 23–25, arranged on 6 larger denticles; total length 20–21·5 mm.

.....*S. wood-masoni.*

(2) Submedian denticles 12–16 only; arranged on 6 larger denticles; with the outermost pair smooth and rounded; total length 17·5–19·0 mm.

.....*S. interrupta.*

(ii) Anterior bifurcation of median carina of carapace weakly or clearly indicated; cornea of eye not markedly wider than stalk.

(1) Median carina of carapace bicarinate behind dorsal pit; total length 18·5–19·5 mm.

.....*S. holoschista.*

(2) Median carina of carapace not bicarinate behind dorsal pit; total length 16–17 mm.

.....*S. nepa.*

Genus *Lysiosquilla* Dana.

First post-larval stage

I. Telson without dorsal spines; submedian spines of telson present or absent; when present, not movable.

(*a*) Submedian spines of telson present but not movable; raptorial dactylus with 11–12 teeth; total length 22–23 mm.

.....*L. maculata.*

(*b*) Submedian spines of telson absent; raptorial dactylus with 9 teeth; total length 21·5 mm.

.....*L. sulcirostris.*

Genus *Acanthosquilla* Manning

II. Telson, with one dorsal spine; submedian spines of telson present and movable.

(*a*) Raptorial dactylus with 6 teeth; intermediate denticles—4; submedian denticles 4–1–4–1–4; total length 9 mm.

.....*A. multifasciata.*†

(*b*) Raptorial dactylus with 7 teeth; intermediate denticles—2; submedians 6–1–6–1–6; total length 10 mm.

.....*A. acanthocarpus.*

(*c*) Raptorial dactylus with 10–11 teeth; intermediate denticles-3; submedians 6–1–5–1–6; total length—9 mm.

.....*A. tigrina.*

† According to Manning (1963) *Lysiosquilla multifasciata*; *L. acanthocarpus* and *L. tigrina* come under his new genus *Acanthosquilla*. He divides the species under this genus into two groups, depending on the possession of three or four pairs of primary marginal spines on telson. However, in the case of *A. tigrina*, the present study has shown that the primary marginal spines of telson are the usual three pairs only [lateral, intermediate and (movable) sub-median] and the four pairs of marginal spines seen in the adult are the lateral and intermediate (primary) spines and the second and fourth intermediate denticles modified into spines.

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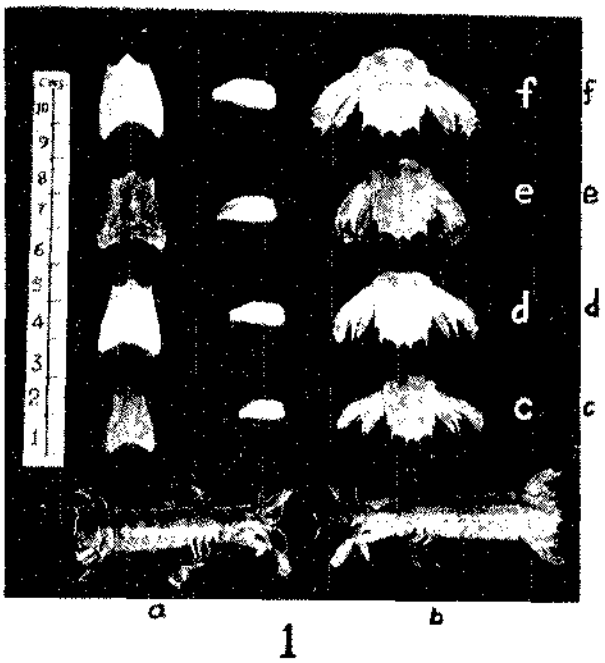

