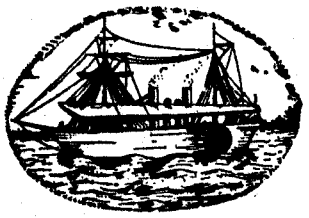
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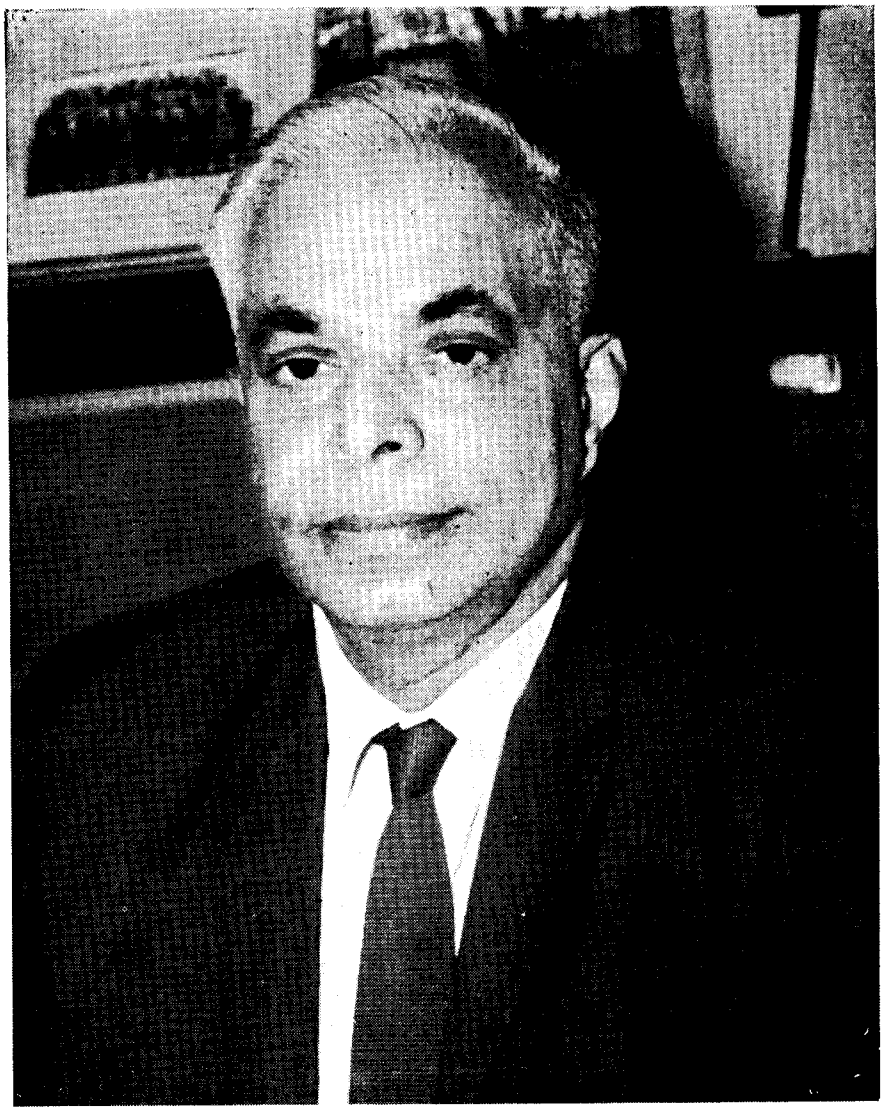
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FOREWORD

With respect and affection, this volume is dedicated to Dr. N. Kesava Panikkar on the occasion of his 60th birthday. The volume has been written by his friends, colleagues and students. For practical considerations, we had to limit the contents to a few invited contributions, and thus had to deny ourselves many more articles that were forthcoming. Even so, the contents of this volume are as varied as Dr. Panikkar would have liked them to be.

By nature, Dr. Panikkar is calm and pleasant. Very often, his mere silence could be as revealing as his other expressions. Not at all fond of irrelevant and verbose conversation, Dr. Panikkar depicts a different image of his personality to different persons. He is best described by his younger colleagues as pleasing and inspiring.

A man of outstanding ability and integrity, Dr. Panikkar became an institution by himself in the scientific circles of India and abroad. He shunned publicity and always tried to provide a solution to the major problems, instead of wasting time on peripheral issues. He seldom allowed himself to be swept by the majority consideration, if it was not, in his opinion, in the interest of a larger cause.

After an outstanding research career at the University of Madras, which earned him the degree of D.Sc at the age of 25, Dr. Panikkar was selected as an overseas scholar by the Royal Commission to work at the Universities of London and Cambridge. His four years' stay in England during the second world war was largely spent at the Marine Biological Laboratory, Plymouth, where he did his classical work on the osmoregulation in prawns. On his return to India, he joined as Professor of Zoology, University College, Trivandrum (Kerala) and later on as Director, Zoological Laboratory, University of Madras. Soon afterwards he was called by the Ministry of Food and Agriculture, Government of India, as Officer on Special Duty to organise fisheries research in India. As a result, the two central fisheries research institutes, viz., marine and inland, came into existence and Dr. Panikkar later became the Director of the Central Marine Fisheries Research Institute. He was again asked to go to Delhi as Fisheries Development Adviser to the Government of India in 1957 and in 1962 he took charge as Director, Indian Programme of the International Indian Ocean Expedition and later as the Director, National Institute of Oceanography. Thus in oceanography, he has had the longest stay, lasting more than ten years.

Dr. Panikkar was elected as Fellow of the Indian Academy of Science, Fellow of the Zoological Society of India, Fellow of the National Institute of Science (now Indian National Science Academy) and Fellow of the Indian Geophysical union. In 1963, he became the Secretary of the Indian National Science Academy and in 1966 was elected as Chairman of the Intergovernmental Oceanographic Commission (IOC). He is at present the President of Indian Geophysical Union, Chairman of the Indian National Committee on Oceanic Research, member of the National Commission on Agriculture and life member of the Marine Biological Association of India. He is associated with numerous scientific committees of India and abroad. On many occasions, Dr. Panikkar represented India at the International conferences on fisheries, oceanography, laws of the sea and living resources of the seas and has worked as member of several Expert Panels of the United Nations agencies. He has recently been honoured with 'Padma Shri' by the President of India.

Dr. Panikkar's research interests have been as varied as the positions he occupied in his very colourful scientific career. This is clearly reflected from his publications which do not fall into the category of any one type of specialisation. His contribution to the development of Indian marine sciences (fisheries and oceanography) has been so immense that it seems hard to comprehend how one person could achieve so many things in such a short time.

The ease with which he changed his employment, according to the needs of the country, and the ability with which he could keep up with his scientific interest, has been one of his major achievements. During his term as Fisheries Development Adviser to the Government of India, he planned the Central Institute of Fisheries Technology at Cochin, and as Chairman of the Committee on Fisheries Education, he became the founder of two more new institutes, the Central Institute of Fisheries Education at Bombay and the Central Institute of Fisheries Operatives at Cochin. His entry into the field of oceanography saw the birth of the Indian Ocean Biological Centre at Cochin and the National Institute of Oceanography at Goa.

In retrospect, one finds it hard to believe that such a busy and vigorous career can ever show signs of fatigue. Many institutions with which he has been associated have had the benefit of his advice and guidance and it would be no exaggeration to say that the Indian marine sciences, as these stand today, owe largely to the efforts of Dr. Panikkar. He has been a source of inspiration to younger scientists and the scientific community would continue to appreciate what Dr. Panikkar did for the development of oceanography and fisheries in India during the past 25 years. Surely he will have the satisfaction that what he did was for others and not for himself.

S. Z. QASIM
MAY, 1973

PUBLICATIONS OF DR. N. K. PANIKKAR

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ECOLOGICAL EFFECTS OF MARINE POLLUTION

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ABSTRACT

The living resources of the sea provide a substantial part of the world population with an essential source of animal protein, and the marine environment is a valuable resource for recreational facilities. In some of our estuaries, these resources are endangered at present by marine pollution, which has already limited our harvest of sea food in polluted estuaries. The remaining areas of the sea suitable for marine life must be protected from additional pollution if we are to maintain and increase our harvest of protein from the sea and to retain the amenities of the marine waters for recreational purposes. Critical marine pollutants are identified, and various methods of assessing the impact of these pollutants on marine life are discussed. Although additional research is needed before we can make absolute recommendations for acceptable levels of pollutants in the marine environment, it is also emphasized that we already know enough to recommend limits which appear, on the basis of present available knowledge, to provide assurance of minimal risk of damage to the marine environment. Some examples of these acceptable limiting concentrations are presented.

INTRODUCTION

The marine environment is subjected to many conflicting demands and uses, some of which are not compatible with others. Historically, the estuaries and harbors were selected for early settlement because of the ease of marine transportation of goods and materials. Even today, our densest centers of population are located either on the sea or in locations where ready access to the sea is available. Today, more than 50% of the population of the United States live in countries bordering the seacoast or the Great Lakes, and the concentration of population in these areas will probably increase in the future. Similar concentrations of coastal populations are found throughout the world. Concomitant with the growth of these coastal populations and for similar reasons, has been the concentration of industries along our seacoast. Thus, the marine environment has been subjected for generations to intensive population pressures and the demands of our ever-increasing technology.

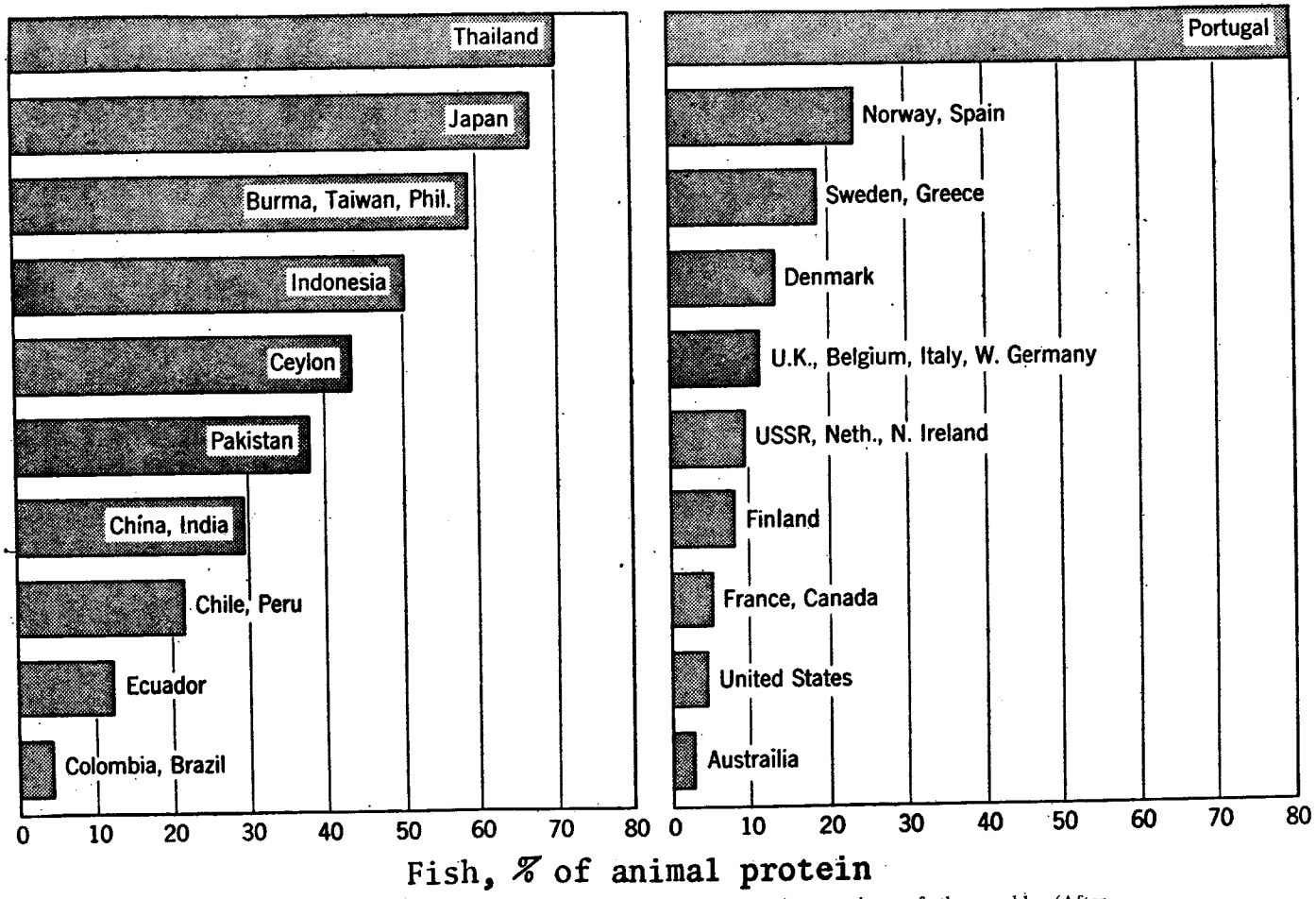


Fig. 1. The value of fish in the nutrition of peop'e in various nations of the world. (After Borgstrom, 1961; Ketchum, 1967)

These combined pressures have led to activities which have greatly modified the marine environment in many places, although some parts of our seashore are still relatively unaffected by man's activities. Harbor development has required extensive dredging and the construction of breakwaters and other structures to protect the shipping. The demand for coastal land and docking space has led to the filling of large areas of salt marsh and wetlands. The waste products of dense populations and of industries have been discharged into these waters with little understanding or appreciation of the possible effects. All of these activities have had impacts on the environment and have produced stresses on the marine ecosystem. So long as the receiving capacity of the body of water is not exceeded, the ecosystem is able to recover from these additional stresses without permanent damage. Today, however, in the most densely populated parts of this country and the entire world, the stresses resulting from man's activity have increased to the point where the marine ecosystem is not able to absorb them without damage, and we now realize that man's mode of action must be drastically changed if we are to retain a marine ecosystem of value to man.

The necessity of maintaining the marine ecosystem in a desirable condition is emphasized by two facts: 1) the animal protein derived from marine products is of great importance in maintaining adequate nutrition for many of the densely populated, developing countries of the world and, 2) the increasing demands for adequate recreational opportunities in aquatic environments supports one of the fastest growing industries in the United States' economy and that of other developed nations. Water of high quality is essential both for recreation and for the survival of the majority of the marine organisms of economic importance.

The annual world harvest of sea food is now nearly 60 million metric tons, (FAO, 1968) and this supplies more than half of the animal protein for about half of the population of the world. The importance of sea food in the nutrition of inhabitants of various nations is illustrated in Figure 1. (Borgstrom, 1961; Ketchum, 1967). Schaefer and Alverson (1968) estimated that the rate of harvest could increase four fold as a result of more effective utilization of all of the fish caught and the discovery of new fish stocks not now being exploited. Ryther (1969) is less optimistic and states that the harvest might double, but that further increases, except by intensive aquaculture, are unlikely. Neither of these estimates takes account of potential damage to the fisheries by increasing pollution impacts, though the deleterious effects of pollution are already obvious in most of the world estuaries.

The value of the marine environment for recreation is also high. It has been estimated by Winslow and Bigler (1969) that, in the United States alone, about 112 million people spent about $ 14 billion dollars seeking recreation in the coastal zone. Using the multiplier suggested by Goldberg (1972, p. 271)

the world value for recreation may be about triple this amount. Clearly, maintaining the quality of marine waters is economically essential, both as a source for food and for recreation.

To give perspective to the problems of global marine pollution, a conceptual framework for water quality evaluation is presented in Figure 2. The imports to the marine ecosystem and the exports from it are important to an understanding of the entire problem (Goldberg, 1972). A toxic chemical which is produced in large amounts, reaches the sea and persists for long periods of time in the marine environment, will have a vastly different impact than a chemical of equivalent toxicity which is produced in relatively small amounts and/or decays rapidly in the marine system. For the former type of pollutant, a screening mechanism should be available which could confine it to the source and not permit it to reach the environment, after which man loses most or all of his ability to control the impact of the pollutant.

Examples of the persistent pollutants which have been known to reach the sea in substantial amounts are the toxic elements, mercury, nickel, zinc, lead, manganese, copper, chromium, selenium, silver, arsenic and cadmium. These elements are listed in the approximate order of their deleterious effects as a function of their toxicity and the rate of mobilization by man and by natural weathering as shown in Table 1. Data from Bertine and Goldberg (1971) on the rates of mobilization by combustion of fossil fuels and by the present-day

TABLE 1. *Toxic elements of critical importance in marine pollution based on potential supply and toxicity*

Element	Rate of Mobilization (10^9g/yr)* A (man) Fossil Fuels	B (natural) River Flow	C Total	Toxicity† D mg/l	Relative Critical Index (10^{12} liters/yr.) A/D	C/D
Mercury	1.6	2.5	4.1	10^{-4}	16,000	41,000
Nickel	3.7	160.0	164.0	2×10^{-3}	1,350	82,000
Zinc	7.0	720.0	727.0	2×10^{-2}	350	36,350
Lead	3.6	110.0	113.6	1×10^{-2}	360	11,360
Manganese	7.0	250.0	257.0	2×10^{-2}	350	12,850
Copper	2.1	250.0	252.1	1×10^{-2}	210	25,210
Chromium	1.5	200.0	201.5	1×10^{-2}	150	20,150
Selenium	0.45	7.2	7.7	5×10^{-3}	90	1,540
Silver	0.07	11.0	11.1	1×10^{-3}	70	11,100
Arsenic	0.7	72.0	72.7	1×10^{-2}	70	7,270
Cadmium	0.002	0.5	0.5	2×10^{-4}	10	2,510

* After Bertine and Goldberg (1971)

† Water Quality Criteria: Concentration considered to pose minimal risk of deleterious effect except for mercury which is the concentration found in sea water and has already produced deleterious effects. After Waldichuk (1972), NAS (in press).

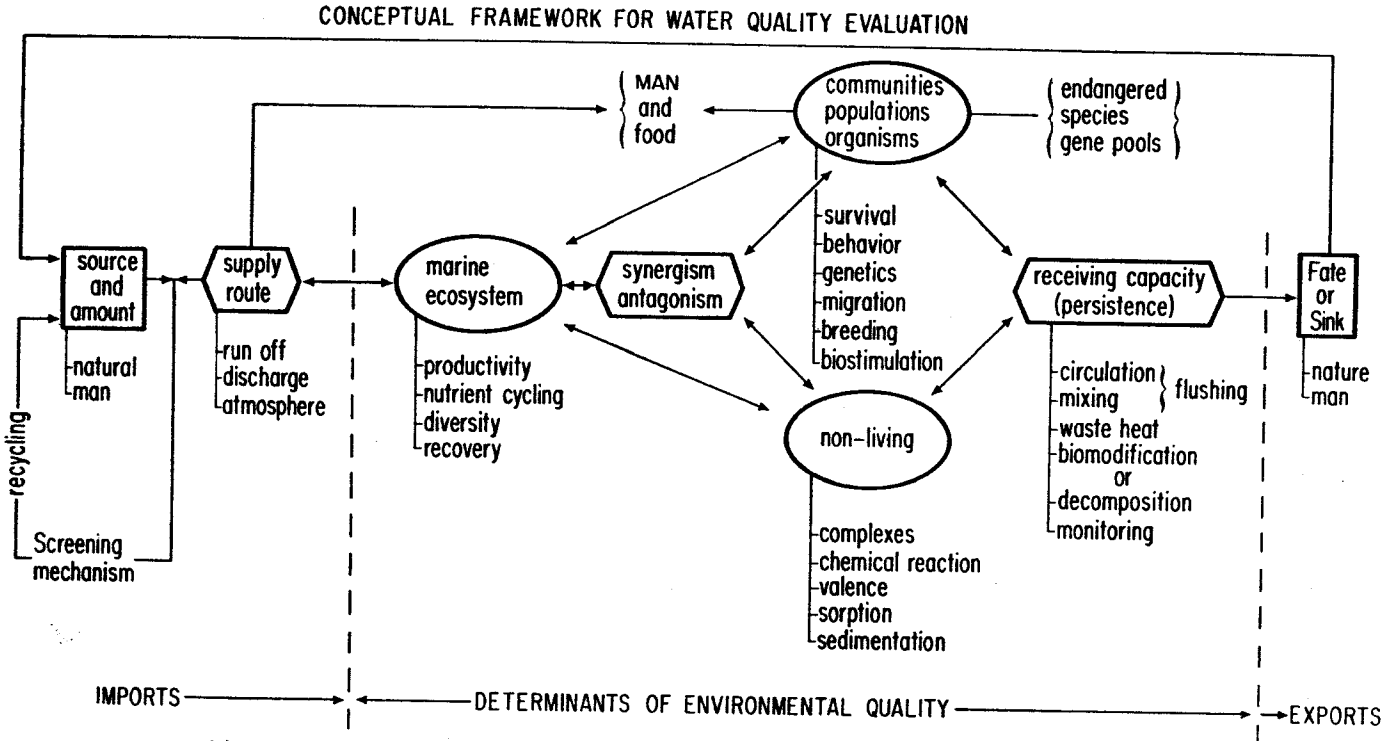


Fig. 2. Conceptual framework for water quality evaluation, showing the various parts of the ecosystem and processes which determine the importance of pollutants in the marine environment.

transport of the element to the sea in river flow are combined with data from Waldichuk (1972, NAS, In Press) on the comparative toxicities. Combined, these data produce an index of how critical the element may be as a marine pollutant. The supply from the combustion of fossil fuels provides a significant part of these materials carried by the atmosphere to the sea. The river transport is based upon analyses of dissolved material in river waters and known rates of flow, and reflects natural weathering, agricultural runoff and pollution sources. There are unquestionably other sources of supply for these elements, but the data used, although uncertain on a global scale, are adequate to rate the relative hazards.

Actually, this index gives the volume of water which would receive an annual increment of the element equal to the concentration shown in Column D (toxicity) at the given rates of mobilization. The unit, 10^{12} liters/yrs., is equal to a cubic kilometer per year. Thousands of cubic kilometers of ocean water are being seriously contaminated by these elements annually. Most of the input is natural geochemical cycling, but for the elements listed, man's contribution is also significant. Since the total water volume of the oceans is about 1.4×10^{21} liters, the time to raise the concentration of the whole ocean to toxic levels could also be calculated giving times, in each case, of many thousands of years. This is really a meaningless computation, however, because the oceans are not uniformly mixed, and the concentration at the locality where the pollutant is introduced will invariably increase more rapidly than the average for the whole ocean.

A wide variety of synthetic organic chemicals are also reaching the environment, particularly the chlorinated hydrocarbons such as DDT and its decomposition products and polychlorinated biphenyls (PCB's). These are not readily biodegradable, and the ocean is the ultimate sink for such compounds. Woodwell *et al.* (1971) have modelled the circulation of DDT in the biosphere and they conclude that the largest reservoir for DDT is in the atmosphere, but also that the amount not decomposed by ultravilot rays in the troposphere will ultimately be added to the surface of the sea. If production of DDT stops in 1974 the model predicts maximum concentrations in the mixed layer of the sea (upper 100 meters) in 1971 after which it would decrease to 10 percent of the maximum by 1993. If production were to increase, however, the concentrations in both the sea and the atmosphere would also increase.

Harvey *et al.* (1972) found substantial concentrations of DDT and its breakdown product, DDE (up to 100 μg/kg wet wt. in a shark) and even higher levels of PCB's (up to 1056 μg/kg wet weight in a dolphin) in a variety of organisms collected from the open sea many miles from land, confirming the probability of atmospheric transport. As expected, these compounds are concentrated in the lipid pool of the organisms with a maximum concentration of 3300 for DDT and DDE and of 21,100 μg/kg lipid for PCB's. None of the concen-

trations observed by Harvey *et al.* (1972) were as great as those assumed by Woodwell *et al.* (1971) for oceanic fish or plankton to estimate the accumulation in the biota (assuming dry weight to be 25% of wet weight). If further evidence confirms this difference, the residence time in the surface ocean waters might need to be modified in the latters' model.

A variety of synthetic organic chemicals, including other pesticides, detergents and pharmaceuticals are also undoubtedly reaching the marine environment with impacts which are virtually unknown. The detrimental effect of DDT on bird breeding potential is well documented and some experiments have been done on a few forms of marine life, but the information is still inadequate for a complete evaluation of the impact on the marine biota of DDT and even less adequate for the other synthetic organic compounds (SCEP Task Force, 1971; NAS, 1971; NAS, in press).

Petroleum, including crude oil, refined products and petrochemicals are also reaching the sea in large amounts. Numerous studies on the toxicity and effects of oil pollution have been made, but more careful studies of selected fractions of this complex mixture of hydrocarbons are needed and virtually nothing is known about the rate or turnover of this material in the marine environment (Revelle *et al.*, 1971). A number of scientific studies are needed for each of the pollutants listed above in order to evaluate adequately the "determinants of environmental quality" shown in Figure 2.

Biological Effects of Pollution

A marine pollutant may have subtle indirect effects on the ecosystem, which may be the result of a more direct effect on a certain species or group of species essential to the ecosystem (Fig. 2). The indirect effects may not be predictable from studies of individual parts of the ecosystem, and a change in the characteristics of the ecosystem may be an early warning indicator of deleterious effects. Laboratory micro-ecosystems, and experiments in ponds or tanks which include several components of the ecosystem can be useful in extending bioassays to longer time scales. Knowledge of ecosystem processes is necessary as a foundation for ecosystem models, which are valuable in defining critical studies or observations (Odum, 1971).

Ecosystem Analysis

The marine ecosystem includes all of the biological, chemical, geological and physical components of the environment and their highly complex interactions. The impact of water quality on the total ecosystem may be greater than the sum of the impacts on individual parts of the system. For example, eliminating or decreasing the abundance of an organism or life stage which is essential as food for another organism might disturb the entire pattern of energy flow throughout the system. It is essential to understand the interrelationships among organisms and between organisms and their environment in order to evaluate these subtle and secondary effects.

Studies of ecosystems must also include the imports to and exports from it. In the marine environment, imports and exports continually occur from coastal runoff, tidal action, oceanic currents, atmospheric fallout and exchanges with adjacent water bodies and with the benthos or the atmosphere. Each local environment is somewhat different from all others but the species inhabiting any given environment have evolved over long periods of time and each individual species in a community plays its own role. Any additional stress, whether natural or man-made, will tend to eliminate some species, leaving only the more resistant and tolerant forms to survive. Stresses which are transient may permit replenishment of the species by recruitment from adjacent unaffected areas. In such a case the impact may be reversible and the ecosystem can reestablish itself. A change which is chronic and permanent, such as the excessive pollution of some of our harbors, will never permit the recovery of the original ecosystem until the source of unusual stress is removed. Although the effects of water quality on the marine ecosystem are difficult to establish and evaluate, methods are now available which makes the interpretation of ecosystem studies much more meaningful than it was a few years ago.

In order to assess the impact of any new pollutant on a body of water, it is necessary to acquire information on the conditions existing before, during and after the addition. Information on the physical and chemical characteristics of the system, on the distribution and abundance of species, and on the normal variations of these characteristics over at least an annual cycle will be necessary. Evaluations of productivity, nutrient cycling, diversity and recovery potential should be emphasized.

Productivity and energy flow

The productivity of marine ecosystems varies from place to place and from time to time depending upon a variety of environmental factors including the availability of essential plant nutrients, the clarity of the water, and consequently the depth of penetration of sunlight of adequate intensity to permit photosynthesis, the stability of the water column, and the import and export of various materials into the system (Ryther, 1963). Methods for the study of primary production or photosynthesis, particularly of the planktonic populations, depend either upon the use of Carbon 14 and its assimilation by the plant in the production of new organic material (Steeman Nielsen, 1952) or by the evolution of oxygen in the process of photosynthesis (Riley *et al.*, 1949). The radiocarbon technique in polluted estuaries requires certain modifications (see Qasim *et al.*, 1969). Similar methods can be used in evaluating the productivity of the sedentary plant populations in shallow waters. It should be emphasized, however, that a high rate of productivity is not necessarily an indication that the ecosystem is healthy. The statement that Lake Erie is "dead" is biologically absurd since it is the most productive of the Great Lakes. It is not, however, necessarily a healthy ecosystem, since the species produced in Lake Erie today are not the ones most desirable for man's use (Hubschman, 1971; Beeton, 1969).

Nutrient cycling

The marine ecosystem provides a natural mechanism for the recycling of those elements which are essential for photosynthesis and growth of both plants and animals. Unlike energy, which follows a one-way path from its fixation in photosynthesis to its ultimate dissipation as heat regardless of the number of transfers through the foodweb, nutrients are returned to the system as a result of decomposition and can be used over and over again (Ketchum and Corwin, 1965). The productivity of the marine ecosystem is frequently limited by the lack of nutrients which are commonly reduced to very low concentrations in the illuminated part of the water column. Various types of pollution, such as domestic or food processing wastes, enrich the waters with nutrients and when present in excessive amounts can result in the replacement of the normal phytoplankton population with noxious species and change the entire biotic structure of the marine ecosystem in the process known as "cultural eutrophication" (NAS, 1969).

We need to develop more precise methods to evaluate the mechanisms and efficiency of nutrient recycling under a variety of marine conditions. In the shallow, inshore waters and estuaries the exchange of nutrients with the bottom sediments is an important part of this process (Sankaranarayanan and Qasim, 1969), though in the waters with depths greater than 100 or 200 meters, most of the organic material formed in the illuminated surface layers decomposes before reaching the bottom (Menzel and Ryther, 1970; Ketchum and Corwin, 1965).

The efficiency of the nutrient cycling system and the concentrations of nutrients which produce objectionable growths in the water require further and intensive study under a wide variety of marine environmental conditions.

Diversity

A wide variety of indices have been developed to evaluate the diversity of ecosystems (Sanders, 1968, 1969; Slobodkin and Sanders, 1969). These all relate the number of different species with the total abundance of organisms. In general the ecosystems with high diversity are also the most stable, in part because there are large numbers of pathways for the transfer of food and energy from one part of the system to another. Even natural and undisturbed ecosystems have, however, different degrees of diversity depending upon the natural stresses on the system. High diversity is generally associated with minimum stress such as is found in the tropics, where the annual cycle of change is small, or in the deep sea where it is continuously cold and dark. Low diversity is generally found in strongly stressed ecosystems such as the Arctic, where seasonal changes are severe, or in estuaries where the ebb and flow of the tide and fluctuating river flow produce severe stresses on time scales ranging from hourly to seasonally. Consequently, before diversity can be used as an indicator of change, the natural diversity of the environment being studied must be known.

Pollution, or any other man-made modification of the environment, can be considered as an additional stress imposed on the ecosystem and will tend to eliminate some species, leaving only the more resistant and tolerant forms to survive. The diversity will tend to be decreased by this additional stress, even under situations where the total productivity is increased. When the natural diversity of the system is known, the disappearance of sensitive species and the consequent decrease in diversity may be the first indication of impending deterioration of the environment. We need to study the diversity of a wide variety of marine ecosystems and learn to interpret changes in diversity as indicators of overall water quality.

Recovery of ecosystems

Very little is known about the ability of ecosystems to recover if the stresses imposed by man are modified or removed. Some man-made modifications are irreversible. A salt marsh which is filled, paved over and built upon or which is dredged for a navigation channel cannot be expected to return to its original condition. There is clear evidence, however, that the removal of sources of pollution, either by improved treatment processes or by transferring the pollutant to a water mass of greater receiving capacity can permit recovery (Edmondson, 1969 and 1970). This is especially true if the original species can be recruited from nearby unmodified areas. Much remains to be learned about the potential for deliberate restocking of a cleaned-up water body with imported species. For anadromous species, such as salmon which return to their birthplace to spawn, intentional restocking may be the only way to re-establish the population in the ecosystem.

When pollution has continued for many years, the sediments may form a large reservoir and may take years to recover. However, for pollutants which remain in solution, and are not changed by biological, chemical or geological processes, the recovery time will be a function of the flushing time of the system (see Fig. 2). The rates of exchange, which determine the flushing time (Ketchum, 1955), need both fundamental studies to improve our understanding of the mechanisms and application to many local situations which have not yet been investigated.

Effects on Communities, Population and Organisms

Knowledge of and an ability to work with organisms, populations, and communities which make up the living part of the marine ecosystem is fundamental to the understanding of the system and the effects of potential pollutants on the system. The biological effects of pollution may be reflected by acute toxicity to individual organisms or by chronic, sub-lethal effects on the survival of populations through modification of behavior, genetics, migration or breeding potential. Some pollutants may stimulate or accelerate biological processes, for example, fertilizers can increase the rate of photosynthesis and increased temperatures can accelerate the rate of respiration. These effects can modify the func-

tioning of the ecosystem, but cannot be evaluated directly without full evaluation of the impact on the system.

Acute toxicity

The acute toxicity of a pollutant is generally evaluated by means of a bioassay test on a selected organism. These tests determine the concentration of a substance which will kill one half of a population of test organisms within a given period of time, usually 48 or 96 hours. The results are reported as the lethal concentration for 50% of the test organisms (LC50), or median tolerance limit (TLm or TL50). The bioassay may be a static test, in which the organism is exposed to the test solution in a tank, or a flow-through system in which the test solution is continuously renewed. Both may determine sub-lethal effects as well as mortality. Methods for routine bioassays are described in standard methods for the examination of water and waste water (APHA, 1971) and their application is evaluated by Sprague (1971). Clearly, the LC50 is not a "safe" concentration and water quality criteria are set at a fraction (application factors of 0.1, 0.01 or less) of the L C 50.

Because organisms, and life stages of organisms, may vary considerably in their resistance to a given toxic substance the selection of the least tolerant life stage or organism is critical to the sensitivity and validity of the test. Research is needed to develop more effective bioassay methods for potential toxicants. The most sensitive marine organisms should be identified and cultivated on an egg-to-egg basis under laboratory conditions to provide genetic variability information on the test species and to form a basis for intercomparison of experiments and results.

Equipment and methods are needed for the collection, isolation, and production of all life stages of important aquatic organisms so that they may be available at all times in sufficient numbers for bioassay studies. The effects of organic and inorganic pollutants on marine organisms should be investigated with controlled variation of environmental conditions, including salinity, temperature, dissolved oxygen, and pressure.

An advantage of bioassays which duplicate existing conditions of the area being studied is that they measure the effect of the substance including the valence state and natural complexing with materials in sea water, and synergistic or antagonistic effects (cf Fig. 2). Thus, the total effect can be estimated without a clear understanding of all mechanisms involved. This does not, however, obviate the need for such an understanding because only with firm knowledge of the mechanisms involved can transfer of information to other systems and prediction of effects be achieved. Application factors relating acute toxicity data (bioassays) to long-term effects must be developed in order to define more precisely tolerable environmental levels.

Chronic, sub-lethal effects

Many biological effects of pollution may not show up in the bioassay test for acute toxicity. This would be true if the effect were slow to develop or if the effect were to produce a general debility which might interfere with some of the normal life functions of the organism rather than killing it directly. Long-term exposures to sub-lethal concentrations may be necessary to produce the effect, and evaluation of this type of action is difficult in a laboratory analysis. Long-term exposures to sub-lethal concentrations may produce effects on migration, behaviour, incidence of disease, life cycle, physiological processes, nutrition or food chains, or genetics which are not revealed in tests shorter than complete life cycles or number of generations. Unfortunately, little is known about these chronic, sub-lethal effects. Behavioural scientists should be encouraged to seek methods for evaluating the effect of pollutants on activities of marine organisms and to identify low levels of pollutants which may have undetectable short-term effects. Long-term studies on sensitive life stages of organisms should be undertaken to provide a basis for application factors.

a. *Migrations*

Sub-lethal concentrations may interfere with the normal migration patterns of organisms. The mechanisms used for orientation and navigation by migrating organisms, though extensively studied, are still not well understood (Hasler, 1966; Bardach and Todd, 1970). In some cases chemotaxis plays an important role. Salmon and many other anadromous fishes have been excluded from their home streams by pollution though it is not always known whether the reason is that a chemical cue has been masked or because the general polluted environment is offensive to the fish.

b. *Behaviour*

Much of the day-to-day behaviour of species may also be mediated by means of chemotactic responses (Bardach and Todd, 1970). The finding and capture of food, or the finding of a mate during the breeding season would be included in this category of activity. Again, any pollutant which interfered with the chemoreceptors of the organism would interfere with behavioural patterns which are essential to the survival of the population.

c. *Incidence of disease*

Long-term exposure to sub-lethal concentrations of pollutants may make an organism more susceptible to a disease. It is also possible that some pollutants which are organic in nature may provide an environment suitable for the development of disease-producing bacteria or viruses. In such cases, even though the pollutant is not directly toxic to the adult organism it could still have a profound effect on the population of the species over a longer period of time.

d. *Life cycle*

The larval forms of many species of organisms are much more sensitive to pollution than are the adults which are commonly used in the bioassay. In many aquatic species millions of eggs are produced and fertilized, but only two of the larvae produced need to grow to maturity and breed in order to maintain the standing stock of the species. For these species the pre-adult mortality is enormous even under the best of natural conditions. Because of an additional stress on the developing organisms enough individuals might fail to survive to maintain the population. Interrupting any stage of the life cycle can be as disastrous for the population as would death of the adults because of acute toxicity.

e. *Physiological processes*

Interference with various physiological processes, without necessarily causing death in a bioassay test, may also interfere with the survival of a species. If photosynthesis of the phytoplankton is inhibited, algal growth will be decreased and the population may be grazed to extinction without being directly killed by the toxic. DDT has been shown by Wurster (1968) to depress photosynthesis in planktonic algae, but only at concentrations greater than its solubility in water (about 1 ppb). Menzel. *et al.* (1968) demonstrated that different phytoplankton species showed various responses to DDT, dieldren and endrin ranging from no effect to toxicity at concentrations of 0.1 to 1 ppb.

Respiration might also be adversely affected as could various other enzymatic processes by sub-lethal concentrations of pollutants. The effect of DDT and its decomposition products on the shells of bird eggs is probably the result of interference with enzyme systems. Mercury is a general protoplasmic poison but has its most damaging effect on the nervous system. In humans this is known to be serious; how it affects fish and other aquatic organisms in sub-lethal concentrations is still unknown.

f. *Nutrition and food chains*

Pollutants may interfere with the nutrition of organisms by affecting the ability of an organism to find its prey, by interfering with digestion or assimilation of food, or by contaminating the prey species so that it is not accepted by the predator. On the other hand, if predator species are eliminated by pollution the prey species may have an improved chance of survival. An example of the latter effect was shown for the Kelp resurgence after the oil spill in Tampico Bay, California (North, 1967). The oil killed the sea urchins which used young, newly developing Kelp as food. When the urchins were killed, the Kelp beds developed luxurious growth within a few months.

g. *Genetic effects*

Many pollutants produce genetic effects which can have long-range significance for the survival of species. Radio-active contamination

can cause mutations directly by the action of radiation on the genetic material. Also oil and other organic pollutants may include both mutagenic and carcinogenic compounds (Blumer, 1970). From genetic studies in general it is known that a large majority of mutations are detrimental to the survival of the young, and many are lethal. Little is known about the intensity or frequency of genetic or developmental effects of pollutants, except for radioactive materials (Donaldson and Foster, 1957). The doses required for serious damage greatly exceed the radioactivity present as pollution in the marine environment (NAS, 1971).

h. *Food value for human use*

Sub-lethal concentrations of pollutants can so taint sea food that it becomes useless as a source of food. Oil can be ingested by marine organisms, pass through the wall of the gut and accumulate in the lipid pool. Blumer (1969, and 1970) states that oil in the tissues of shellfish has been shown to persist for several months after an oil spill in Wets Falmouth, Mass. The polluted area was closed for shellfishing for a period of 18 months. Sea food may be rendered unfit for human consumption because of the accumulation of pollutants. California mackerel and Coho salmon from Lake Michigan were condemned because they contained more DDT than the permissible amount in human food (5 ppm,. Likewise tunafish and swordfish were removed from the market because the mercury content of the flesh exceeded the allowable concentration (0.5 ppm). There was no evidence that these concentrations had any adverse effect on the fish, but their removal from the market has adversely affected the economics of the fisheries.