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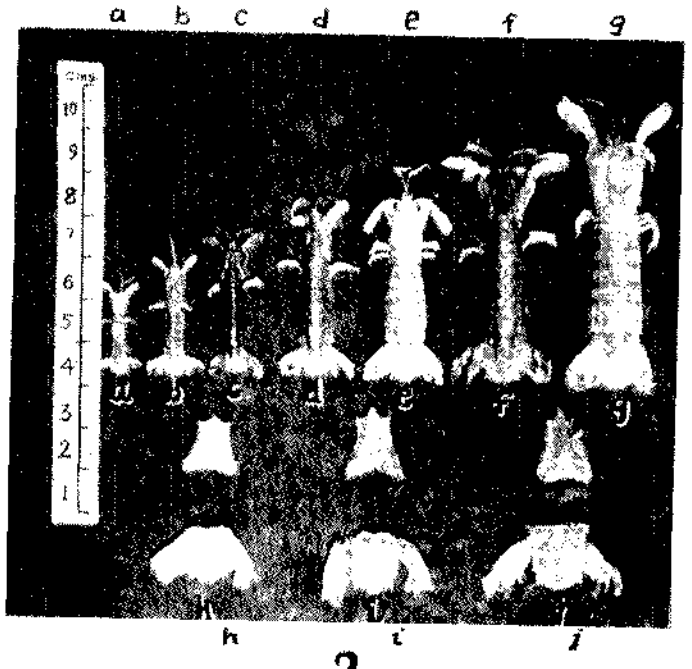

2

FIGS. 1 2. Fig. 1. *Squilla nepa*. (*a*) A male specimen, 86 days old, which moulted for the sixth time, on the 44th day after metamorphosis; (*b*) A male specimen, 84 days old, which moulted for the seventh time on the 52nd day after metamorphosis. *a* to *f* Carapace, two terminal segments of the raptorial claw and uropods and telson during the 8th, 9th, 10th, and 11th post-larval stage respectively—moults only.
Fig. 2. *Squilla holcochirus*. (*a*) Post-larva before the first moult; (*b* to *g*) Post-larva after the first, second, third, fourth, fifth and sixth moults, respectively; (*h* to *j*) Carapace and uropods and telson during the seventh, eighth and ninth post-larval stages respectively—moults only.

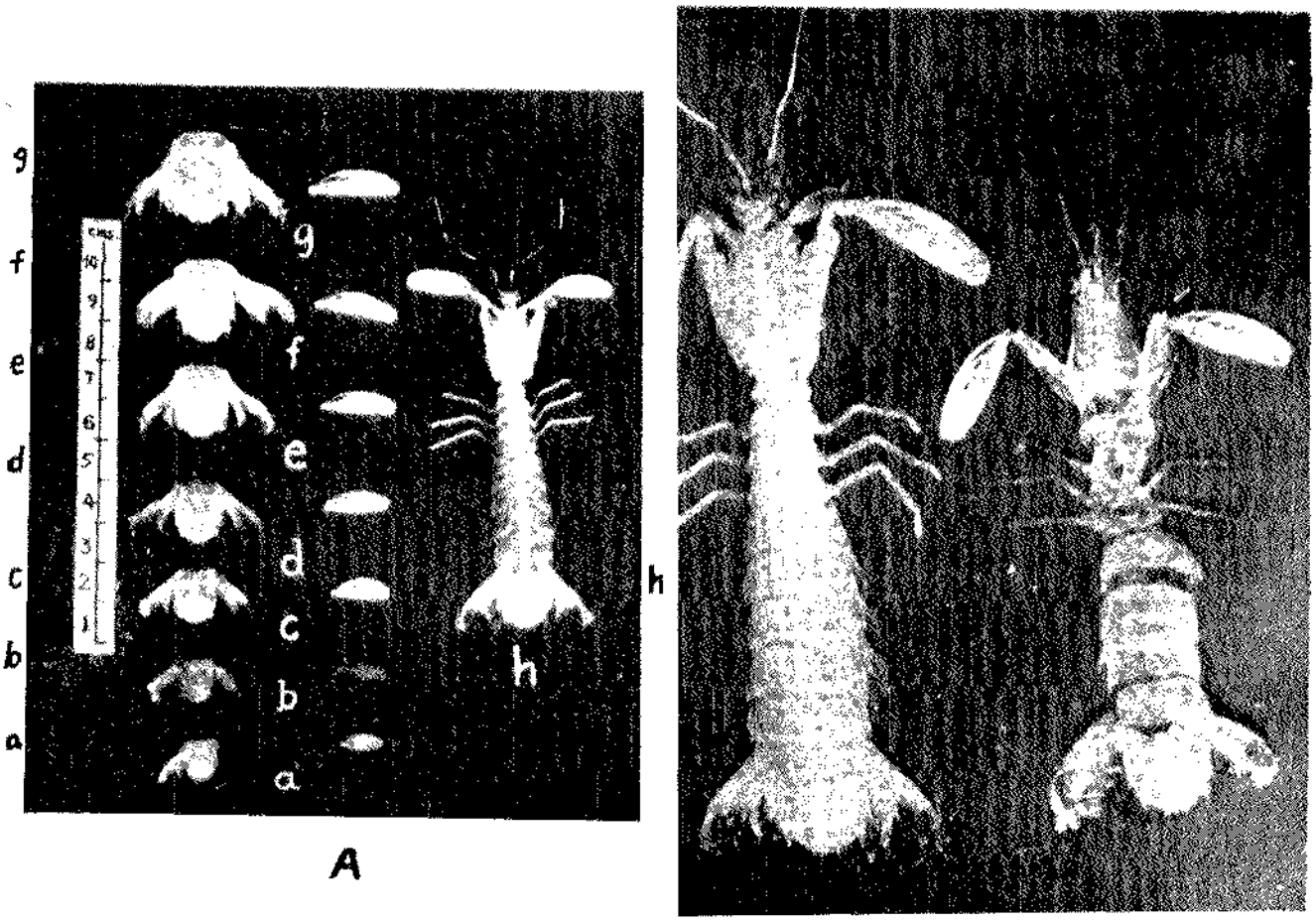

FIG. A. *Harpiosquilla raphidea*. *(a* to *g)* Uropods and telson and two terminal segments of the raptorial claw during the 8th, 9th, 10th, 11th, 12th, 13th and 14th post larval stages respectively—moults only; *(h)* A specimen after the ninth moult, 80 days old after metamorphosis. FIG. B. *Harpiosquilla raphidea*. *(a)* The moult (ninth after metamorphosis) of a specimen 80 days old; *(b)* The same specimen, after moulting. Note the difference in size as compared to the earlier stage represented by the moult.