Sub-lethal effects on chemotactic responses, reproductive efficiency, survival, growth, vigor, behaviour, and general activity should be studied. A debilitation index developed from this type of research could provide indications of incipient toxicity. Studies of metabolic rates under multifactorial combinations of various environmental components in the presence of pollutants are needed.

Non-living Components of the Marine Ecosystem

The aqueous chemistry, biochemistry, and geochemistry of substances within the marine system control the form of substances available to react with and affect marine organisms. Relatively little is known about the reactions of substances in sea water, the dynamics and equilibria involved or the rates. There is a need to understand the natural chemical system of sea water and the interaction of man introduced substances with the system. Of particular concern are the role of synthetic organics in complexing inorganics, the role of surface films in water-atmosphere exchanges, and the residence times of organic and inorganic constituents.

Because of the presence of a large number of salts in sea water of various concentrations, it can be expected that in some cases there may be an antagonis-

tic effect and, in some cases, synergism with respect to certain inorganic constituents in sea water. This should be carefully studied on species that are extremely sensitive to small changes in pollutant concentrations. The effects of sea water on the synergistic and antagonistic aspects of inorganic chemicals in the marine environment need further study. When heavy metals are present in combination in effluents, synergism or antagonism can be expected. A series of combinations and permutations should be tested under different conditions in both fresh water and sea water to understand more fully the mechanisms involved.

Many inorganic chemicals exhibit different degrees of toxicity when they are present in different valence (oxidation) states. There may be some logical order, according to the periodic classification, for toxicity of inorganic constituents, based on atomic number, molecular weight, number of electrons in the outer orbit, etc. Preliminary examination has already shown some measure of consistency with respect to the periodic classification, in acute bioassays.

Different elements vary widely in toxicity according to their chemical form. For example, the methyl mercury form is highly toxic compared to the ionic mercury form (Ui and Kitamura, 1971). There may be other metallo-organic forms of the elements which are highly toxic also, and which we do not recognize at the present time. Organic complexes such as those formed with NTA Nitrilotriacetate) and EDTA (Ethylene diamine tetraacetic acid) appear to be relatively harmless and tend to detoxify the heavy metals. However, there have been shown to be some side effects at high concentrations of NTA complexes and these should be further investigated. The complexing and dispersion of inorganic constituents by various organic materials in water, both natural and introduced, must be more fully examined.

We require more sensitive methods of chemical analysis for the detection and measurement of both inorganic and organic constituents in water and organisms. This particularly applies to sea water where there is a great deal of interference from the numerous elements and compounds present. Identifying effects of concentrations of substances in aquatic organisms have been hampered by the lack of adequate methods of detection of the particular material in the water or organism. Recognition of the importance of various pollutants in the sea has followed improved methods of analysis. This is particularly true of mercury and DDT. Improved methods of chemical analysis for many organic and inorganic chemicals are needed. Intercalibration or comparison of results obtained by investigators in different laboratories or using different methods is essential.

The Assimilative Capacity of Marine Systems

We need to learn more about the receiving capacity of various marine areas in order to evaluate the amount of waste materials which can be introduced

without exceeding the concentration recommended for water quality criteria. The receiving capacity of a system is determined both by the physical processes of circulation and mixing and by the biological and geological processes which modify, decompose or remove the pollutant from the system. Fundamental studies of these processes are needed to develop the methodology which can be applied to a variety of locations. Each location, however, will have some unique characteristics so that local conditions and the processes operating there which determine the fate, concentration and distribution of a pollutant must be studied in order to assure that a proposed rate of disposal will not exceed levels harmful to the ecosystem.

Flushing times

A conservative pollutant is, by definition, one which is not modified by biological, chemical or geological processes. If such a pollutant remains dissolved or suspended in the water column its distribution in the marine system is determined by the same circulation and mixing processes which determine the distribution of salt or river water (Ketchum, 1955). The average retention time or the half life of the material in the system can be used to estimate the average concentration which the pollutant will achieve in the system if it is added continuously at a uniform rate. If the disposal is stopped, the rate of removal from the system can be evaluated if the rates of circulation and mixing are known. The faster the flushing time of a system the greater the receiving capacity of the system will be without exceeding unsatisfactory levels of concentration. Also the recovery from a stress imposed by a pollutant will be more rapid if the circulation and mixing provide a rapid flushing.

Estimates have been made of the rate of flushing of numerous estuaries (see Wyatt and Qasim, 1973 for Cochin Backwater), but additional fundamental studies are needed in order to improve our capability to predict and evaluate the flushing rate of a variety of systems. The methods developed in these fundamental studies can be applied to different systems, but always with the caveat that the model selected must be validated for each system in order to assure that it is applicable.

Waste heat

Disposal of waste heat from power plants requires accurate knowledge of the volume of water available for dilution which is a function of the circulation and mixing of the water column which determine the rate of flushing. It is a special case because the warm water modifies the circulation and mixing. The density of heated water is less than that of the receiving body of water so that it tends to accumulate at the surface. Heat is not a conservative property since it is dissipated to the atmosphere at a rate which depends upon both the gradient of temperature in the water column and the difference bet-

ween the temperatures of the heated water and the atmosphere. Better methods are needed to predict the fate and extent of warm water plumes as a function of the permissible temperature increase. Information is needed concerning the rate at which the heat is dissipated to the atmosphere under a variety of conditions.

Biological, chemical and geological modifications

A non-conservative pollutant is, by definition, one that changes with time by processes which are additional to circulation and dilution. Pollutants may be decomposed biologically or chemically or they may be precipitated or sorbed onto particulate matter and sedimented to the bottom deposits. The half life of non-conservative materials in the environment is the product of these processes and the processes of circulation and mixing. The materials of greatest concern as pollutants in the marine environment are those which are most stable and persistent in the environment, such as the toxic heavy metals which can be removed from the water column only by accumulation in the biota or by sedimentation, and the stable chlorinated hydrocarbons which are only decomposed slowly with the production of by-products which may be as toxic as the original. Petroleum hydrocarbons are intermediate in their persistence in the marine environment but, again, the products of decomposition may be more toxic than the original oil from which they are derived. Organic materials which are similar to those which are naturally found in the sea, such as domestic sewage and food processing wastes, are decomposed more rapidly, with, however, the release of elements essential for plant nutrition and productivity, leading at high concentrations to eutrophication (Qasim and Sankaranarayanan, 1972). We need to know precisely the rates of modification in order to evaluate the long-term impact of various pollutants on the marine ecosystem. Research is needed on the rates of biological degradation and decomposition, on the chemical reactions which various compounds or elements undergo when introduced into sea water and on the rates of sorption and precipitation to the sediments.

Even when materials are incorporated into the sediments they may not be permanently removed from the water column. Decomposition of organic material within the sediments or exchanges between the sediments and the water column. proceed at rates which are virtually unknown. This is exemplified by our lack of information on the ultimate fate of the sewage sludge which has been dumped off New York Harbor for the past 40 years. Until we know the rate at which this is being modified, decomposed or recycled it is impossible to predict whether this is a safe and acceptable procedure or what quantity of such sewage sludge can safely be disposed in this manner.

Various chemicals can be accumulated by organisms to concentrations within their body several orders of magnitude greater than in the surrounding

water. For some materials, DDT for example, the concentration may increase at each succeeding step of the food chain. The extent of bio-accumulation for various pollutants and the effects of transfer from organism to organism will determine or modify the magnitude of the biological effect.

Monitoring And Information Exchange

In attempting to evaluate water quality or pollution problems, both scientists and administrators are often faced with a lack of adequate information. It is generally impossible to extrapolate from information on a few local areas to evaluate the total or global impact of a given activity, and frequently the information available on one area is not readily transferable to another one of different characteristics. A monitoring system and a mechanism for the retrieval and dissemination of monitoring data is needed. However, it is abundantly clear that we cannot monitor for all possible pollutants in all possible places so that careful thought has to be given to the design of the system. Any effective monitoring system must satisfy at least the following objectives :

a. To establish present-day baselines
b. To detect and evaluate trends of change
c. To give advance warning of approaching critical conditions
d. To detect accidental critical events
e. To provide an adequate system for data storage retrieval and dissemination

Various international groups such as GESAMP (Joint Group of Experts on the Scientific Aspects of Marine Pollution), GIPME (Global Investigation of Pollution in the Marine Environment) and SCOPE (Scientific Committee on Problems of the Environment) are considering the details of monitoring the global environment for pollution. To insure that such a monitoring system is effective it will be necessary to select the critical materials which should be monitored in the marine environment and the critical locations where the measurements should be made. Research for these purposes should include studies of the necessary frequency, both in space and time, required to give significant information adequate to achieve the objectives listed above for a monitoring system. Standard methods of analysis, or at least intercomparison and intercalibration of the results will also be needed. Chemical, physical, and biological methods of analysis should all be evaluated in this regard. An adequate information storage and retrieval system will be required so that the critical monitoring data are readily available not only to the scientific community but especially to administrators and the elected officials so that appropriate and justifiable decisions can be based upon the best available information.

Discussion And Conclusions

The disposal of wastes to the marine environment has long been an accepted practice but it has been done without understanding or considering the possible consequences. The sea, however, has a finite assimilative capacity for any given type of pollutant. Locally this capacity of the marine system has already been exceeded in many places. For example, Ketchum (1969) estimated that the Hudson River estuary is now receiving 5 to 10 times more domestic pollution than can be absorbed by the ecosystem within a forty-mile length of the estuary. Beyond this distance, dilution reduces the nutrient concentration to acceptable limits. Some pollutants, such as mercury, are naturally present in sea water at concentrations which have already produced deleterious effects. In other cases, particularly the chlorinated hydrocarbons, the material is not naturally produced and organisms capable of metabolizing them rapidly have not evolved, so that these compounds persist for long periods of time in the environment. In cases such as these, further additions as a result of man's activities should be prohibited. The concept of zero discharge rates for pollutants which can be assimilated by the marine ecosystem, however, is not reasonable, but it is essential to know the assimilative capacity and, by further treatment or diversion, maintain the ambient concentrations within acceptable limits for ecosystem maintenance and survival.

Throughout this paper, the need for additional scientific investigations has been repeatedly emphasized. We should recognize, however, that we already know a great deal about the marine ecosystem and that reasonable models already exist and can be applied in many cases to evaluate discharge rates which will maintain acceptable limits of pollutant concentrations. We can evaluate the impact of many pollutants on living marine resources, and can specify the degree of treatment or type of approach necessary to stay within acceptable limits of water quality (FWPCA, 1968; NAS, in press). Generally the technology is available to permit industrial development while maintaining, at the same time, acceptable environmental conditions. It is abundantly clear, however, that we can no longer continue to be indiscriminate in our actions and that drastic changes will have to be made in man's activities in order to maintain the marine environment in a condition of desirable quality for posterity. To achieve this goal will require the best efforts of scientists and engineers of government officials and industrial leaders and of diplomats and international organizations. Marine pollution is no longer a local problem, or one that can be ignored. It is encouraging that the United Nations Conference on the Human Environment in Stockholm in June 1972 recognized the urgency of marine pollution problems, among others, and recommended cooperation among member states and international action to reverse the trend of deterioration of our environment for the benefit of all mankind.

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FOOD AND THE STABILIZATION MECHANISM IN FISHES

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ABSTRACT

A study of stock/recruitment processes in model form suggests that the natural mortality of fishes is a density dependent function of age. With an estimate of the larval mortality of the plaice in the Southern North Sea, the trend of natural mortality with age was estimated. A critical age was defined as that at which the specific growth rates and specific mortality rates become equal and it was suggested that in older age groups mortality might become senescent. In the models used, mortality rate in the larval stage depends upon the variability of food and there is a sense in which subsequent recruitment is determined by the patchiness of the food. There is a distinction between such an exploratory character in the density dependent mortality that may establish the magnitude of recruitment and the conservative character of the stock dependent on which the initial numbers are based. Differences in the ratio of specific growth rate and specific mortality rate during larval life might express competitive differences which would affect the magnitude of recruitment and eventually the quantity in the stock. A consequence is that possibly high diversity is the result of low competitive pressures and vice versa.

It is a truism that the numbers of animals depend upon the supply of food, and it was the central theme of Lack's (1954) book on the "Natural regulation of animal numbers". The reproductive rate was considered to be adapted by natural selection to the food supply and numbers were controlled by density-dependent mortality. The same principles apply to fishes, where the mechanism of stabilization operates during juvenile life through density-dependent mortality (which may be linked to density-dependent growth). Fecundity cannot be the driving force during adult life because density-dependent growth is by then more or less absent. Variation in stock is expressed through fecundity in the initial numbers of eggs and larvae. However, the mechanism of stabilization itself is linked to fecundity (Cushing, 1971) in that density-dependent mortality is probably higher in the more fecund fishes (Cushing and Harris, in press, *a*).

The very large reduction in numbers during immature life is often regarded as a loss or a wastage in the face of a hostile environment. Because the fecund fishes can stabilize their population well, it does not follow that they must live in adverse conditions. Further, if the numbers are really wasted, the evolutionary processes which operate across the food chains must appear to be inefficient. In this paper another explanation is put forward which may be more relevant to the mild and benign environment in which fishes live.

There are two developing models of the growth and mortality of fishes during larval life. Jones (in press) shows that haddock larvae grow at 12%/d and die at 10%/d, and he suggests that they grow through a succession of predatory fields and that they live on 'private' food sources which develop at the same time as the larvae. A density-dependent mortality is generated by varying the numbers of larvae. Jones suggests that the coefficient of variation of gadoid year-classes in the North Sea is correlated with probable ranges of food available to the different populations.

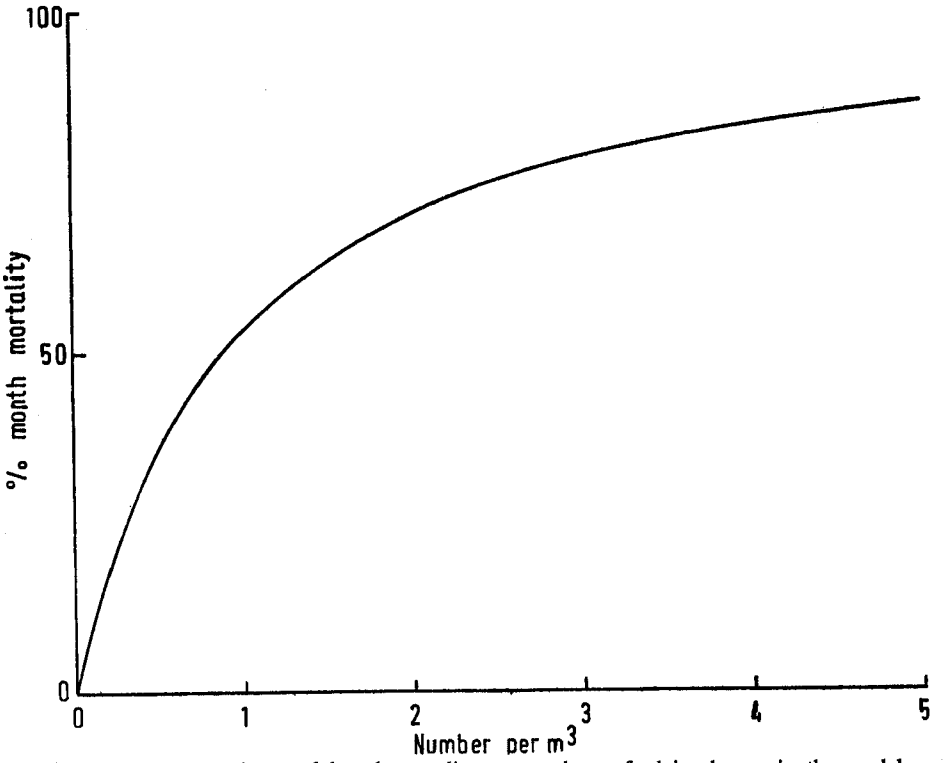


Fig. 1. Dependence of larval mortality on numbers of plaice larvae in the model described.

The second model, that of Cushing and Harris (in press, *a*) and Cushing (in press), proposes that, in rich food, larvae eat well, grow well, swim quickly and minimize predation; in scarce food, however, for converse reasons predation is greater. Variations in the numbers of larvae generate density-dependent mortality and variations in food alter the degree of density dependence. Fig. 1 shows how the larval mortality (as percentage per month) depends upon the numbers of plaice larvae in the sea, in model terms. The numbers per m^3 correspond to those in the sea and the observed mortality rate of plaice larvae is 80% per month (Harding and Talbot, in press), so the external constraints to the model are approximately right. Fig. 2 shows how in the model the weight

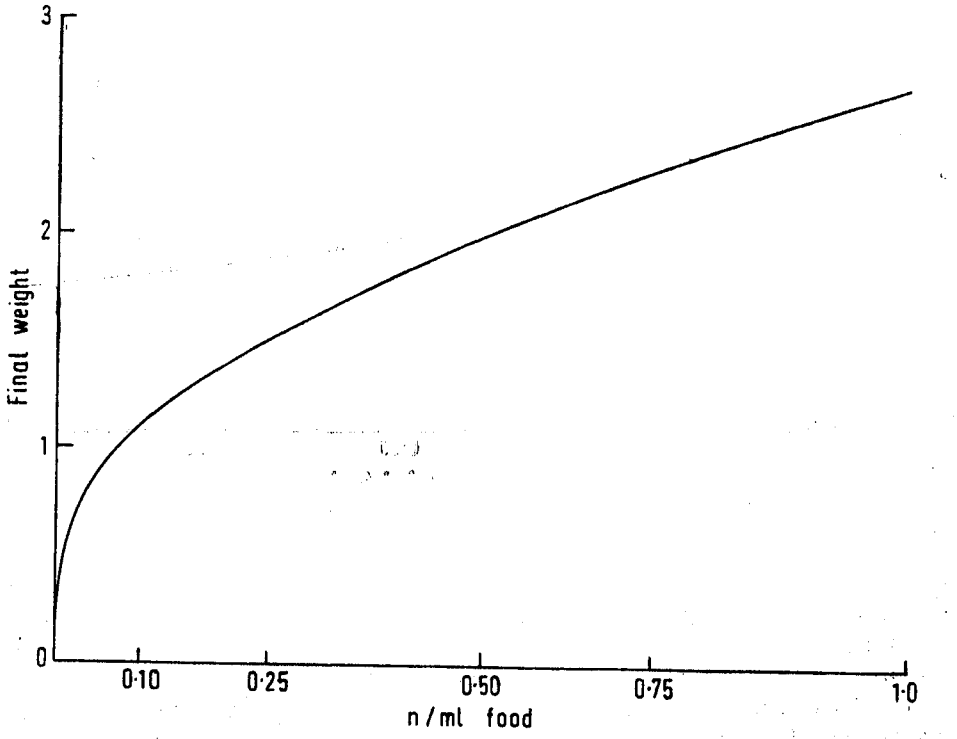


Fig. 2. Dependence of larval weight on food in the model described.

after 30 days depends upon food density, that is, the weight of larvae increases with food in roughly the form of an Ivlev curve. Fig. 3 shows how the percentage mortality per month varies with food density for a constant number of larvae; the mortality rate is high (but corresponds with that observed) and the differences between food levels are low. The growth rates and mortality rates are roughly those observed. It is shown that density-dependent mortality can be generated in the larval stages of plaice as a function of the food available. Such models have been proposed in the past (Ricker and Foerster, 1948; Beverton and Holt, 1957) for short periods during larval life. However, the processes

described in the two models are very general and could be applied, in principle, to fish of any age; however, such processes must be much sharper in larval life, and conversely in adult or older fish they are slight.

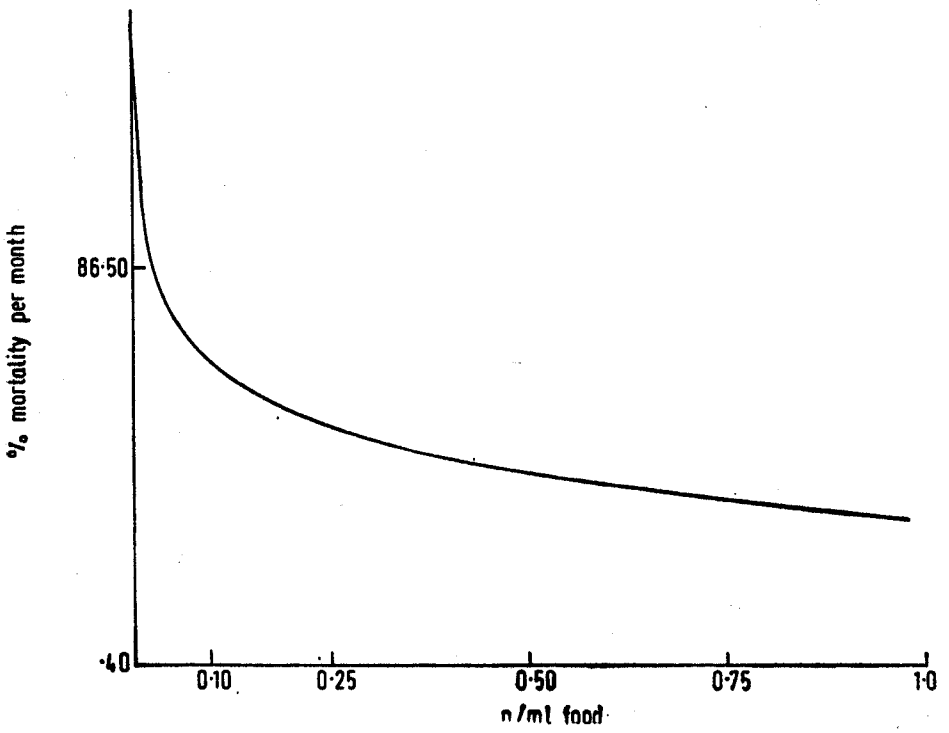


Fig. 3. Dependence of larval mortality rate on food in the model described.

Fisheries biologists have usually considered that density-dependent mortality was a small proportion of the total. One of the reasons for this belief is that the variability in recruitment is very high as compared with that in stock (as, for example, in a stock and recruitment curve). The density-independent mortality is usually considered to be the wastage in a hostile environment. If, however, we suppose that the natural mortality of fishes were density dependent throughout life (primarily because predation must be considred as a density-dependent process; the time to capture and eat a prey organism is constant, but the time to search is inversely proportional to prey density and as the ratio of the first to second increases with density, predation is density-dependent), the variability of recruitment is considered as the end product of a continuous process during immature life. Ricker's equation (1958) relating recruitment to parent stock supposes that the tangent to the curve at the origin represents density-independent mortality. He supposed that control as density-dependent mortality is generated by the aggregation of predators on to the initial numbers of eggs and

larvae. Beverton and Holt (1957) arrived at the same curve in formal terms in supposing that fish larvae grow through a critical period at different rates according to the food available, which generates density-dependent mortality, according to the numbers of larvae. Both processes were considered to be active amongst the eggs and larvae in the sea, but there can be no distinction between the eggs produced by one fish and those produced by more than one. If all mortality were density-dependent, the distinction would not matter because only the single process is effective. Then any density-independent mortality is an instantaneous loss which is subsequently modulated in a density-dependent manner during the remaining life-cycle. If we suppose that natural mortality is a density-dependent function of age (because predation is also density-dependent), it can be shown (Cushing, in press) that $N_t = N_0/(1 + M_0 t)$ and that $N_0 = (N_0 - N_t)/N_t \cdot t$, where N_0 is the initial number of eggs or larvae, N_t the number at time t and M_0 the initial mortality rate. The curve of number in time descends sharply and tends to flatten in adult life. Such trends of numbers of larvae, O- and I-group fishes with age have been presented on a number of occasions (e.g., Pearcy, 1962).

In different species of fish, the specific mortality rates $\left(M^X = \ln (N_{t+1}/N_t)\right.$, where N_t and N_{t+1} are numbers in a cohort in successive years calculated from the density-dependent curve on age$\left.\right)$ are practically the same at a given age during adult life. Then the differences in natural mortality between species are really differences in the age of first maturation and the duration of adult life. The growth of adult fishes is not density-dependent as a general rule (an exception is the large Pacific halibut, in which density-dependent growth is evident in the youngest adult age-groups only; Southward, 1967); consequently, the specific growth rate, G, can be readily determined. Then a critical age (corresponding to Ricker's, 1945, critical length) can be defined as that at which $(G - M^X) = 0$. Between the age of first maturation and the critical age in the virgin stock, the population fecundity increases, but at greater ages it must decrease and the animals might well then become senescent. Indeed, Greer-Walker (1970) has shown that the white muscle fibres of older fish decrease in size as they grow older—at about the critical age of 16 in cod. In the older fish, the escape speeds and the attack speeds must therefore decrease with age. If senescence is a reality in fishes, the population fecundity is limited by the critical age. Hence, on average, and only on average, the population should replace itself by the critical age. A larger stock would be corrected by density-dependent processes in the subsequent generation and a smaller stock would be augmented by the fecundity of the senescent population. If the population replaces itself by the critical age, two adults should be generated by

n gonads, where n is the number of age-groups between the age of maturation and the critical age; thus a scale is provided for the equation given above. It can be located by the observed larval mortality rate of 80%/month in the plaice of the southern North Sea; then the estimates of 40%/month in the first summer and of 10%/month in the first winter and of 10%/year from the ages of 5 to 15 (Beverton and Holt, 1957) can be derived and they correspond in fact to the observed mortalities. For the plaice, at least, the trend of natural mortality with age is well described by the density-dependent function. At first sight it is an improbable conclusion, but not on later consideration. A fuller account is given in Cushing (in press) and in Cushing and Harris (in press, *b*).

Harris (in press), in a study of the equations which relate recruitment to parent stock, has distinguished stock dependence and density dependence. Ricker (1954, 1958) suggested that fish populations were controlled by the aggregation by predators on to the initial numbers of eggs or larvae. Such stock dependence can perhaps be generated in other ways, but it must always play an essential part in control. Density dependence, in the new and narrow

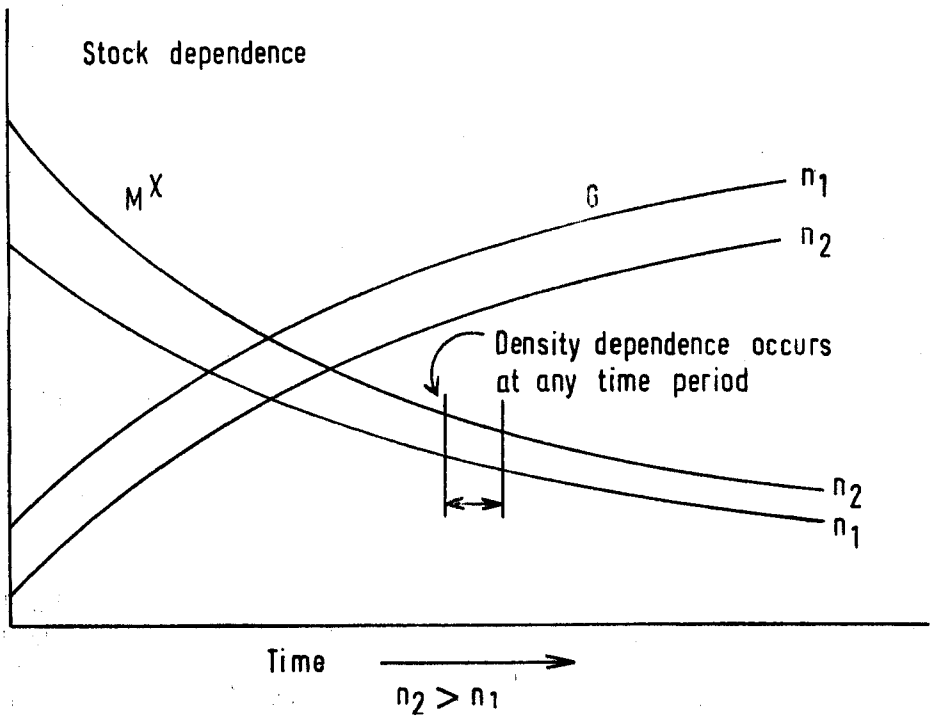


Fig. 4. Stock dependence and density dependence in an ideal state.

sense, occurs later, in larval life or in juvenile life and it may well be generated as in the models described above. An important point, which Dr Gulland has made to me, is that density dependence must operate during a period of time.

The distinction between the two forms of control is reminiscent of Gulland's (1965) distinction between a coarse control and a fine control. Fig. 4 illustrates the distinction as a trend of numbers with age: stock dependence represents the movement of initial numbers of eggs and larvae on the ordinate, whereas density dependence represents the shift of the curve in age upwards or downwards, that is, between n_1 and n_2 on the figure. For a given initial number of eggs and larvae, the trend of density-dependent natural mortality with age must represent an average condition. The variance about the curve is represented by the variation in recruitment. Another form of variation may be represented by differences in the numbers at the critical age; if it remains at 2.1 for a number of year-classes the population expands rapidly, and vice versa. These considerations show that the trend of natural mortality with age is not quite the rigid structure which was proposed above.

During the first year or so of life, at least, differences in the initial number generate differences in the specific mortality rates at given ages, that is, from month to month. In the models described above, it was shown that density-dependent mortality was a function of the availability of food. Fig. 5 illustrates the trend of specific mortality with age during an early period of life. At a middle period, I have supposed that a marked change in food availability occurred and that it persisted for a period of time, say a month, and that then the change was reversed, that is, the decrement of food later equals the earlier increment. During the period of rich food, the specific mortality rate is less at the new rate than at the old; then when the food availability change is reversed, the trend of mortality must take a different course in age (because it is a little less during the period of time). Thus, recruitment may be partly controlled by variation in the availabllity of food; Jones and Hall (in press) reached the same conclusion by a quite different route, but with an analogous model. However, it is not the only conclusion. A much more important one is that because the distribution of food is always variable in space, as well as in time, there may be a continuous modulation of the potential recruitment by the variability in the availability of food. It is an active and continuous process of extracting energy from the environment and it should be contrasted with the concept of loss or wastage in the face of an environment which was named as hostile. It should not be implied that there is no such thing as density-independent mortality, but its real effects are instantaneous losses and hence modulations of the form of density dependence. It has long been thought that variability in space should generate temporal variation; indeed Steele (1961) showed how it might occur. A much more important point is that the stabilization mechanism itself should be rooted in the variability of food.

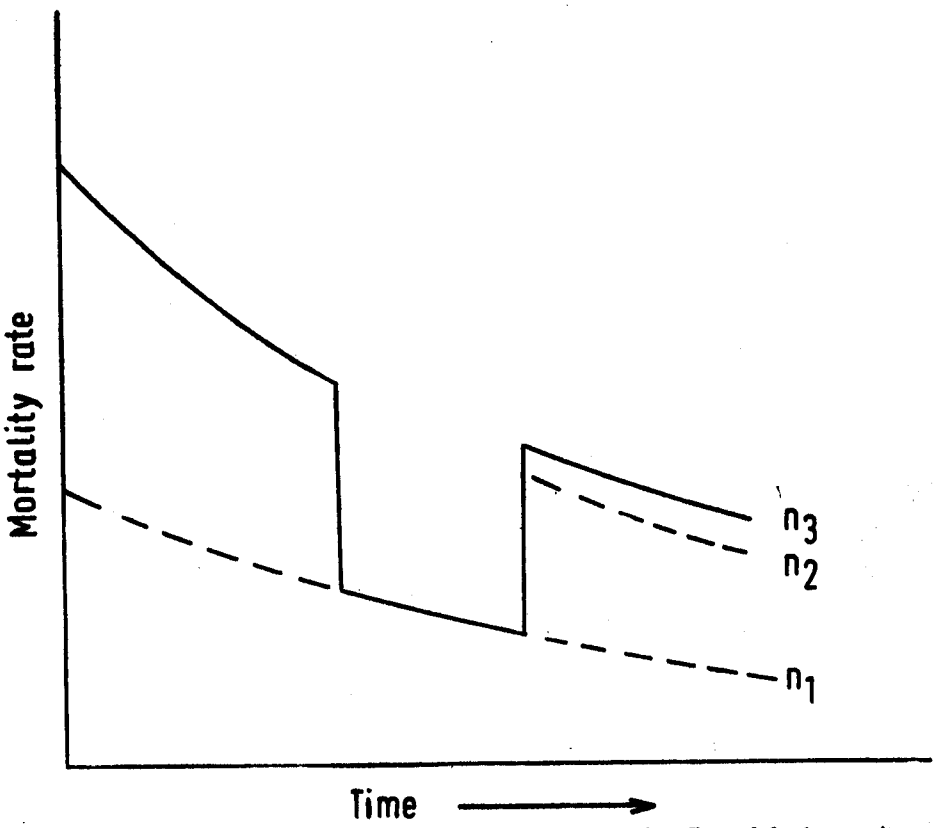


Fig. 5. Trend of specific mortality rate with time and the effect of food upon it.

We may return to the distinction between stock dependence and density dependence. Whereas density dependence is a continuous process of the exploratory extraction of energy from the food available, stock dependence has a conservative character. That is, in each generation, stock summarizes the exploratory activity characteristic of recruitment. Each cohort extracts the most energy from the food available during its life, but stock represents the average of a number of cohorts. The average represents the energy conserved, or in another idiom, information stored. It has long been recognized that the variability of recruitment is damped by the number of year-classes, but it is averaged in time rather like a moving mean—for the same reason, because the variability in a time series is conserved by such a procedure. Perhaps the variability in recruitment should not be regarded strictly as a random variable, but as one which is generated in climatic trends (Ottestad, 1942).

If we contrast stocks of high and low abundance, the difference in specific mortality rate at a given low age is much less in low stock than in high. Not only is the dependence of mortality on density during a time period less, but the

growth is less if growth and mortality are linked. Less food is extracted, the animals are perhaps smaller and the variance of recruitment is probably less. To put the argument the other way round, the abundance of stocks depends on the availability of food.

Differences in number between species are the results of competition, and from cohort to cohort they will be expressed in the proportion of recruitment to parent stock, or in another terminology, in differences in the net rate of increase. During any time period in the juvenile life-histories, such differences between species would be expressed in the ratio (G/M^x) which would be high in abundant stocks $(G/M^x)_1$ and low in less abundant ones $(G/M^x)_2$. Competition is then high between abundant populations and low between the less abundant ones. Hence there is a greater chance of a species being eliminated under conditions of abundance than under conditions of scarcity. The number of species is less where food is abundant in the sea than where it is scarce. The argument assumes that the competitive advantage or disadvantage expressed in the two ratios $(G/M^x)_1$ and $(G/M^x)_2$ for short periods in larval life can be maintained from generation to generation. Diversity is then explicable as the result of processes within the two stabilization mechanisms.

The processes of production in the sea may be classed in two groups, the continuous cycle of the open ocean in tropical and subtropical seas and the discontinuous one of high latitude and upwelling areas. The difference between the two in primary production may be of an order of magnitude or more. Cushing (1972) suggested that the transfer from primary to secondary production was three times as efficient in the continuous cycle as in the discontinuous one, so in secondary production the difference is probably reduced to a factor of 3 to 10. Efficient transfer occurs where competition may be less intense. Where (G/M^x) is high, feeding is intense and so is predation; that is, the competion for food is great in the face of predatory mortality. The continuous production cycle with efficient transfer is perhaps one of muted competition, whereas in the discontinuous one transfer is inefficient because competition is more severe. In the long term of evolution more species would survive in the continuous cycle, where food is not abundant, than in the discontinuous one, where it is. The inverse relationship between diversity and abundance is thus seen to be one of the degree of competition, itself a function of the part played by food availability in the stabilization mechanism.

Fishes grow through a number of trophic levels during their lives : their initial food may be algae and then they move on to copepod nauplii, copepods, worms or fish. Except for sharks, they are rarely the top predators, but they

are usually at a high position in a food chain. During the whole of their lives they exploit a considerable part of the chain. Consequently, they compete not only with analogous fishes, but with animals in the plankton or in the benthos. The competition will be most severe in the juvenile stages. If a density-dependent form of natural mortality in age were characteristic of fishes, perhaps it is also so of other animals in the chain, if only because of the important part played by fishes in the food chain structure. More to the point, the processes described briefly in the models above are of general application and could perhaps be used in invertebrate population studies.

If such an extension is permissible, there are two general conclusions :

1 that high diversity in evolutionary time periods is linked to low abundance of food because the intensity of competition is less;

2 that the structure of food chains depends upon the stabilization mechanism of the component populations.

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INDIAN OCEANOGRAPHY IN PERSPECTIVE

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ABSTRACT

The paper gives a brief review of the progress in oceanography in India since the middle of the nineteenth century when this important field of science had its beginning in this country. In order to make future planning more purposeful and for the proper growth of the subject, the need for a stock-taking and development of strong schools specializing in different aspects of oceanography is emphasized. The inescapability of a co-operative approach in oceanography, if substantial progress is to be achieved, is reiterated. The paper concludes with a tribute to Dr. N. K. Panikkar who has been the main architect in planning and organizing the many National Institutes dealing with oceanography, marine biology and fisheries.

THE middle of the nineteenth century saw the beginning of marine biological and oceanographical investigations along the coast of India. The interest and enthusiasm of the medical officers working on board the ships of the Royal Indian Navy in the marine environment sowed the seeds of oceanographic studies in this country. Subsequently with the appointment of Surgeon Naturalists on the staff of the Marine Survey Department an organized effort to gather knowledge of the conditions of life in our seas was started. The interest kindled by these Surgeon Naturalists gradually spread resulting in the establishment of marine biological studies in the Zoological Survey of India, the Fisheries Department and Government Museum, Madras, etc. Following these, universities began to evince interest in the study of marine life. With the setting up of the Central Marine Fisheries Research Institute the need for oceanographic investigations as an integral part of marine fisheries research was recognized. In the chronological order of events, the next landmark is the formation of the Marine Biological Association of India. Soon, the world community of oceanographers recognized the fact that Indian Ocean was the least explored and a co-operative effort to study this ocean, the International Indian Ocean Expedition, was organized. This was also prompted by the fact that it is one of the unique oceans subjected to the influence of monsoons. India actively participated in this and as a further step of recognition of this important field of study a full-fledged institute, the National Institute of Oceanography, was set up.

A Century of Oceanographic Research

Beginning with a simple survey, India has been able to build up a sound base for oceanographic studies during the past ten or twelve decades. The popularity of this field of science is also reflected in the fact that some of the universities have established regular courses in oceanography and marine biology. During the last few years, there has been a noticeable increase in the number of trained marine biologists and oceanographers and one finds a steep upward trend in the number of publications coming out in this field. Investigations in almost all aspects of oceanography are being conducted by different organizations including universities. Physico-chemical, geological and geophysical studies such as bathymetry, temperature, currents, nutrients, thermodynamic conditions at the air-sea interface, sediments, faults and structural features of the ocean floor, magnetic and gravity anomalies, mineral resources, etc., and biological investigations dealing with marine flora and fauna in general, plankton, nekton and benthos are all being carried out at various centres.

As early as in the 1920s interest was evinced in the study of the fauna of the deeper waters around India. But after the work of the survey ship "Investigator" was discontinued in 1926 the addition to our knowledge of this was contributed mainly by various expeditionary vessels such as *John Murray, Galathea, Albatross, Xarifa, Vitiaz, Meteor, Anton Bruun, Akademik Knipovich* and others which have worked in this region from time to time. In very recent years the work of R. V. *Varuna* and one or two of the bigger vessels of the Indo-Norwegian Project has contributed to our knowledge of the fauna of the deeper water especially along the west coast of India. Ecological, physiological and developmental studies of selected animals have also been receiving attention but the nature of biological work in most of the Institutes continues to be, by and large, the conventional natural history type of a qualitative nature, while the experimental and quantitative approach are still very much lacking. Thus, no doubt, a fairly good knowledge of the fauna and flora is available but considering the bewildering assemblage of species in our waters and the need for a better understanding of these much more remains to be done.

Even though the country has an extensive coastline with good prospects for search of hydrocarbons, very little marine geophysical work has been done so far. Investigations relating to mineral exploration and marine geology have also been confined more or less to beaches, explanation of certain offshore phenomena and studies of marine samples collected from deeper regions by outside agencies, while geochemical investigations have been taken up only in very recent times. Recognizing the importance of these and allied disciplines there has been currently evidence of increasing attention being paid to these.