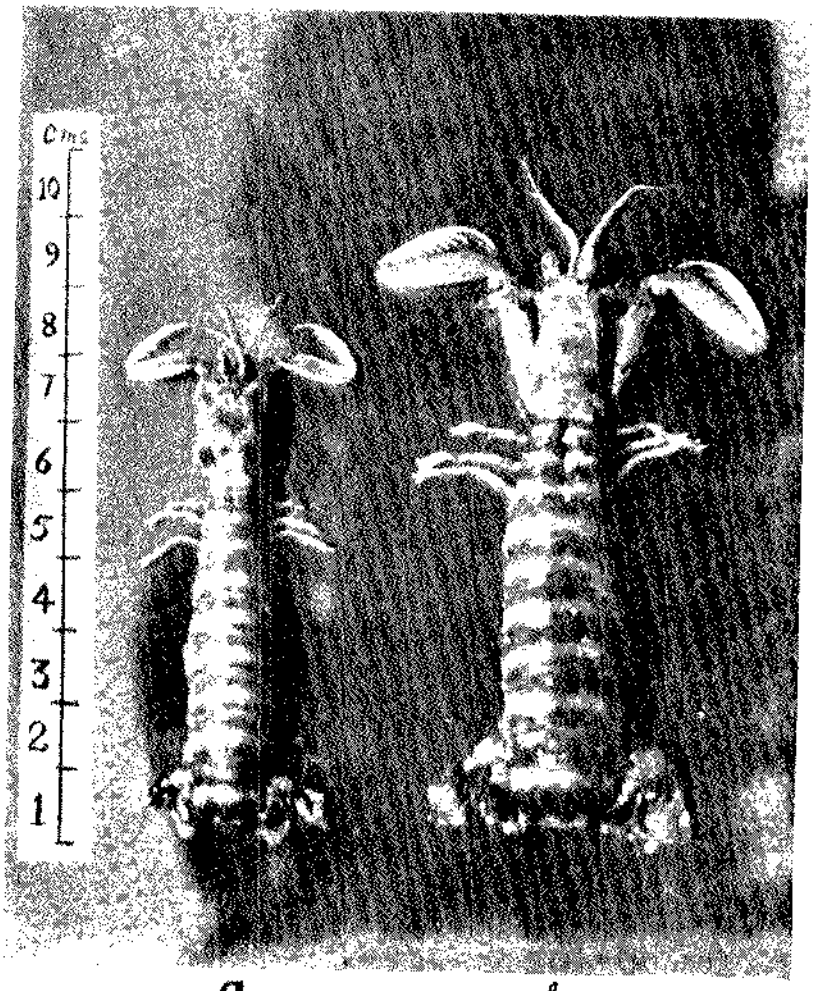

FIG. (a) *Lysiosquilla sulcirostris*. A specimen, after the sixth moult, 81 days after metamorphosis, 63·0 mm. long.
FIG. (b) *Lysiosquilla maculata*. A specimen moulting for the seventh time (died while moulting); 88 days old after metamorphosis; 77·0 mm. long

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* Not referred to in original.

RECENT ADVANCES IN THE LABORATORY CULTURE OF DECAPOD LARVAE[1]

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ABSTRACT

The development in recent years of successful methods for the laboratory culture of decapod larvae, based primarily on the use of *Artemia* nauplii as food, has stimulated widespread interest in the study of larval development of this group. Several laboratories in the United States have established long-term programs for the investigation of decapod larvae. One of these is the Institute of Marine Science of the University of Miami where, in 1960, the first successful attempts to rear larvae led to the establishment of a research and training center to concentrate upon the decapod larvae of the tropical western Atlantic. A cross-indexed literature file was set up and is maintained to permit ready reference to papers published since Gurney's bibliography. Since the initiation of the program, larvae of nearly 100 species of Decapoda have come under observation and approximately one-third of these have been reared from hatching to metamorphosis. The species are distributed through all the major groups of the Decapoda with special emphasis on taxa of particular interest to collaborating workers. Initially effort was concentrated on common inshore species which were considered more likely to offer success in rearing experiments, but it was soon discovered that pelagic larvae of some forms could be maintained for extended periods when captured at sea. Special effort has been made to collect ovigerous females from considerable depths in the Florida Straits and elsewhere. Some of these have yielded numbers of viable larvae which were reared in the laboratory to various stages of development.

The availability of successful, uncomplicated techniques for the laboratory rearing of decapod larvae has made possible reliable identifications of planktonic material. Formerly scarce material of early stages of many species can now be produced in quantity under controlled conditions permitting detailed studies of morphology and experiments on physiology, nutrition and other aspects of the ecology of larval forms.

A plea is made for expansion of similar studies on the decapod fauna of the Indo-Pacific and other regions.

AN examination of the pertinent literature will show the historical trends in the field of larval studies on the Decapoda. The very early studies were made on embryos obtained from preserved adults or upon planktonic forms whose ancestry was in most cases quite uncertain. Observations soon were made upon the recently hatched larvae of shallow water species which could be kept alive for some hours or even days with facilities which existed at that time. With few exceptions for most of a century, the study of larval decapods was concentrated upon material captured in the plankton or hatched from ovigerous adults taken at the seashore. Efforts to maintain larvae alive for more than a few days were usually unsuccesful and as a result, information on biology of larvae or the sequential morphology of early developmental stages, and the identity of planktonic forms was slow to accumulate. With the eventual realization that most decapod larvae are carnivores preferring live food, searches for convenient food supplies for developing larvae became more successful. Lebour (1928) was able to get various crab larvae to live on mollusc, echinoderm and polychaete larvae, and some other foods, but most of these foods require considerable effort or depend upon convenient timing of natural spawning of the food species. The major difficulty in using macerated flesh of any species as food is the tendency for bacterial contamination and fouling of the water in culture vessels; moreover, it was found that most larvae would not feed on material resting on the bottom but require active food. The elaborate and varied methods used to provide circulating water were cumbersome and would have been largely unnecessary if adequate supplies of living food could have been provided.

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The advent of the use of *Artemia* nauplii marked a new era in the study of crustacean development. Gurney himself was one of the first to advocate use of this food. The eggs of the brine shrimp, being capable of long periods of dry storage, make available within 24-36 hours any quantity of a small, highly concentrated living food. The convenience of this food as well as its cheapness combine to make it a highly desirable tool for laboratory studies, especially now that it has been demonstrated to be sufficient for the attainment of metamorphosis by a wide variety of crustacean larvae. Representatives of virtually all major groups of decapods have been reared to metamorphosis on a diet of *Artemia* alone or, in some instances, on *Artemia* in combination with supplementary items such as echinoderm embryos or phytoplankton. The particular problem of penaeid early stages which require rather small food was solved by combining various species of phytoplankton with young *Artemia* for the first few larval stages of the shrimp, after which *Artemia* alone sufficed (Ewald, 1965). For the rearing of phyllosoma larvae, *Artemia* nauplii alone suffice for the early portions of development after which larger items are apparently needed by the phyllosoma because of the physical problems of capture (Inonue and Nonaka, 1963; Robertson, unpublished). *Artemia* is not a cure-all, for there are some species of decapods the larvae of which are so small as to require other techiniques, but it cannot be denied that no other food for larval decapods is at the present time of such wide applicability in laboratory culture.

The traditional tendency to attempt culture *en masse* obscured for many years the phenomenon of individual variability in larval history. Only when it became possible to rear numbers of larvae of the same brood in isolation could a comparison be made of the stages through which individual animals passed. Many species are able to attain metamorphosis after a varying number of larval instars. Certain groups, anomurans and many carideans in particular, are especially susceptible to such variation (Boyd and Johnson, 1963; Provenzano and Dobkin, 1962; Tsurnamal, 1963) but other groups, notably most brachyurans, are remarkably consistent in the number of larval instars through which they pass (Costlow and Bookhout, 1960, 1961, 1962, unpublished; Yang, unpublished). That some larvae do vary in their laboratory development indicates that they are at least *capable* of doing this in the field where there would be survival value in postponing metamorphosis until sufficient growth, rather than a certain instar, has been attained. In fact, Boyd and Johnson (1963) did find evidence for such variation in planktonic larvae. Costlow (1963) has shown that the hormones governing growth and metamorphosis in *Callinectes* are distinct. Although these hormones generally are synchronized in action, they are capable of acting out of phase, as indicated by the occasional appearance of imperfectly metamorphosed specimens. Such intermediate forms have been reported for a number of systematic groups (Kurata, 1960; Provenzano and Dobkin, 1962, and Provenzano, unpublished).

Just as the use of *Artemia* has solved the food problem for the rearing of many forms, so another tool has made it convenient to rear quantities of larvae in isolation. This is the compartmented plastic tray or "Trans-box" method first developed at Duke University Marine Laboratory by Costlow and Bookhout (1959) and now used extensively at the University of Miami. A major advantage of these trays or boxes is the small space required for a considerable number of isolated individuals and the ease with which these can be handled. Even with the transparent tops of the boxes closed, there seems to be no oxygen problem for most species and changing to new containers is needed only once a day at most, frequently only every second day depending upon temperature (Fig. 1). Starved animals can be maintained unchanged for many days.

Sometimes there are difficulties in maintaining females with egg masses until hatching takes place. Some female crabs and lobsters for instance will remove their eggs from the pleopods if disturbed or when subjected to the artificial environments of the laboratory. Moreover, it is not uncommon with some deep-water forms that the female will die during the prcocess of collection and eggs from such individuals are also lost unless the aeration and treatment of the eggs normally provided by the female can be replaced by suitable artificial conditions. A method for keeping and hatching brachyuran eggs artificially was given a few years ago by Costlow and Bookhout (1960). Basically the method consists of placing portions of the egg mass in individual compartments of plastic trays and after the addition of antibiotics, the trays are then placed on a variable