Oceans being the primary generator of much of the weather, the interdependence of meteorology and oceanography is leading to detailed investigations into the problems of ocean-atmosphere interactions. These investigations are of importance in a variety of fields such as agriculture, fisheries, offshore oil industry, marine transportation, etc.

Recently man has begun to wake up to a possible danger threatening his well-being as well as that of the future generations on this planet—the environmental pollution. Fortunately, pollution has not yet reached alarming proportions in India but this is evident in certain coastal areas and studies have been initiated in this direction.

Undoubtedly, there has been an overall increase in the study of the ocean and in the broad geographical zone in which the country is located we have made a mark in oceanographic research. But in view of the various proposals to intensify substantially the efforts to study the ocean an introspection and evaluation are called for to assess our achievements during the past century in relation to the effort and financial inputs. Elsewhere, oceanography in the last one or two decades has made rapid strides, but to us the horizon does not seem to widen. The development in oceanographic instrumentation has been spectacular, yet the Institutes in this country dealing with oceanography have neither ocean-going research vessels nor the many sophisticated equipments. The oceans are to-day a major area for the application of new technology and consequently the tremendous advancements in space technology are being increasingly made use of in oceanographic studies such as ocean temperature, pollution, ecology, fish resources and a host of other aspects with the help of earth-orbiting satellites. Several years back one of the leading scientists in this country is reported to have advocated 'oceanography without research vessels'. There might have been a tone of sarcasm in it, but it could be that oceanography now is moving in that direction although due entirely to technological advancements. Despite the spectacular achievements of satellite technology, today the concept of oceanography without research vessels may sound bizarre and it would be unrealistic to hope that the situation will change radically in the near future.

Another disturbing factor is that more than a century of oceanographic researches in this country have not led to the development of different schools specializing in particular aspects of oceanography and this has impaired the proper growth of the subject. This leads one to the inference that there is evidently an inadequacy of dynamic and dedicated leadership. Coupled with this is the bottleneck created by the prevailing cumbersome administrative and procedural methods thoroughly unsuited for the present day requirements of a science-oriented planning and development. For this the administration should be performance-oriented. The emphasis should be on action and results, and there should be a minimum of red tape. In the words of the Nobel Laureate,

Norman Borlaug, a stage seems to have come when "we need to develop a mutant strain of man who will have the enzyme cellulase in his gut which will thereby permit him to eat, digest, and grow fat on the mountains of paper and red tape that are being produced in ever-increasing abundance by the world's planners, bureaucrats and press." In recent years there has been a perceptible re-awakening to the importance and potential the oceans hold for our well-being but the problems facing the oceanographers are challenging and need a bold and relentless approach.

Co-operative Oceanography

Oceans have always been a link between the nations and peoples. From mere highways of communication, oceans are now assuming greater significance to humanity as a whole. The wealth of the ocean in terms of living and non-living resources was the first to receive the attention of the nations. In recent years, the oceans have been considered as a common heritage and it is not only the nations with a sea-board that claim a right but the land-locked nations too feel that they should have a share of the oceans' vast riches. Present trends in oceanographic investigations have led to the realization of the dependence of man on his ocean environment. From weather through food, minerals, fuel, bio-medicines, etc., man is depending more and more on the sea. With these ramifications and the increasing range of research in the field of marine sciences a stage has come when we have realized that no Institute or even no country alone will be capable of carrying out all aspects of oceanographic research necessary for making any tangible progress in the utilization of the ocean and the exploitation of its vast resources.

This concept of international co-operation in oceanography was first tried during the International Geophysical Year, 1957-58. This created a very favourable impact and achieved a good deal of successful results because this co-operation was not only in terms of participation but also in the sharing of new knowledge acquired about the global marine environment. Encouraged by this, the international co-operation in oceanography entered a new phase in 1961 with the establishment of the Inter-governmental Oceanographic Comimssion which was mostly responsible for the organisation of the 7-year International Indian Ocean Expedition. This international venture provided abundant and valuable information about the least known Indian Ocean. International co-operative efforts are now continued to work in the tropical Atlantic and the Kuroshio region.

At the national level too co-operative research programmes are being formulated and executed between organisations having common interests. One of the best examples of this is the California Co-operative Oceanic Fisheries Investigations organised about two decades back for studying resources of the California current system. In the United States it is not only the Governmental

and academic agencies that co-operate but the Federal, State and local governments, private industry, academic and other research institutions all co-operate and collaborate to contribute to the nation's progress. Consequently the progress has been substantial.

Proliferation of organizations, lack of co-ordination and co-operation, unhealthy compartmentalization, etc., have led to avoidable duplication, fragmentation and consequent retardation of progress of marine sciences in this country. In a country like ours there is an inescapable need for better camaraderie amongst scientific organisations in view of the fact that the overall budget for scientific and technological research and development is pitifully small compared to the host of problems to be solved. Therefore, there is little doubt for the need to create foundations of mutual confidence. That will be the only way to avoid needless suspicion and rivalry leading to wastage of huge resources.

Strangely enough, apprehensions have been expressed by some that co-operative investigations might affect the committed programmes of the participating institutes. This fear is unjustified and this attitude can be interpreted only as a facade to cover up the reluctance to participate in co-operative programmes. The illogicalness of this would be obvious if we analyse what the committed programmes of an Institute are. The ultimate objective of the work of any national institute should be to contribute to the betterment of the country and its people. Proceeding from this axiom it follows that the objectives of the institutes dealing with problems directly or indirectly related to a particular field of science cannot be divorced from the national objectives, as these are only pieces of a mosaic picture of the overall national goal. This brings up the most important and primary requirement, i.e., the need for identifying problems and assigning national priorities for each of these. Having done this, the programmes should be formulated in an integrated and co-ordinated manner, taking into account the possibility of maximum inter-institutional collaboration. Such collaboration apart from saving funds and ensuring better and fuller utilization of the existing facilities and manpower would break the communication barrier and promote cross-fertilization of ideas. Co-operative efforts do not in any way imply that participating institutes should sacrifice their individuality or they will cease to be discrete entities. Thus, separately and together we should strive to achieve our goal and, to borrow a jargon used by the musicians, the institutes should not aim at performing only solos but should also have tutti in which each institute makes its individual contribution towards a harmonious whole.

Indian Ocean Exploration in the Seventies

We are now at the threshold of the Second Development Decade launched by the United Nations. Recognizing the need for greater knowledge of the oceans and their resources, international co-operative programmes such as the 'Global Ocean Research', 'International Decade of Ocean Exploration', 'Long-

term and Expanded Programme of Oceanic Exploration and Research', etc., have been formulated. In this context a long-term programme of ocean research for India also has been prepared by the Indian National Committee on Oceanic Research. These programmes heralded an important step towards providing a foundation of fundamental knowledge essential for the better use of the oceans. Working co-operatively the national programme of ocean exploration offers an excellent opportunity to share the responsibilities and results and we can turn the oceans to greater use and simultaneously gather the knowledge required to preserve the quality of the marine environment.

The sea is an untold storehouse of wealth, waiting for man's use. Considering the vastness of the problem of effective and rational utilisation of this wealth and the relatively limited resources for implementing a purposeful programme, the emphasis should be on the utilization of the ocean in order to produce the much-needed protein and mineral resources and weather forecasting. The Indian programme, therefore, aims at developing the scientific content of a long-term programme to study the Indian Ocean for a better management of the living resources, an assessment of the economic potential of the non-living resources and to develop the necessary capacity to predict oceanic conditions and control the marine environment to the extent feasible for the betterment of the economic condition of our people, especially of the weaker section.

A Tribute

In the gigantic task of laying the foundation for a modern approach to oceanographic research in India, Dr. N. K. Panikkar, to whom this volume is dedicated on the occasion of his 60th birthday, occupies a pre-eminent position. His mission in life has been to put India in a prominent place in the oceanographic map of the world through a comprehensive understanding of the Indian Mahasagar. Apart from his valuable contributions in furthering the frontiers of our knowledge in biological oceanography and fisheries, he has been the main architect in planning and organizing the many institutes in this country dealing with oceanography, marine biology and fisheries. To him, the best tribute that we can pay on this occasion would be to re-dedicate ourselves to the cause of marine science and team ourselves to co-operate in the study of the seas around us to get the maximum benefit within the minimum possible time.

SPACE TECHNOLOGY AND OCEANOGRAPHY

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ABSTRACT

Space Technology has developed modern sensing devices which carried on aircraft and spacecraft platforms can obtain repetitive synoptic data over large oceanic areas. It has also developed aspects of systems-theory, information-theory, data processing methodology etc., which can be applied to the large volumes of data collected over the oceans. This integrated technique of surveying oceans for its resources is known as **Remote Sensing.** Water colour, sea-state, surface winds, temperature, chlorophyll, surface-currents, sediment transport and surface salinity are some of the parameters collected through Remote Sensing. The data so collected have applications to shipping, meteorology, coastal geography and marine biology. It is suggested that it is time for drawing up plans for taking observations over specific sites in the Arabian Sea and the Bay of Bengal from aircraft and ocean-craft platforms simultaneous with the expected overflights of NASA's Earth Resources Technology Satellites, already orbited and to be orbited in future.

Dr. N. K. Panikkar has played a significant role in the development of modern Oceanography in India. This he has done both through his personal scientific contributions of high calibre as well as through his remarkable ability of organising scientific Institutions. Young scientists have been thereby enabled to work in Institutions and find out ways and means of utilising our oceanic resources for the economic betterment of our country. I am happy to associate myself with the Marine Biological Association who is dedicating this special number of their Journal to Dr. N. K. Panikkar, on his Sixtieth Birthday, and to wish him many more years of useful work in his chosen field of Oceanography.

It is well known that the earth is a space ship with no external supplies except solar insolation. Humanity inherited all the terrestrial resources at its birth and we will be supplied with nothing more. The oceans, which constitute about 70% of the earth surface, probably has within them far more resources than the land

areas, although tapping them may be more difficult. So far, the oceans have been explored through ship-borne instrumentation and visual observations. Ocean vessels have limited capabilities and are slow moving. Unlike the static ground, the oceans are dynamic— subject to continuous change. The expanse of the oceans coupled with their dynamic nature, make the conventional method of ship observations inadequate. It is here that space technology can be of great help.

Remote sensing

Space technology have developed modern sensing devices which carried on aircraft and spacecraft platforms can collect data on phenomena and features appearing on the ocean surface. These sensing devices include passive and active systems and employ different bands in the visible spectrum, in the near infra-red, in the far infra-red as well as in the centimeter radio waves. Fortunately, the atmosphere is transparent for all these bands when cloud free, and to some even when clouded. The reflectivity and the emissivity of ocean surface in the various bands of the electromagnetic spectrum are quantitatively registered by these sensing devices.

Space technology has also developed aspects of large systems theory, information theory, data processing methodology etc. which can be profitably applied to large volumes of data that can be collected with sensors on aircraft and satellites, particularly the latter. An integrated approach to earth resources studies using all these has now become feasible. Such an approach called Remote Sensing, when applied to oceanographic problems and carried out in conjunction with the conventional methods using ship-borne instrumentation, can be expected to yield substantial economic benefits.

Remote Sensing applied to oceanography, or any other field, produces imagery and analogue data, whose deciphering and interpretation require special skills. When oceanographic data are derived from the imagery, it is also necessary to validate them through independent ship-borne observations. Hence the need to carry out spacecraft and aircraft remote sensing observations in conjunction with conventional, ship-based observations.

Applications To Oceanography

The present state-of-the-art of remotely sensing oceanographic and related parameters from aircraft and satellite platforms has provided tools for collecting data simultaneously over a wide area. This has not been possible with ships. Within the last decade a variety of sensor-mounted spacecraft and aircraft, both manned and unmanned, have provided directly or indirectly oceanographic data on parameters like: water colour, sea-state, surface-winds, temperature, chlorophyll, surface-currents, sediment transport and surface salinity. With these parameters, the anticipated oceanographic applications can be: study of

ocean waves and sea conditions; delineation of shoals and mapping of coastal areas; ocean currents, their variations and meanderings; ice surveillance; coastal marine processes with particular reference to erosion in coastal areas; biological phenomena including characterisation of productive and non-productive areas; sea-level and sea-slope and sub-surface structure, etc.

The evaporation from the oceans is the ultimate cause of all clouds and precipitation even over the land areas. The role played by the location of abnormally warm oceanic areas in causing the vagaries of the rainfall (including that of the Indian Monsoon) is gradually being realised by meteorologists. Thus, a survey of the oceans becomes essential for the forecasting of weather over land and sea. As stated in the earlier chapter, on behalf of the World Meteorological Organisation and the International Council of Scientific Unions, a group of meteorological scientists are now involved in the GARP Project. They have realised that the tropical oceans play a large part in the generation of global weather systems. In order to investigate the details of this role, plans are afoot for conducting an experiment in the northern equatorial Atlantic in 1974. The planners have definitely stated that a geosynchronous and a couple of sunsynchronous satellites, for surveying the oceanic area under investigation, are essential requirements for the experiment.

The Gemini Manned Spacecraft Missions, brought several colour photographs of the earth's surface taken during the flights. Made with hand-held cameras, these pictures revealed the potential of surveys of the earth and its resources by means of remote sensing from space. The pictures were remarkably clear, clearer than those taken from aircraft. Their clarity was obviously due to the fact that the camera's lens was many miles away from the atmospheric scattering medium. These pictures covered thousands of square miles at one time, shownig large patterns and formations which cannot be seen in aerial photographs.

A vertical view of some coastal areas in Florida, showed shoal areas and underwater detail through colour tones. Sedimentation patterns over large lakes were clearly discernible. Several atolls 60 miles or less in diameter appeared in the central Pacific. Such ocean photographs have already been used to revise hydrographic charts.

Biological productivity of plankton and fish are perhaps the most important oceanic resources. In the years ahead this resource must be surveyed, monitored, conserved and wisely harvested. There is a significant correlation between ocean temperature gradients and the location of large schools of fish, so that information on the ocean temperature through infra-red sensing would prove valuable to the fishing industry. Surface temperature measurements also help to identify loca-

tions of highest plankton concentration and therefore possibly locations of high population of fish.

The oceans absorb surplus carbon-dioxide in the atmosphere via phytoplankton which converts it into oxygen. Some scientists feel that the overload of industrially emitted carbon-dioxide might have already saturated the ocean's capacity to effect this conversion. This also makes it necessary to monitor the areas of phytoplankton. Phytoplankton can be killed or their vigour impaired through oil slicks or pollution films. With so many oil tankers the risk of such films is large over the Arabian Sea. With many countries going in for underwater drilling operations for oil, the risk of oil slicks spreading over oceans is on the increase. It is desirable to monitor them. A satellite sensor scanning in the near ultra-violet and thermal infra-red can detect oil slicks, those which are only a few hours old and those which are several days old.

It is not known definitely whether schools of fish create detectable thin films of fish oil. If so, the same technique of ultra-violet sensing may detect schools of fish swimming just below the surface.

Subtle gradations in ocean colour shown in the Gemini photographs correlated well with ocean flora. Hence this technique can be used to indicate areas of high food content where fish are more likely to be found. As already mentioned ocean colour gradation in shallow waters can be used to update hydrographic charts. This is very necessary as the action of tides and currents are continuously changing the contours of the sea bottom, faster than the classical hydrographic surveys. From a space platform, small difference in colour can be detected through the use of multi-spectral photography or scanning imagery, using narrow band filters.

The areas and intensities of the "sunglint"—the area of an ocean surface which reflects sunlight into the observing camera provide data on the surface waves, which can be related to the surface wind. The state of the sea also produces differences in the sea colour when viewed vertically. Remote sensing techniques for these features installed in spacecraft can provide information on the state of the sea. The state of the sea can be inferred more definitely using microwave radiations. The information about the state of the sea can be used for appropriate re-routing of ships along routes offering less resistance to the ship's motion.

The space oceanographers say that they will now strive for data on the following: the surface wind field, wave systems; ocean currents, their boundaries and speeds; eddies and divergences; areas of upwelling; depth of the mixed layer; water temperatures and their gradients; biological productivity; fluxes of heat, moisture and carbon-dioxide.

The following table gives some of the applications of Space Technology to Oceanography:

Application	Type of data	Inference drawn from the data
Shipping	Wave height	State of the sea
	Surface temperature	
	Surface temperature gradients	Currents
	Water colour	
	Temperature anomalies	Hazards like icebergs
	Water/ice inference	
Meteorology	Wave heights	
	Water colour	Winds
	Surface temperature	Evaporation
	Temperature anomalies	Cyclone development
Coastal Geography	Land/water interface	
	Colour tones and contrast	Shore line topography
	Water colour tone	Effluents from rivers and sediment deposits
	Water surface elevation	Sea level and slopes
Marine Biology	Colour tones	Bioluminescence
	Colour tones	Plankton
	Colour tones	Schools of fish and algae
Physical Oceanography	Sea surface temperature gradient	Upwelling
	Water temperature gradient	Current and eddies
	Water colour	
	Wave refraction and colour tones	Bottom topography
	Ultraviolet or other vapour features	Oil slicks of petroleum origin or of fish origin

Earth Resources Technology Satellites

Sensor systems aboard the unmanned ERTS-A (Earth Resources Technology Satellite) flown in July 1972 is providing, and the manned Skylab/EREP (Earth Resources Experiment Package) to be flown in 1973 will provide, thermal and visual imagery applicable to oceanography. The mission of ERTS-A, to be followed by ERTS-B in 1973, is the repet.tive acquisition of high resolution multispectral spectra of the earth's surface. The ERTS-A satellite carries two sensor systems one of which is a four channel Multi-spectral Scanner (MSS), while the other is a three-camera Return Beam Vidicon (RBV). Apparently the RBV system has been turned off due to some technical reasons; the performance of the MSS system has been reported as better than anticipated.

However, to use the information gathered from these programmes—ERTS-A, ERTS-B etc.—it is necessary to have data gathered simultaneously from *aircraft and ocean-craft over pre-defined test sites.* The data gathered from spacecraft, aircraft and ocean-craft then should be correlated with one another, so that scientists can draw reliable inferences about the appropriate ocean-craft data given only the spacecraft data. It is only then that the spacecraft data can be used efficiently for fisheries development and utilisation.

It is suggested that the Marine Biological Association take initiative and draw up plans for taking observations over specific sites in the Arabian Sea and the Bay of Bengal from aircraft and ocean-craft platforms simultaneously with the expected overflights of the ERTS-A, ERTS-B, EREP satellites over these areas during the years 1973 and 1974.

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COMMENTS ON THE DIEL PERIODICITY OF PHYTOPLANKTON PHOTOSYNTHESIS, WITH AN EXAMPLE FROM THE INDIAN OCEAN

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ABSTRACT

The well known diel periodicity of phytoplankton photosynthesis under constant light can be explained, to a large extent, by diel periodicity of the photosynthetic activity per unit of chlorophyll; thus, to the same extent, this rhythm is independent of chlorophyll concentration or biomass, and it reflects an endogenous cycle. On the other hand, the periodicity which results from long term (24 hours) exposures under "simulated **in situ**" conditions belongs to a quite different type. Both phenomena are discussed here on the basis of parallel experiments made during cruise 8 of R/V "Anton Bruun" in the Mozambique Channel (International Indian ocean Expedition).

In the natural environment, this periodicity interfers with a number of physical and physiological parameters, so that the background of primary production on the 24-hour scale is not less intricate than the annual pattern, and deserves as much interest as the latter.

INTRODUCTION

The paper by Doty and Oguri (1957) has now become a classical one; it demonstrated that photosynthetic intensity of phytoplankton samples incubated under constant artificial light for a few hours (photosynthetic "capacity") varies according to time of sampling. This so-called "diurnal" rhythm [1] has been then confirmed by several workers, but it is still interpreted quite diversely in the literature. The fundamental question as to whether this periodicity reflects changes in biomass or changes in the production/biomass ratio, has been rather neglected. The former hypothesis, in fact, could only be sustained by the single observation by Yentsch and Ryther (1957) that variations in photosynthesis are accompanied by parallel variations in chlorophyll content; parallel changes are

1 "Diurnal", as the opposite of "nocturnal", is inadequate when applying to a 24-hour cycle : "diel" seems to be here more appropriate. See Sournia and Frontier (1968).

also mentioned by Shimada (1958) and Lorenzen (1963), but with a smaller range for the pigment values; in all other cases, changes in pigment content are opposite or undetectable (Doty and Oguri, 1957; Holmes and Haxo, 1958; Angot, 1961; McAllister, 1963; on monospecific cultures: Hastings *et al.*, 1961, and Palmer *et al.*, 1964). Thus, a diel rhythm of chlorophyll activity, i.e. in photosynthesis per unit of chlorophyll, must be taken into account : such a rhythm has been briefly or hypothetically considered by Lorenzen (1963), McAllister (1963) and Newhouse *et al.* (1967), and demonstrated on natural populations by Hansen (1962), Endo (1967), Newhouse (1967) and Sournia (1967), and on laboratory cultures by Eppley and Coatsworth, 1966 (*Dunaliella*), Jorgensen, 1966 (*Skeletonema*) and Eppley *et al.*, 1967 (*Ditylum*).

An other type of diel periodicity has been described by Ryther and Menzel (1961) and Ryther *et al.* (1961) and was left unexplained by these authors: as resulting from 24-hour experiments in the so-called "simulated *in situ*" conditions (i. e. : samples in a water bath under natural illumination, with appropriate filters "simulating" the fractions of incident light at the respective depths), the highest rates of ^{14}C assimilation occurred for experiments beginning at midnight (or at night), and the lowest for those initiated at midday (or in the day), while chlorophyll concentrations behaved in a rather opposite way.

In this paper, the diel trends of ^{14}C uptake *per unit of chlorophyll* will be discussed comparatively from both types of experiments: 1) short-term incubations under constant light, 2) 24-hour simulated *in situ* experiments.

Methods

The present example [2] is taken from R/V "Anton Bruun" investigations in the Mozambique Channel from September to November, 1964 (I. I. O. E., cruise nr. 8).

Samples were taken at any hour of the day or night and from five photometrical depths (100, 50, 25, 10 and 1% of incident light); they were used for : 1) spectrophotometric determination of chlorophyll *a* 2) photosynthetic uptake of ^{14}C during 4 hours under fluorescent lamps of approximately 1000 foot-candles (or approximately 10000 lx or 3,6 ly.h $^{-1}$), 3) photosynthetic uptake of ^{14}C during 24 hours on deck in incubator bottles being covered with neutral mesh wire filters which simulated the *in situ* percentages of transmitted light. Hourly rates were obtained by dividing 4-hour rates by 4, and 24-hour rates by 12 (an approximation of daylight length, excluding night time).

2 Thanks are expressed to the National Science Foundation and to Dr. J. H. Ryther (formerly Director for U. S. Program in Biology, International Indian Ocean Expedition), for inviting the author on board R/V "Anton Bruun" to participate in the cruise.

Further details on the cruise are available from the following papers: Menzel, 1962 (a manual of methods), Woods Hole Oceanographic Institution, 1964-65 (methods and stations data) and Ryther *et al.*, 1966 (methods and a synopsis of primary productivity and hydrology).

Short-term Experiments Under Constant Light

Timing of maximum and minimum (fig. 1) as well as amplitude agree quite well with the characteristics of the photosynthetic periodicity as described by Doty and Oguri (1957) and others (see a brief compilation in Lorenzen, 1963). Thus, the photosynthesis/chlorophyll cycle can explain to a large extent, if not fully, the photosynthetic cycle. Let us consider now the possible causes of the former cycle.

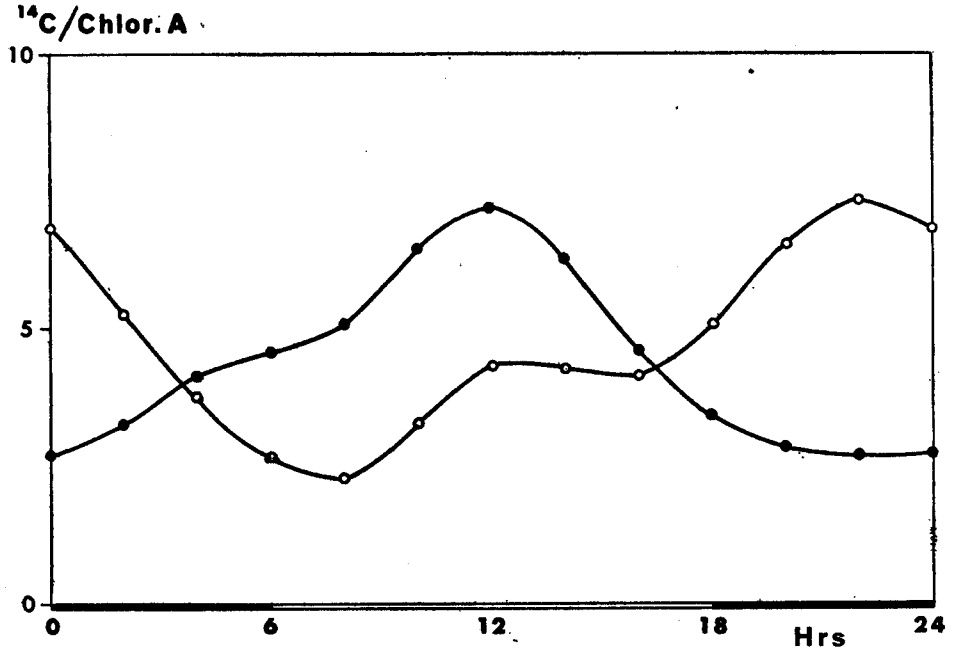


Fig. 1. Photosynthetic uptake of ^{14}C per unit of chlorophyll (mg C/h/mg chlor. a) as a function of sampling time.

● 4-hour experiments under artificial constant light,
O 24-hour experiments under "simuated **in situ**" conditions.

As far as production/biomass ratio is concerned, one must exclude variations of biomass itself, though such hvpotheses are commonly found in the literature : cell division, transport, migration, sinking, grazing by zooplankton, or amount of pigment per cell. It is hardly to be expected that diel changes in respiration rates could account for so a large range of variations (see e. g. Ohle, 1958 and Lorenzen, 1963). On the other hand, since this rhythm extends to

all levels in the euphotic zone—and since it is measured under constant illumination—injurious effect of light, called forth by Hansen (1962) and Steemann Nielsen and Jorgensen (1962, 1968) must also be discarded. The role of nutrients is suggested by Vollenweider and Nauwerck (1961) but experiments made by Ryther *et al.* (1961) failed to establish a direct relation between diel variations of photosynthesis and availability of nutrients; moreover, work on algal cultures, in which nutrients are supplied at a constant rate, leads to exclude this possibility.

Now, if this phenomenon is replaced in the general frame of plant physiology, an analogy immediately appears with the well known "afternoon depression" (or "midday depression", "diurnal depression", "afternoon nap"), which consists in a drop in photosynthetic activity during the second half of the light period, followed by a progressive recovery during the night. Several explanations have been proposed for this depression (Rabinowitch, 1951, chapter 26; Talling, 1961) but the most satisfactory one, in the case of unicellular algae, is an accumulation of photosynthetic products or by-prdoucts, or, as pointed out by Sweeney (1965, 1969), an inactivation of enzymes. Whatever the precise cause, it must be looked for inside the cells, that is to say : the rhythm is endogenous.

Studies on synchronous or semi-synchronous cultures of algae suggest that this depression could be connected with the cell division cycle (Hastings and Astrachan, 1959, and Hastings *et al.*, 1961 on *Gonyaulax;* Palmer *et al.*, 1964 on *Phaeodactylum;* Eppley and Coatsworth 1966 on *Dunaliella;* Jorgensen 1966 on *Skeletonema;* Eppley *et al.*, 1967 on *Ditylum;* see also numerous papers by Pirson, Sorokin, Tamiya and others on *Chlorella,* reviewed by Tamiya 1966). However, a photosynthetic rhythm is known in non-dividing (enucleated) cells of *Acetabularia* (Sweeney and Haxo, 1961). Furthermore, natural (mixed) populations of phytoplankton are not likely to divide synchronously and, according to Sorokin (1960), "the amplitude of changes in metabolic activity during the life cycle is expected to be larger in non-synchronized population." Thus, division cycle must be considered as a connected phenomenon rather than as a causative process.

It should be recalled that we are dealing here with experiments under artificial constant light, so that "capacity" of photosynthesis is measured instead of actual *in situ* photosynthesis. If we refer for a moment to *in situ* conditions, it will be noticed that the afternoon depression in this case is not so general as it appears in artificial conditions: when measuring *in situ* primary production, some workers observe that photosynthesis is more active during forenoon than during afternoon (Verduin, 1957; Ohle, 1958; Vollenweider and Nauwerck, 1961), but this is far from being the rule. The reason is that, besides changes in natural illumination, some environmental factors such as turbulence must be taken into account (Verduin, 1957; Ohle, 1961). So, the afternoon depression, which is of general occurrence in the plant kingdom, is expected to undergo fre-

quent exceptions in natural populations of plankton living in actual *in situ* conditions.

Simulated *In Situ* Experiments

The "simulated *in situ*" experiments are subjected to natural day-to-day variations of incident light; on the other hand, such prolonged expositions over 24 hours can be suspected of some unreliability, particularly in oligotrophic waters (Steemann Nielsen, 1964). However, it is clear from fig. 1 that photosynthesis is higher in night samples and the lowest in morning samples.

These observations agree with the periodicity described by Ryther and Menzel (1961) and Ryther *et al.* (1961), who could not explain it. Explanation, however, looks very simple (Steemann Nielsen, 1964) : when experiments begin during daylight, a notable fraction of photosynthetized ^{14}C is subsequently lost through respiration in the course of the night, whereas this effect is minimum for samples taken during night (moreover, the afternoon depression is expected to interfere at some degree with this cycle and make it more complex). It follows that, unlike the cycle resulting from short-term exposures under constant light, the present cycle can hardly be considered as a photosynthetic rhythm and should be merely designated as a pseudo-rhythm.

Fig. 1 shows that the two cycles described in the present paper are nearly opposite with respect to time; this is explained by the different processes which are involved in each of them. In the two cases, on the other hand, timing is expected to vary if other conditions of light and duration of exposures are used. This is probably the reason why the two cycles described by Doty *et al.* (1967) and Newhouse *et al.* (1967) do not differ markedly from each other, and differ slightly from our own curves; procedure used by these workers were *a*) short-term experiments: 2 hours, 1500 foot-candles, *b*) 24-hour experiments: using this artificial light source, instead of natural daylight, between 06.00 and 18.00 hours.

Conclusions

The well known diel periodicity of photosynthetic capacity, as described by Doty and Oguri (1957) and others, mainly reflects a periodicity of photosynthesizing ability of chlorophyll. To what extent the latter cycle can account for the former one is difficult to say but, whatever that may be, indisputable evidence is now available of diel variations in photosynthesis per unit chlorophyll or, as diversely called by workers, "assimilation number" or "assimilationszahl". Such variations are of the utmost importance in field studies of primary production.

First, this constitutes one reason more to think that chlorophyll measurements can provide only but a rough estimate, or a mean estimate, of potential productivity. So the "chlorophyll-radiation" method of Ryther and Yentsch

(1957) and similar ones cannot be used without extreme caution. In fact, a constant value of the photosynthesis/chlorophyll ratio would be found if "plankton originates from approximately the same area, the same season, the same depth and the same time of the day" (Steemann Nielsen and Jorgensen, 1962), that is nearly to say: if duplicate samples are considered. It must still be added, concerning chlorophyll, that all the data presented or cited in this paper apply to total concentrations of both active and inactive or "dead" pigment; further researches are needed on possible diel variation of active and inactive chlorophyll proportions.

A second consequence of practical interest concerns the choice of adequate sampling time and duration of experiments in routine work, in view of assessing daily production. This problem has been approached by several workers (e. g. : Angot, 1961; Vollenweider and Nauwerck, 1961; Doty *et al.*, 1963, 1967; Strickland, 1965; Newhouse, 1967; Qasim *et al.*, 1969; Doty, in press). In fact, it seems doubtful that a standard procedure could be established, as diel characteristics depend on experimental conditions : then, it would be necessary to standardize experimental conditions too, but this subject is beyond the scope of the present paper. Furthermore, in addition to the diel photosynthetic periodicity, the time course of primary production *in situ* is subjected to a number of factors such as light intensity, turbulence, cell growth, synthesis of chlorophyll, excretion of photosynthesized matter, respiration, horizontal transport and grazing. For these reasons, any extrapolation of *in situ* daily production, whether gross or net, from a single experiment, encounters insuperable difficulties. Actually, as far as natural populations of phytoplankton are concerned, diel variations are not less complex than seasonal ones, and there is no doubt that a single measurement during the course of the year could hardly be extrapolated to annual production. Much more information about the numerous aspects of diel phytoplankton cycle must be gathered before the problem of daily primary production could be reasonably treated.

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SEASONAL DISTRIBUTION OF THE PLANKTON IN SINGAPORE STRAITS

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ABSTRACT

The physical and chemical characteristics of the environment in Singapore Straits are described. Mention is also made of the currents and drift throughout the year. The general distribution, both qualitative and quantitative, of the phytoplankton and zooplankton is given. At the same time the main genera of phytoplankton which contribute to the phytoplankton calender are highlighted. The interrelationships between phytoplankton, zooplankton and fish in Singapore Straits are briefly discussed.

INTRODUCTION

Singapore Straits is a narrow stretch of water situated a little over 1 north of the equator and bounded by Singapore in the north and the Rhio and Lingga Archipelago in the south. At the eastern end it is connected with the South China Sea, whilst at the western it is connected with the Durian Straits and the Straits of of Malacca. In the south it is connected with Java Sea through the maze of channels in the Rhio and Lingga Archipelago. In view of its geographical position, the plankton of Singapore Straits may be expected to have many forms which are common in the South China Sea and the Java Sea. The plankton of Singapore Straits was first studied by Tham (1953) and later by Wickstead (1961). After the establishment of the Fisheries Biology Unit at the University of Singapore in 1963, the study of various groups of planktonic organisms was carried by research students of the Fisheries Biology Unit under the supervision of the author. With the establishment of the Regional Marine Biological Centre at Singapore in 1968, the study of the plankton of Singapore Straits including total counts of the samples taken was carried out by members of the staff.

Physical and Chemical Environmental Characteristics

The climate of Singapore is characterised by two monsoons, the south-west monsoon from May to September and the north-east monsoon from November to March the following year, with two inter-monsoon periods of about eight weeks each during which weather conditions are changeable and windforce is at a minimum. On the whole the north-east monsoon brings more rain than the south-west monsoon. Usually the wettest months are from November to January the following year and the driest months are July and August, although in some years this pattern may not be followed. On the average the total annual rainfall is of the order of 237.5 cm, but it could be as much as 300.0 cm during certain years.

In Singapore Straits there are, generally speaking, one high water and one low water, succeeded by a second high water and low water of lower range, during each day. During neap tides the difference between the heights of this inferior high and low water may be only a few inches. The range between two consecutive low waters is generally greater than the two consecutive high waters.

According to Berlage (1927) and Wyrtki (1961), the general direction of the currents in the South China Sea during the north-east monsoon is south-west. At the eastern entrance to Singapore Straits this stream bifurcates—one branch flowing westwards into Singapore Straits and then northwards through Malacca Straits and the main stream flowing through Gaspar and Carimata Straits into the Java Sea. During the south-west monsoon the currents from the Java Sea filter through the Rhio and Lingga Archipelago into Singapore Straits, after which the bulk of the water leaves Singapore Straits through its western entrance and flows into Malacca Straits. From the studies carried out by Robinson *et al.* (1953) and current meter readings carried out in Singapore Straits recently it would appear that the general drift in Singapore Straits during the months of June to August is from west to east. This is confirmed by the movement of an oil slick in Singapore during the latter part of June 1972. Recent studies carried out with current meters in Singapore Straits indicate that the current directions in the territorial waters of Singapore in Singapore Straits form a very complex picture because of the large number of small islands to the south of Singapore and there is much turbulence during certain states of the tides.

The general pattern of water temperature fluctuations in Singapore Straits during the years 1948 and 1949 was shown by Tham (1953) to be characterised by a minimum (around 27° C) during December/January, with the temperature rising to a maximum (around 30°C) during April/June and then receding to another minimum (around 29°C) during August/September, thereafter rising slightly in October and then receding to the minimum in December/January.

From the records of the Meteorological Department the monthly average number of hours of sunshine per day for the different months of the year varies from 4.5 to nearly 7, with lower figures during November/December and higher

figures during February/March and May/August. There does not appear to be a statistically significant correlation between the sunshine data and the water temperature data, but Tham (1953) found a statistically significant inverse correlation between the windforce data and the water temperature data.

Tham and Hon (1969) in their recent study of light penetration in Singapore waters found that near the middle of Singapore Straits off Raffles Lighthouse the percentage penetration of visible light around 11 a. m. in September 1967 was about 50% at a depth of 2 metres, about 22% at 5 metres and 7% at 10 metres, with a deck cell reading of around 20,000 lux of visible light. These results are in line with those obtained for tropical coastal waters in other parts of the world (cf. Raymont, 1963).

The dissolved oxygen content of the sea water in the middle of Singapore Straits at the surface and down to a depth of 2 metres is between 5 and 6 cc. per litre. The value decreases as one approaches the shore.

The general pattern of salinity fluctuations in Singapore Straits during the years 1948 and 1949 was shown by Tham (1953) to be characterised by a minimum of around 30‰ during December/January, thereafter rising to a maximum of 31.5‰ from February to April. From May the salinity decreases to a minimum of about 28.5‰ during July/August, thereafter rising again to a maximum of between 30.5‰ and 31.5‰ from September to November. This general pattern was confirmed by Robinson *et al.* (1953) and Ommanney (1961).

The fluctuation of dissolved inorganic phosphate content in the surface layer down to 2 metres in Singapore Straits was studied by Tham (1953) during 1948 and 1949. The results showed that throughout the two years the values fluctuated between 5 mg P_2O_5/m^3 and 20 mg P_2O_5/m^3, except from January to March 1948 when the values were 81, 28 and 40 mg P_2O_5/m^3 respectively. This was due to land drainage resulting from the abnormally heavy rainfall (24 inches) during January 1948.

PHYTOPLANKTON

The study on the phytoplankton in Singapore Straits was carried out by Tham (1953) in 1948 and 1949 by pumped hauls. It was found that there were two major blooms and one minor bloom in 1948. The major blooms occurred in February and April whilst the minor bloom was in November 1948. In 1949 the pattern was more or less similar but there was an additional bloom in July, whilst the major blooms occurred in January and May and the minor bloom in December 1949. The January/February blooms were due mainly to *Coscinodiscus* spp. whilst the April/May blooms were due mainly to *Chaetoceros* spp. The November 1948 bloom was due mainly to *Rhizosolenia imbricata* and *Coscinodiscus* spp., whilst the December 1949

bloom was due mainly to *Coscinodiscus* spp. and *Chaetoceros* spp. The July 1949 bloom was due mainly to *Chaetoceros* spp. with *Coscinodiscus* spp., *Biddulphia sinensis* and *Ditylum sol* being present in fairly large numbers. Species of the genera *Coscinodiscus, Hemidiscus, Biddulphia, Ditylum, Chaetoceros, Bacteriastrum, Thalassiothrix* and *Rhizosolenia* were found in the plankton in most months of the year, although sometimes only in small numbers.

The pigment content in Harvey units has been determined. High values of about 1,300 Harvey units were found for February and May 1948 and values of about 1,000 Harvey units were found in October and November 1948. These high values correspond with the blooms noted in 1948. However, in 1949 high values correspond with the blooms noted in 1948. However, in 1949 high values of 2,350, 1,100 and 920 Harvey units were found in May, August and October respectively so that except for the bloom in May 1949 there does not seem to be such close correspondence between the blooms and the high values of pigment content. In spite of this there is a statistically significant correlation between the phytoplankton count and the pigment values in Harvey units for the data of the two years taken as a whole.