speed shaker. The method was highly successful and avoided potential loss of the entire egg mass through fungal or ciliate infection. Eggs from a single female could be subjected to various environmental conditions prior to hatching in order to study effects on pre-adapted embryos and larvae. A modification of this method has been used at our laboratory with considerable success. Many decapods other than brachyura (caridean and penaeid shrimps, anomurans and lobsters) have been studied in this fashion. We have found that if the eggs are washed thoroughly before being isolated in clean sea-water, the addition of antibiotics is not necessary in most cases. A new and very inexpensive shaker has been developed recently to substitute for the rather high cost variable speed shaker originally used in the development of the basic method. The new shaker, consisting of a sliding, mounted plate over a base plate with an inexpensive DC or AC electric motor is small enough to be placed inside an ordinary household refrigerator, yet can hold several trays with hundreds of eggs. These shakers, which generate very little heat, are especially valuable for keeping eggs of deep sea species agitated under cold conditions in a limited space (Fig. 1).

Among the requirements for successful rearing of decapod larvae is that the sea-water be as clean as possible. The salinity and temperature must be somewhat similar to that where the species is found in nature, for Costlow and Bookhout (numerous publications) have shown for a number of species the effect of variations in temperature and salinity on survival of larvae. Aside from that, however, there are characteristics of the water which should be considered before using it for culture work. It is well known that water masses of different origins have subtle differences in characteristics associated with the ability of animals to grow in those water masses. Inshore species are generally more tolerant of foreign water conditions than are pelagic or oceanic species. Thus, salinity and other gross characteristics being equal, inshore species may be reared in bay water or oceanic water, but the larval of species from oceanic habitats may not survive long in bay water.

The use of stored water assures that water of the same salinity will be available for rearing a given brood of larvae completely through to metamorphosis without the complications of daily fluctuations in physical characteristics of the water. Sea-water should be filtered to remove the maximum amount of living and detrital organic material. We have used with good success water stored in carboys for periods of several months.

Except for very delicate species we have not found it necessary to change water more often than every two days at temperatures of 20° C. and lower. After two days the *Artemia* nauplii have become too large for the decapod larvae to capture easily, have begun to starve to death, and have been reduced in number through predation. Hence, fresh food and water is required about every second day, but daily at temperatures from 25–30° C. More frequent changing increases possibility of damage to larvae in transfer but may be offset by higher water quality and food conditions for critical experiments. For animals reared in isolation, the number of actions needed to transfer and record data for individual animals restricts the total number which can be handled by a single worker to a couple of hundred and minimal changing consistent with reliable results is necessary for practical reasons. The *Artemia* itself should be collected when less than 24 hours old. In fact if the screen into which they are siphoned is sufficiently fine, best results will be achieved by collecting nauplii just a few hours old, since the younger ones will live longer in the trays without food than older nauplii will. In practice it is usually necessary to allow the earliest hatched *Artemia* to remain in the hatching jars for several hours in order to be able to collect a large number of nauplii at once. Hatching generally continues for several days from the same initial stock of eggs, but the quality of the nauplii for rearing deteriorates rapidly after the first 24 hours.

In 1960 a small pilot study at Miami showed the feasibility of rearing larvae of tropical decapods in the laboratory, several species of hermit crabs and carideans being reared for the first time to metamorphosis. Grants from several government agencies aided in the establishment of a research program to study the development of tropical decapod larvae as part of the long-term activities of our Institute. Nearly 100 species have been studied to at least some degree and about one-third of these have been reared from hatching to metamorphosis. We have not concentrated on species

of commercial value, but an economically important species of shrimp was reared for the first time at our laboratory using basic methods worked out as a result of this program (Ewald, 1965).

Having discovered that local inshore species were not particularly difficult to rear with our methods as they had been developed at that time, we began to investigate some of the deep water species whose eggs and larvae were becoming available to us through the activities of our research vessels. We have obtained for study living material from the Straits of Florida, the continental shelf off the eastern United States, the waters near Bermuda, the Bahamas and from off West Africa. Bottom dwelling species are captured with otter trawls and eggs are removed from female decapods. The process of capture frequently kills the adult, but the eggs usually survive being brought through the warm surface waters, even from depths as great as 1,200 fathoms (approx. 2,300 meters). Foxton (1964) reported keeping eggs of a bathypelagic caridean for a month or two in the laboratory prior to hatching. He pointed out the difficulties usually attendant on keeping embryos or larvae of pelagic or deep-water organisms alive for any length of time. Before the availability of the modified shakers we were not able to agitate eggs removed from deep-water specimens which died in the course of being brought to the surface, but by placing the eggs in cold water of sufficient volume, some remarkable records have been established for holding embryos in the laboratory. Larvae of a number of forms have been obtained after holding the eggs for many months. Our present record is for a caridean shrimp, *Glyphocrangon spinicauda*, embryos of which were kept at approximately 7° C. for as long as 11 months. At capture, the eggs were undifferentiated, and by the end of the 10-month period the larvae were completely formed. Although those particular eggs did not hatch because of an equipment failure which permitted the temperature to rise to fatal level, other more advanced eggs kept for a shorter time did hatch (Dobkin, 1965).

In addition to eggs of benthic species we have captured pelagic larvae by means of Isaacs-Kidd midwater trawls. This gear will capture organisms which usually escape the slower plankton nets. As the specimens are taken by the trawl, they wash into a protective bucket which keeps the material in relatively good condition so that many crustaceans reach the ship's laboratory alive and active. The animals are placed into pre-chilled water and examined, the more important and prominent larvae being selected for individual care and placed in the plastic compartmented trays. Many of these animals have been maintained for extended periods, some as much as several months. Usually when a specimen is able to survive the first 48 hours, it is in good enough condition to take food and moult successfully one or more times in the laboratory.

Thus, we have been able to identify larvae which have metamorphosed into postlarvae or juveniles of described species. In some cases, the larval forms have been known from plankton for many years, but by observing the moult to postlarva or beyond it is possible to establish the identity of these forms. Many of the crustacean larvae captured with the high speed midwater trawl are very large in comparison with anything usually taken by plankton net. Nevertheless, we have found that of the larvae which we have kept through metamorphosis, even the largest are apparently normal larvae of species which may or may not be large as adults. One published example is the zoea and megalopa of a *Homola* species (Rice, 1964). The captured megalopas produced a first crab stage having 40% the linear size of an ovigerous adult.

In all tropical areas the lobsters of the scyllarid and panulirid groups are of considerable importance economically. It has been very difficult in the past to study the biology of phyllosoma larvae other than by means of plankton collections, because rearing in the laboratory from the egg has been very difficult. In fact perhaps the earliest instance of prolonged maintenance of phyllosomas in the laboratory is that of Inonue and Nonaka (1963) who succeeded in rearing *Panulirus japonicus* from hatching to 7th instar (about 6 weeks). As development proceeded they observed apparent dietary deficiencies. At our laboratory, Robertson has reared a scyllarid and a panulirid from hatching nearly to metamorphosis (up to 3 months from hatching) using basically the same technique already demonstrated to be successful for many other groups. He too has found an apparent dietary deficiency however, in the later stages. It appears that phyllosomas are mecha-

nically unable to capture sufficient food if only *Artemia* nauplii are provided but they are capable of capturing larger prey. If there is any considerable amount of debris in the water, phyllosoma larvae quickly become fouled and fail to swim. However, even unfed phyllosomas captured in good condition can be maintained for many days and through at least one moult if kept in clean sea-water, free of debris.

The identification of many decapod larvae is becoming possible through laboratory rearings from known adults or even from direct evidence of metamorphosis in some pelagic forms. Material once rare or unobtainable for experimental purposes can now become available in quantity for studies on morphology, physiology and ecology of larval forms. Every taxonomic group the larvae of which are studied will present problems of its own because of the peculiarities of those larvae, but there are some problems of general applicability.