In 1968 and 1969 a further study was carried out by Tham *et al.* (1972) by means of horizontal surface hauls with a muslin net at a station in Singapore Straits further inshore than the 1948/49 station. There was much turbulence at the 1968/69 station because of its proximity to a number of small islands immediately to the south of Singapore. The specific composition of the phytoplankton was found to be different from that found in 1948/49 by Tham (1953) in so far as there was a predominance of pennate diatoms throughout the year. Blooms were noted in May 1968, September 1968 and a minor one in November/December 1968. Whilst the blooms in May and November/December in 1968 are consistent with the pattern found by Tham (1953) in 1948 and 1949, the September 1968 bloom appears at first sight to be a new development but on further study it was found to be made up of 91.5% Biraphideae (of which 99.8% consists of *Nitzschia* spp.), 2.6% Araphideae (mainly *Thalassionema*), 4.1% Biddulphioideae (mainly *Bellerochea, Chaetoceros, Cerataulina* and *Biddulphia*) and 1.7% Discoideae (mainly *Coscinodiscus*). It has been established by Tham (1953) that during September south and south-west winds are very strong in Singapore Straits and these winds have caused great turbulence. It would appear that this has brought the pennate forms from the bottom up to the surface. Taking the distribution of the Centriceae alone the broad pattern of quantitative distribution of phytoplankton in Singapore Straits established by the findings of Tham (1953) for the years 1935, 1948 and 1949 appears to be still valid for the period April 1968 to March 1969 studied by Tham *et al.* (1972).

It is significant that the major phytoplankton bloom in Singapore Straits occurred in April/May during all the years studied, i. e. 1935, 1948, 1949 and

1968. This corresponds with the spring blooms recorded in various parts of the northern hemisphere (vide Raymont, 1963), and in these cases the blooms coincided with a rise in water temperature and an increase in solar radiation. But in Singapore Straits the annual temperature variation is of the order of only 3° C. and in any case the rise in water temperature takes place around February each year. Also the light intensity does not vary much during the year and during this period the nutrient content of the water is not high, so that this April/May bloom could not have been brought about by any rise in water temperature or any increase in solar radiation. Raymont (1963) in discussing the spring blooms stated that it appeared probable that some degree of stratification was necessary in the euphotic zone for effective phytoplankton production, at least in the early spring, and that the start of the spring increase was delayed if some degree of stability did not occur. This was emphasised by Rilev (1942, 1946) and was investigated by Sverdrup (1953). In Singapore Straits, April/May is the inter-monsoon period when the change-over from the north-east monsoon to the south-west monsoon occurs and during this period it was shown by Tham (1953) that windforce was at a minimum. Recent current meter readings taken during these two months showed that the direction of drift was uncertain and the resultant drift was comparatively low. It was also observed that during this April/May bloom the sea surface in Singapore Straits was extremely calm. It would thus appear that the April/May bloom in Singapore Straits has been brought about by the stability of the water column. The same would apply to the minor bloom during November which is the other inter-monsoon period when the south-west monsoon changes over to the north-east monsoon.

The January/February bloom and the occasional July/August bloom in Singapore Straits cannot, however, be explained in this way. During the early part of January at least, the water temperature is at a minimum, solar radiation is generally low and the nutrient content is high. It would thus appear that the January/February bloom could have been brought about by rising temperature, increase in solar radiation and high nutrient content of the water. The high nutrient content is due to the heavy runoff from the Malay Peninsula and Singapore as a result of the heavy rainfall during December/January each year and there is no doubt that there should be present in the water a host of other nutrients and trace elements which could spark off a bloom. The occasional July/August bloom could perhaps be due to the increased content of nutrients and trace elements in the water brought about by the turbulence caused by the strong south, south-east and south-west winds which are prevalent in Singapore Straits during this time of year.

Attention has been drawn earlier to the succession of species in the phytoplankton in Singapore Straits. This phenomenon has been observed and studied extensively. Raymont (1963) reviewing this subject came to the conclusion that although temperature and, to a lesser extent, light intensity and perhaps nutrient concentration may play a part in the changes, more subtle differences, particularly the biological history of the water, have an important role. In Singapore Straits it is most unlikely that temperature and even light intensity play an important role in the species succession of phytoplankton. It is more likely that the biological history of the water, the stability of the water column and turbulence play a role in species succession. In Singapore Straits, which receives water from the South China Sea mixed with coastal water from the Gulf of Thailand and eastern coast of the Malay Peninsula during the north-east monsoon and from the Java Sea and the maze of channels among the cluster of islands to the south-east of Sumatra during the south-west monsoon, it seems probable that seeding from these currents may also play a role in species succession.

There is one other phenomenon which should also be mentioned and that is the occurrence of fairly large quantities of a blue-green alga (Cyanophyceae), *Trichodesmium erythraeum,* in Singapore straits during the south-west monsoon (June to September). They are found mainly floating on the surface in patches and appear at first sight to be patches of floating sawdust. This was first mentioned by Tham (1953) who noted that it was very abundant in 1948 but was comparatively rare in 1949. Tham (unpublished) noted fairly large quantities again in September 1967.

ZOOPLANKTON

Generally speaking, zooplankton numbers are higher during the period from March to November every year. Invariably the plankton is dominated by copepods and their larval stages, the numbers varying from 40% to 70% of the total zooplankton count. The other dominant forms in descending order are the appendicularians, cirripede larvae, molluscan larvae, decapod larvae, siphonophores and chaetognaths. Other forms which are present throughout the year are fish eggs and fish larvae, echinoderm larvae, pteropods, *Lucifer,* amphipods, ostracods, polychaete larvae, cyphonautes larvae, other medusae and foraminiferans. Forms which occur sporadically are *Noctiluca,* ctenophores, cladocerans, euphausiids, heteropods, salps, isopods, brachiopod larvae and ascidian larvae. *Noctiluca,* when present, may dominate in numbers.

Noctiluca

In February 1948 a bloom of *Noctiluca* was observed by Tham (1953), but in 1949 no such phenomenon was observed. Wickstead (1961) found it very abundant during September and October 1955. Tham *et al.* (1972) found

three periods of abundance in 1968 in respect of this organism, a major bloom during August/September and two minor ones during May and November.

Coelenterata

The siphonophores in Singapore Straits belong to species of *Diphyes* and *Lensia,* the former being more abundant (Lim, 1968). They are usually present in the plankton throughout the year. From the work of Tham (1953), Wickstead (1961) and Tham *et al.* (1972), there appears to be four periods during which these organisms may be abundant in Singapore, viz :– December/ January, March/April, June and September/October/November.

Small medusae have never been observed in large numbers during the studies carried out so far, but large medusae may sometimes be present in Singapore Straits to such an extent that they become a nuisance to fishermen and people swimming along the beach.

Polychaeta

Polychaetes and their larvae are not usually common in the plankton but they may be observed in large numbers sporadically.

Chaetognatha

The chaetognaths in Singapore Straits are represented by two genera, *Sagitta* and *Krohnitta* (To, 1966). *Sagitta enflata* is the dominant form. Other species which may be present are *S. robusta, S. bedoti, S. johorensis* and *S. demipenna.* The genus *Krohnitta* is represented by the species *K. pacifica.* From the work of Tham (1953), Wickstead (1961) and Tham *et al.* (1972), there are three periods during the year, viz:- March/April, June/July and October/November/December, when chaetognaths may be found in Singapore Straits in large numbers in the plankton.

Cladocera

The cladocerans in Singapore Straits belong mainly to the genera *Evadne* and *Penilia,* species of the former genus being more common. Tham *et al.* (1972) have never observed them in large numbers in the plankton, but Wickstead (1965) states that *Penilia* can range from being completely absent to being present in numbers like 2,500/m^3, forming over 50% of the total plankton numbers.

Ostracoda

The ostracods are represented mainly by the genera *Pyrocypris* and *Euconchoecia* in the plankton of Singapore Straits. Tan (1966) found 250 to 450 ostracods per half hour horizontal haul in April, June and August in 1964 and in June and September in 1965, but the number never exceeded 40 in any month in 1966. Tham *et al.* (1972) found between 300 and 800 organisms in June and October 1968 and in January 1969.

Copepoda

The copepods in Singapore Straits are represented by the following sub-orders, families and genera :—

Sub-order	Family	Genus
Calanoida	Paracalanidae	*Paracalanus*
	do.	*Acrocalanus*
	Acartiidae	*Acartia*
	Eucalanidae	*Eucalanus*
	Pontellidae	*Calanopia*
	do.	*Labidocera*
	Calanidae	*Canthocalanus*
	Arietellidae	*Metacalanus*
	Temoridae	*Temora*
	Tortanidae	*Tortanus*
	Centropagidae	*Centropages*
	Pseudodiaptomidae	*Pseudodiaptomus*
	Candaciidae	*Candacia*
Harpacticoida	Ectinosomidae	*Microsetella*
	Macrosetellidae	*Macrosetella*
	Clytemnestridae	*Clytemnestra*
	Tachydiidae	*Euterpina*
Cyclopoida	Oithonidae	*Oithona*
	Oncaeidae	*Oncaea*
	Corycaeidae	*Corycaeus*

The families of each order have been listed in the order of dominance in the plankton catches during 1968. Tham (1953) in his study of the copepod population in Singapore Straits found that during the years 1948 and 1949, copepod numbers were highest during April/May, July (and also June in 1948) and October/November (and also December 1949). Tham *et al.* (1972) in a more detailed study from April 1968 to March 1969 found that, among the Calanoida, most genera were abundant during July and October, the months of greatest abundance for the total copepod count. These genera, viz:— *Paracalanus, Acrocalanus, Acartia, Eucalanus, Canthocalanus, Temora, Tortanus, Pseudodiaptomus* and *Candacia* were apparently brought into Singapore Straits by the currents of the south-west monsoon, although *Paracalanus* and *Acrocalanus* are believed to breed in Singapore Straits. Most of these genera were also found in fairly large numbers in March or May indicating that they were also brought into Singapore Straits by the north-east monsoon currents. The exceptions were *Labidocera* which were found in fair numbers in January, March and September, and *Metacalanus* which were found in fair numbers only in November.

The sub-order Harpacticoida appears to be common during two periods of the year, from September to November and again from January to April. Members of the sub-order Cyclopoida were present throughout the year but were more abundant from July to November. Among the three genera the genus *Corycaeus* was the most abundant.

From the point of view of total copepod numbers, Tham (1953) found for 1948-49, by pumping a measured quantity of sea water and filtering through a No. 20 (173 meshes per sq. in.) bolting silk net, a minimum of approximately 3,000 organisms per m^3 in January 1948 and 1949 and a maximum of approximately 40,000 organisms per m^3 in October 1948. Wickstead (1961) did not agree with these findings because his maximum record for 1955-56 was only 523 copepods per m^3 or 534 per m^3 including the nauplii, but his method of sampling was a vertical haul with the International coarse silk net and a 1 m stramin net similar to those used by Russell and Colman (1931) at the Great Barrier Reef. Tham *et al.* (1972) found, with a half hour horizontal haul with a muslin net, as many as 39,000 copepods in October 1968 and this agrees well with the figure (40,500/m^3) found in October 1948 by Tham (1953). In order to check further the figures obtained by Tham (1953) and by Tham *et al.* (1972), several pumped hauls of one m^3 were made at noon on 23 April 1970 with a mechanical pump and filtered through a Norpac Type Plankton net (mesh GG52 or 50.5 meshes per sq. in.) and the whole sample was counted by the staff of the Regional Marine Biological Centre at Singapore. The results were as follows :— (i) 22,358 copepods/m^3 at the surface, (ii) 9,467 at a depth of 5 fathoms and (iii) 13,538 at a depth of 10 fathoms. Tham (1953) found 23,000 copepods/m^3 in April 1948 and 28,900 copepods/m^3 in April 1949. The figures are therefore in fairly good agreement. This underlines the fact that the method of sampling as well as the net used is important. It was also found by Dr. Takashi Minoda that, by using simultaneously one pair of nets designed by Professor S. Motoda, viz:— (a) a Norpac type net which consisted of Pylen No. 60 (0.35 mm. x 0.35 mm. mesh) and (b) a double Norpac type net with a small net of Pylen No. 60 inside and a larger net of Pylen No. 200 (0.1 mm. x 0.1 mm. mesh) outside, a much larger number of copepods (at least double and as much as 56 times) was caught by the (b) double Norpac net. These samples were sorted and counted at the Regional Marine Biological Centre at Singapore. It is now the concensus of opinion among scientists engaged in the Co-operative Study of the Kuroshio (CSK) that, in the South China Sea and adjacent areas where the Paracalanidae are dominant in numbers, coarse nets are not adequate for sampling copepods on a quantitative basis.

Cirripedia

Cirripede larvae were observed by Tham (1953) in the plankton of Singapore Straits throughout the year but not in large numbers. Tham *et al.* (1972) found a maximum of about 11,000 organisms per half hour haul in Singapore

Straits in November 1968. Yang (1967) working in Johore Straits also found maximum numbers in November 1966 but the numbers were highest (100,000) inside Johore Straits and decreased to 60,000 at the entrance to Johore Straits and in the inshore waters of Singapore Straits it dropped to 4,500.

Lucifer

Tham (1953) reported that *Lucifer* was comparatively rare in the plankton of Singapore Straits for the years 1948 and 1949. From the work of Khoo (1967) and Chua (1967), *Lucifer* appears to be extremely rare in Johore Straits. Tham *et al.* (1972) found that *Lucifer* was more common in Singapore Straits during the north-east monsoon, the highest numbers being recorded in November 1968 and January 1969. Wickstead (1961) found that *Lucifer* was more common in Singapore Straits during November 1955, February 1956 and April 1956. These findings indicate that *Lucifer* in Singapore Straits are carried in with the South China Sea current.

Other Decapoda

Other decapods in the plankton consist mainly of brachyuran larvae as well as some penaeid and caridean larvae. Tham *et al.* (1972) found the largest number (3,500 in a half hour haul) of other decapods in the plankton in October 1969. Tham (1953) found that they were more common in 1948 and 1949 during March, June/July/August and October/November/December, the number being highest during June/July. Wickstead (1961) found peaks of abundance in June/July 1955, October/November 1955 and April 1956.

Mollusca

Tham *et al.* (1972) found a fair number of mollusca and molluscan larvae in the plankton of Singapore Straits in 1968/69, with peaks of abundance during March/April, July and October/November. Gastropods made up 75% of the total numbers, whilst the remaining 25% consisted of lamellibranch larvae. The bulk of the gastropods were larval stages, whilst pteropods and heteropods were comparatively rare. Wickstead (1961) found the peaks of abundance of molluscan larvae in 1955/56 during February, May/June, September/October and December.

Echinodermata

Tham et al. (1972) found echinoderm larvae to be very rare in the plankton except during February/March and May. Echinoderms, especially asteroids, are fairly abundant along the south coast of Singapore especially in the deeper portions of Singapore Straits so that March and May may be the spawning months.

Tunicata

Tham *et al.* (1972) noted fair numbers of appendicularians in the plankton of Singapore Straits being more common during March, May, August and November. They belong mainly to the genus *Oikopleura.* Gan (1968), who made a study of *Oikopleura* abundance in Singapore Straits during 1965 and 1966, found that they could appear in numbers during any month in the periods, March-April-May-June, August-September and November-December-January.

Salps are usually rare in the plankton, but they could suddenly appear in large numbers for a short period of time. The writer noted a very large swarm in June 1936.

Fish eggs and fish larvae

The work of Tham (1953) in 1948 and 1949 and that of Wickstead (1961) in 1955-56 show that fish eggs and fish larvae were never abundant in the plankton of Singapore Straits. Tham *et al.* (1972) in their study in 1968-69 sorted out and counted all the fish eggs and fish larvae in the plankton collected. They found that the average number of fish eggs never exceeded 400 in any half hour haul and a similar count for fish larvae never exceeded 500. It is believed that only a few inshore fish spawn in Singapore Straits and that the main spawning areas are in the South China Sea. Tham and LeMare (1954) found a preponderance of juvenile fish in the inshore fish population of Singapore Straits during the first few months of the year (January to April). These juvenile fish are brought into Singapore Straits from the South China Sea by the monsoon currents of the north-east monsoon and they aggregate there because of the density of planktonic food.

Other groups

The other groups which occur in the plankton of Singapore Straits are, in descending order of abundance, Foraminifera, cyphonautes larvae, crustacean nauplii (excluding copepod nauplii), ascidian larvae, brachiopod larvae, Thaliacea, Amphipoda, Isopoda, Euphausiacea, stomatopod larvae, Mysidacea, Phyllosoma larvae, Ctenophora, Tomopteridae, actinotrocha larvae, Cumacea, Nemertinea and Platyhelminthes. Tham *et al.* (1972) found that in any one haul the number of organisms never exceeded 400 for Foraminifera, 250 for cyphonautes larvae and Ascidian larvae, 200 for crustacean nauplii (excluding copepod nauplii), 100 for brachiopod larvae and Isopoda and 50 for the others.

Interrelationships between Phytoplankton, Zooplankton and Fish

A close study of the variations in phytoplankton and zooplankton in Singapore Straits in 1948 and 1949 as given by Tham (1953) shows that, whilst the abundance of phytoplankton usually alternates with that of zooplankton, during April/May an abundance of phytoplankton coincides with an

abundance of copepods and other zooplankters. The alternation of rich populations of phytoplankton and zooplankton can be explained by the grazing theory put forward by various workers including Harvey *et al.* (1935). The coincidence of rich populations of phytoplankton and zooplankton is however not so easy to explain. In the case of Singapore Straits the rich populations of phytoplankton during April 1948 and May 1949 were dominated by *Chaetoceros* spp. which made up 96% and 62% of the population respectively. Harvey (1937), studying selectivity in the diet of copepods, found that when *Calanus* was fed with a mixture of *Chaetoceros* and *Lauderia* the latter was readily consumed but *Chaetoceros* was hardly consumed. It is thus possible that the rich populations of phytoplankton in April 1948 and May 1949 were due to the fact that the *Chaetoceros* portion of the population was not consumed by the copepods. During these periods, conditions were optimal for the growth of the phytoplankton population because solar radiation was high and drift was at a minimum.

With regard to the relationship between the plankton and fish, the work of Tham (1950) has shown that the bulk of the fish caught in Singapore Straits are plankton feeders and even in the case of well known predators such as the lutianids, scomberomorids, trichiurids, the post-larval and small specimens also feed on zooplankton. Tham (1953) also noted that in 1948 and 1949 large catches of *Stolephorus* spp. as well as *Clupea (Harengula) fimbriata* and *Clupea (Harengula) perforata,* all plankton feeders, coincided with the peaks of abundance of phytoplankton and zooplankton. The large number of juvenile fish in the catches of Singapore Straits also indicates that Singapore Straits is the feeding ground of the juveniles of many species of fish and this appears to be due to the larger quantity of plankton in Singapore Straits as compared with the offshore areas of the South China Sea. Whilst the abundance of plankton in Singapore Straits results in an abundance of *Stolephorus* spp. and *Clupea (Harengula)* spp., the presence of these groups of species of fish, in turn, attracts large numbers of *Scomberomorus* spp. and *Chirocentrus dorab* which feed on them. This underlines the importance of plankton not only for the aggregation of plankton feeders but also indirectly for the aggregation of predacious fish which feed on plankton feeders.

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PHOTOSYNTHETIC AND RESPIRATORY RATES, AND PHOSPHORUS CONTENT OF ALGAE GROWN AT DIFFERENT PHOSPHATE LEVELS

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ABSTRACT

Amphidinium carteri and **Cylindrotheca closterium** were grown for 42-65 hr in stagnant batch-cultures using media containing $2\mu gP/ml$ (normal phosphate) and $20\,\mu gP/ml$ (tenfold phosphate). Phosphorus content of the cells was determined after washing several times with 3.5% NaCl until no more P was removed.

After growth the pH of the media ranged from 8.57 to 9.96. In media containing $2\mu gP/ml$ the total phosphorus in 10^6 cells ranged from 0.33 to $1.38\mu g$ for **Amphidinium** and 0.35 to $0.83\mu g$ for **Cylindrotheca**. The corresponding values for tenfold-phosphate were 0.87 to $1.53\mu g$ and 0.63 to $1.23\mu g$. The ratios of respiration of tenfold-phosphate cells to respiration of normal-phosphate cells ranged from 0.59 to 1.16 **(Amphidinium)** and from 0.60 to 1.03 **(Cylindrotheca).** Corresponding ratios for photosynthesis were 0.61 to 0.99 and 0.45 to 1.02. Therefore the supply of extra phosphate increased the total phosphorus of the cells but decreased, rather than increased, the rates of photosynthesis and respiration.