There is the matter of adequate nutrition for larvae too small or physiologically too specialized to use *Artemia*. There is evidence that even for forms capable of reaching metamorphosis on a diet of *Artemia* alone, the quality or quantity of food has definite effects on development (Broad, 1957). Only when mortality rates are extremely low or can be demonstrated to be results of other environmental factors, can we say that we know adequately the nutritional requirements for a given species. Moreover, since *Artemia* does not occur in the natural habitat of decapod larvae, it is obviously a substitute for normal foods and the comparison of effects of diet of field and laboratory populations has yet to be investigated in detail for any species. The role of phytoplankton in larval nutrition is still poorly understood. It is known to be detrimental to some species when fed in the laboratory, but it seems to be required for some penaeids at least and possibly for some very small carideans. There is need for development of adequate artificial or processed food for maintenance of juvenile and adult Crustacea for long periods of time. Macerated shrimp or fish flesh or other "natural" foods are sufficient for keeping small numbers of animals alive, but if large-scale commercial culture of decapods (as well as other organisms) is to be practical, convenient and inexpensive manufactured foods will have to be developed much as modern feeds for poultry and other domesticated animals have been. Successes in recent years at a number of laboratories have made feasible investigations into the larval ecology of a number of commercial and potentially commercial decapod crustaceans. The kinds of information which can be gained from small-scale laboratory studies can be applied with great profit to the development of techniques for mass cultivation.

The decapod fauna of the western Atlantic is being investigated by a number of laboratories in that area, those of Duke and the University of Miami being examples. There are a number of workers studying species from the western American waters also, but there are relatively few life histories well known for that region. The larvae of western Europe and the Mediterranean are relatively well known taxonomically but there are still undescribed larvae in those fairly well studied areas. Almost every marine area offers much raw material for investigation of life-histories and the biology of larval forms, but the richest of all is the Indo-Pacific faunal region. It is here that the number of species and genera is highest and the larvae relatively, and perhaps in absolute numbers, the least known. It will be many decades before the decapod larvae of this area will be adequately described even with greatly increased effort. Everything possible should be done to encourage this work.

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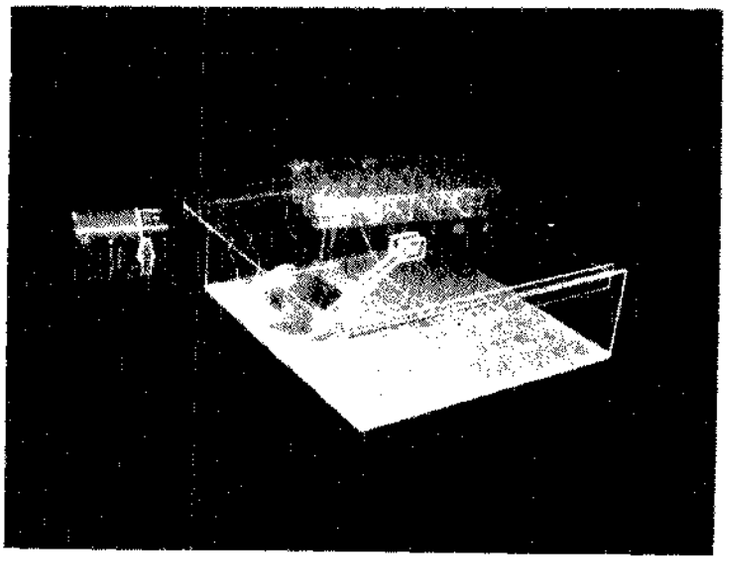

FIG. 1. A "*grass-box*" or rearing tray on the shelf of a specially built shaking device. The tray contains 18 individual compartments of 30 ml. capacity. Normally, each compartment is filled only with 15–20 ml. of sea-water, leaving the remainder of the volume as air. The cover prevents evaporation and keeps out dust. From one to five decapod larvae may be conveniently reared in each compartment. The shaker is not ordinarily used for agitation of trays containing larvae, but only for those with eggs which have been taken from the female decapod. The gentle agitation apparently aids in keeping the micro-environment of the egg well oxygenated. The volume of sea-water bathing eggs should be approximately 10 ml. for compartments of 30 ml. capacity.

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