The NaCl washings contained large amounts of inorganic phosphorus, probably precipitated from the media by the high pH. Using many assumptions in recalculating data of other authors, the phosphorus content of these washed cells was compared with the phosphorus content of cells of other species.

INTRODUCTION

The photosynthetic and respiratory rates of phytoplankton are often used in models of marine productivity. It would be preferable to use cells reared under natural conditions when determining these rates, but it is not yet possible to culture unicellular algae under conditions even approximating to natural ones. The commonly used stagnant batch-cultures, shaking batch-cultures, chemostat cultures, and turbidostat cultures are therefore worth investigation to see what ranges of values are obtained for cells produced by these different methods.

It is already known that within each method, the values of the rates depend greatly on growth conditions and many other factors. For example, Humphrey and Rao (1967) using stagnant batch-cultures of *Cylindrotheca closterium* found that photosynthesis was greatest on the first day and decreased to about 50% of this at three days, and to about 10% at fourteen days. During these periods the cultures were depleted of much of their carbon source for photosynthesis as was shown by increases in pH to 9 or more. There was also considerable loss of phosphate, but not nitrate, from the culture medium.

In the present investigation, stagnant batch-cultures of *Cylindrotheca closterium* and *Amphidinium carteri* were used to determine the effect of extra phosphate on the magnitude of photosynthesis and respiration.

METHODS

Bacteria-free cultures were grown for periods between 42 and 65 hours at 19-21° in 25 ml of culture medium (2 μgP/ml) or the same medium containing 10 times this normal amount of phosphate, in 50 ml conical flasks over white fluorescent lamps giving 1.2–1.3 mW/cm^2 (Humphrey and Rao, 1967). The flasks were shaken gently twice daily. Inocula were 5 ml of 2 or 3-day cultures. Duplicate cell-counts were made in a haemocytometer.

A Rank (Rank Brothers, Cambridge, England) oxygen-electrode was used at 0.65V to measure respiration and photosynthesis. The electrode was calibrated with N_2, 10% O_2 in N_2, and air. A sample of the culture was mixed with one-tenth of a volume of 0.1 M $NaHCO_3$ containing 0.01M K_2CO_3, and 3 ml of the mixture placed in the glass electrode-compartment. The stirrer was set on its slowest speed; water at 20° was circulated through the clear plastic jacket. Respiration was determined for a period of 5-10 minutes while the jacket was covered by black cloth. Photosynthesis was then determined for a period of 10-20 minutes after removing the cloth and while irradiating with white light from a tungsten lamp to give 16 mW/cm^2 inside the electrode-compartment. This intensity was slightly more than enough to saturate photosynthesis. After these determinations the cells were still whole, but their motility was considerably reduced; the pH of the suspensions after the determinations varied from 7.89 to 8.60.

Phosphorus was determined by the method of Murphy and Riley (1962), total phosphorus involving an extra stage of digestion with $HClO_4$. The culture supernatant was obtained by centrifuging 1 to 6 ml of culture for 15 minutes at 15,000 g. The cells were then suspended in 6 ml of 3.5% NaCl with the aid of mechanical vibration for a few seconds. The suspension was centrifuged as before.

This washing procedure was repeated several times to ensure removal of soluble phosphorus.

RESULTS

Tables 1 and 2 give the results of two of the experiments; in these two, cultures were grown for 48 hours. In the 17 experiments carried out, the culture pH on sampling ranged from 8.57 to 9.96 and the amounts of phosphate in the supernatants were, on the whole, lower at the higher pH values. In normal phosphate, the total phosphorus in 10^6 cells ranged from 0.33 to 1.38 for *Amphidinium* and 0.35 to 0.83 for *Cylindrotheca;* the corresponding values for tenfold phosphate were 0.87 to 1.53 and 0.63 to 1.23. The ratios of respiration of tenfold-phosphate cells to respiration of normal-phosphate cells ranged from 0.59 to 1.16 (*Amphidinium*) and from 0.60 to 1.03 (*Cylindrotheca*). Corresponding ratios for photosynthesis were 0.61 to 0.99 and 0.45 to 1.02.

TABLE 1. *Phosphate Concentration and Amphidinium*
P_i and P_t are the inorganic and total phosphorus values referred to 1 ml of the culture
(– signifies below the analytical limit)

	NORMAL PHOSPHATE		TENFOLD PHOSPHATE	
Culture pH	9.78		9.78	
Cell number	1.3×10^6/ml		1.0×10^6/ml	
	μg P_i / ml	μg P_t / ml	μg P_i / ml	μg P_t / ml
Culture supernatant	0.04	0.09	0.38	0.75
First washing	0.42	0.57	9.74	9.64
Second washing	0.33	0.44	7.52	7.44
Third washing	—	—	3.98	4.09
Fourth washing	—	—	2.00	2.06
Fifth washing	—	—	0.73	0.75
Sixth washing	—	—	—	0.34
Seventh washing	—	—	—	—
Eighth washing	—	—	—	—
Ninth washing	—	—	—	—
Washed cells	—	0.43	—	0.87
	μl $O_2/10^6$ cells/hr		μl $O_2/10^6$ cells/hr	
Respiration	−10.9		−10.8	
Photosynthesis	+12.7		+12.2	

TABLE 2. *Phosphate Concentration and Cylindrotheca*
P_i and P_t are the inorganic and total phosporus values referred to 1 ml of the culture
(– signifies below the analytical limit)

	NORMAL PHOSPHATE		TENFOLD PHOSPHATE	
Culture pH	9.3		9.3	
Cell number	1.1×10^6/ml		1.0×10^6/ml	
	μg P_i / ml	μg P_t / ml	μg P_i / ml	μg P_t / ml
Culture supernatant	0.91	0.96	1.92	2.07
First washing	0.21	0.27	8.56	8.25
Second washing	0.15	0.23	4.04	3.84
Third washing	0.11	0.13	1.73	1.56
Fourth washing	—	—	0.74	0.79
Fifth washing	—	—	0.62	0.65
Sixth washing	—	—	0.45	0.45
Seventh washing	—	—	—	—
Eighth washing	—	—	—	—
Ninth washing	—	—	—	—
Washed cells	—	0.37	0.15	0.63
	μl $O_2/10^6$ cells/hr		μl $O_2/10^6$ cells/hr	
Respiration	−4.8		−2.9	
Photosynthesis	+7.0		+4.1	

Although the cultures were bacteria-free, there was much suspended matter not recognisable as algal material. Often, *Cylindrotheca* had several particles attached to the outside of the frustule, and these progressively disappeared as washing proceeded. The suspended matter, particularly the particles, might have been hydroxy-carbonate-phosphate complexes with calcium and/or iron.

DISCUSSION

The results presented here show that under the growth conditions used, extra phosphate inhibited rather than increased the magnitude of photosynthesis and respiration. Recently Ebata and Fujita (1971), have shown that photosynthesis by *Phaeodactylum tricornutum* was increased by 40% if cells were grown in five times the normal phosphate; in both normal (0.9μgP/ml) and five-fold phosphate photosynthesis was greatest after 60 hours growth, and the decline thereafter was slower with the higher phosphate. The difference between these results and those with *Amphidinium* and *Cylindrotheca* might be explained by the

different species used or by the differing culture conditions e.g. *Phaeodactylum* was grown in the presence of 0.5% CO_2 and at 60 hours was just starting the logarithmic phase of growth.

Previously reported values for the phosphorus content of unicellular marine algae have usually been calculated indirectly by equating the loss of phosphorus from the culture medium to the uptake of phosphorus by the cells. The experiments with *Amphidinium* and *Cylindrotheca* show that this method can be erroneous because phosphorus compounds are precipitated in the alkaline, seawater-based media often used. This precipitation is further increased as the pH is allowed to rise. Previously published studies (Table 3) do not give information on pH or its variation during culture. Values were probably sufficiently high to cause phosphate precipitation unless there was some mixing, especially by bubbling gaseous CO_2.

Table 3 was compiled by recalculating data and measuring graphs designed for purposes other than to give the phosphorus content of cells. Because many assumptions were made in these arithmetic procedures and because experimental conditions differed greatly between the various investigations, no specific conclusions can be made. The general order of magnitude of the phosphorus content per cell and per volume of cell provide a base for further chemical work and for considerations on phosphorus metabolism.

TABLE 3. *Phosphorus Content of Algae*
Time refers to duration of contact with medium

SPECIES	INITIAL μg P /ml medium	TIME	CULTURE METHOD	μg P/10^6 cells	μg P/μl cell	REFERENCE
Phaeodactylum tricornutum	0.04	9hr	Stagnant batch	0.6	0.6	Ketchum (1939*a*)
,,	0.25	6hr	,,	0.2	0.2	Ketchum (1939*b*)
,,	0.9 and 2.5	12hr	,,	2.0	2	Kuenzler and Ketchum (1962)
,,	0.9	160hr	CO_2 mixing	0.2	0.2	Ebata and Fujita (1971)
Asterionella japonica	0.03	some days	Stirred batch	1.6	0.7	Goldberg *et al.* (1951)
Cyclotella nana	0.1	few days	Turbido-Chemo-stats	0.2	3	Fuhs (1969)
Thalassiosira fluviatilis	,,	,,	,,	3.1	5	,,
Amphidinium carteri	2	42–65hr	Stagnant batch	0.9	0.9	Present paper
,,	20	,,	,,	1.2	1.2	,,
Cylindrotheca closterium	2	,,	,,	0.7	0.9	,,
,,	20	,,	,,	0.9	1.2	,,

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EXPERIMENTAL ECOLOGY OF TROPICAL MARINE PHYTOPLANKTON

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ABSTRACT

Experiments dealing with the influence of three environmental factors namely light, salinity and nutrients on the photosynthesis of laboratory cultures indicate that the light requirement for optimum photosynthesis in tropical phytoplankton is much greater than that of temperate forms. At saturating light intensity, photosynthesis seems independent of wavelength. Maximum photosynthesis in many organisms occurs at low salinity which seems an adaptation to regulate their peak production during the monsoon months when nutrients in the nearshore waters are high and salinity is low. Growth kinetics and nutrient requirements of **Biddulphia** and **Ceratium** indicate that **Biddulphia** has a higher value of half saturation constant (K_s) than that of **Ceratium.** The former becomes abundant during the monsoon months when the nutrients in the environment are high, and the latter, with a lower K_s, becomes a better competitor at low concentrations of nutrients found during the pre-monsoon months.

INTRODUCTION

The measurements of a set of environmental factors in the sea along with phytoplankton productivity can give only broad relationship between the two. Our inability to relate, very often, the results properly is because many of the finer details on which the activity of phytoplankton is based are still unknown. Therefore, precise experimental work on isolated environmental factors with laboratory cultures is perhaps what remains the only satisfactory approach of determining the optimum effect of one factor or the limitation imposed by the other. The ecological implications of such experiments can easily be tested by field data. Thus, the purpose of this communication is to summarize the results of laboratory studies undertaken on tropical phytoplankton and to draw generalizations of ecological significance. The factors taken into consideration here are: (a) light (b) salinity and (c) nutrients.

MATERIAL AND METHODS

Experiments with light: Laboratory cultures of several species of diatoms and dinoflagellates were taken, and equal quantities of each organism were innoculated in bottles containing Millipore-filtered sea water. The bottles were clamped in an incubator provided with graded neutral density filters. The incubator was exposed to sunlight and the rate of phytosynthesis in each bottle was measured by ^{14}C assimilation. The incident light falling on each bottle was measured by a calibrated lux-meter and the results were expressed as the intensity effect of light on photosynthesis. Each experiment was conducted for a duration of 2 hours.

In addition to the intensity effect, the quality effect of light was also investigated. Bottles containing each organism were exposed to a portion of the visible spectrum, starting from the longest wavelength. Sharp cut-type glass filters were used in a specially designed incubator for cutting off the transmittance of light (for detail see Qasim et al., 1972 *a*).

Experiments with salinity : Each organism was innoculated in bottles containing sea water of varying salinities, from 5-35‰, and the bottles were exposed to constant illumination of 7 kilolux for 3-4 hours. The rate of photosynthesis under each salinity was determined by ^{14}C uptake (see Qasim *et al.*, 1972 *b*).

Experiments with nutrients : Nutrient-depleted cells of two organisms—a diatom, *Biddulphia sinensis* and a dinoflagellate, *Ceratium furca*—were innoculated in 4 litres of Millipore-filtered sea water containing varying concentrations of phosphate and nitrate, either singly or in combination. From each flask, 50 ml aliquots were drawn at regular intervals and these were incubated for 3 hours under constant illumination and their rates of photosynthesis were measured by ^{14}C assimilation (see Qasim *et al.*, 1973).

RESULTS AND DISCUSSION

Influence of light

Fig. 1 gives the rate of photosynthesis in two organisms (*Biddulphia sinensis* and *Ceratium furca*) as a function of light intensity. As can be seen from the figure, each curve is divisible into three portions—the linear portion of the relationship at low light intensity, the portion of less rapid increase or plateau which indicates optimum photosynthesis at light saturation, and the portion of progressive inhibition of photosynthesis at high light intensity. The point of intersection between linear and saturation regions, which is shown by the I_k, is the point from where the onset of light saturation occurs. In *Biddulphia,* the I_k was at about 17.5 kilolux and in *Ceratium,* it was approximately 13.0 kilolux. Similarly, 10 more organisms were subjected to changes in light intensity and their I_k values were determined. These ranged between 11-18 kilo-

lux, excepting in *Rhizosolenia styliformis* and *Dinophysis miles,* where the I_k values were exceptionally high—23.5 and 34.5 kilolux respectively (Qasim *et al.*, 1972 *a*).

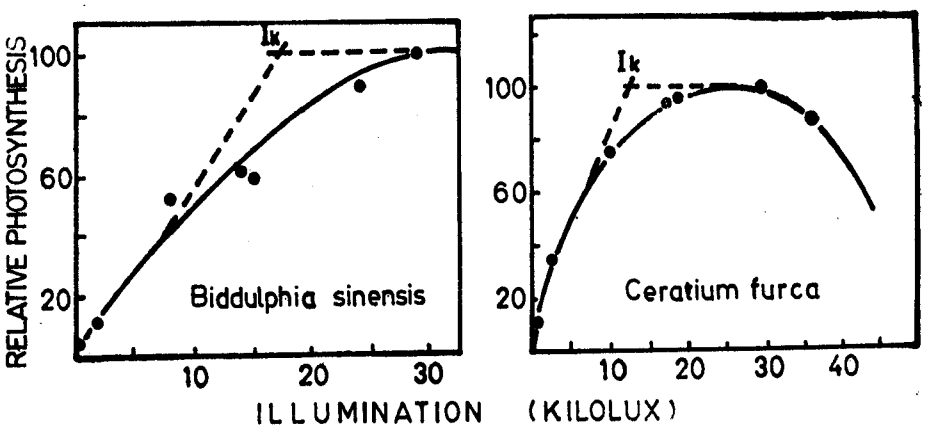


Fig. 1. Photosynthesis in two organisms as a function of light intensity. The point of intersection (I_k) in each curve indicates the point of the onset of photosynthesis at light saturation.

Fig. 2 gives the rate of photosynthesis as a function of illumination in two natural phytoplankton populations taken from the Cochin Backwater (see Qasim *et al.*, 1969). The relationship was almost similar to that of the laboratory cultures and the I_k values in these two cases were found to be 13.6 and 20.8 kilolux.

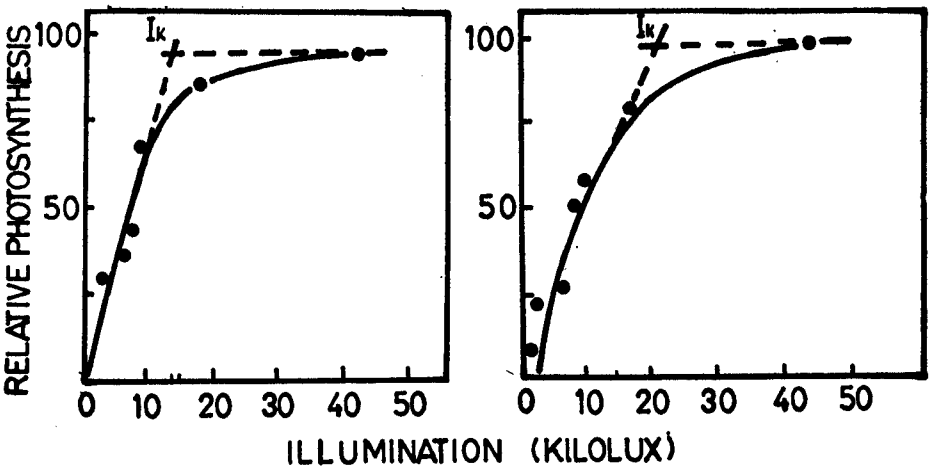


Fig. 2. Photosynthesis in relation to light intensity in two samples of natural phytoplankton population taken from the surface of Cochin Backwater. The I_k values indicate the saturation points in relation to illumination.

The quality effect of illumination on the photosynthesis of *Biddulphia* and *Ceratium* has been shown in Fig. 3. Maximum photosynthesis in both the organisms occurred in the spectral range 700-402 mμ and 700-430mμ. The rate of photosynthesis in both the organisms for the entire visible spectrum 700-400mμ declined because the intensity was too high. The photosynthetic rates in several other organisms in response to quality effect was almost similar to those shown by *Biddulphia* and *Ceratium*. There was no dependence on wavelength in saturating light (Qasim *et al.*, 1972 *a*).

When the photosynthetic rates of the two organisms were plotted against the radiant energy transmitted through the sharp cut-type filters (Fig. 4), the curves obtained were similar to those of the intensity effect, that is, a linear phase at low energy, a saturation phase at optimum energy and an inhibition phase at higher energy (compare Fig. 4 with Fig. 1). This indicates that as long as the light energy available is optimum for photosynthesis (saturation intensity), almost all regions of the visible spectrum are effective.

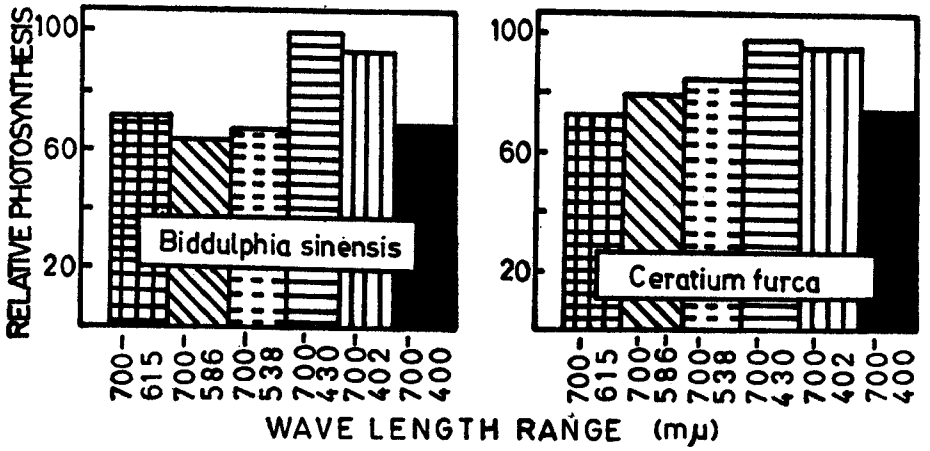


Fig. 3. Photosynthesis in two organisms in relation to different regions of the spectrum.

Ecological significance of light effect

From the I_k values determined for the different species of phytoplankton, the optimum energy for maximum photosynthesis seems to range from 11.50-34.50 kilolux or 0.2–0.6 ly/minute. For natural phytoplankton of the Cochin Backwater the I_k was 13.6–20.8 kilolux or 0.24–0.37 ly/minute. For the tropical phytoplankton of the open ocean, Steemann Nielsen and Jensen (1957) give the I_k as 30 kilolux or 0.52 ly/minute. All these values are close to those determined by experiments. These experiments also indicate that the optimum light requirement of the tropical phytoplankton is much greater than that of the temperate forms. The average solar radiation falling on the sea surface at Cochin during the year ranges from 205-550 ly/minute. Thus even in highly

turbid environments such as the Cochin Backwater, where the light penetration is greatly reduced, optimum illumination is available within a few metres from the surface (Qasim *et al.*, 1968).

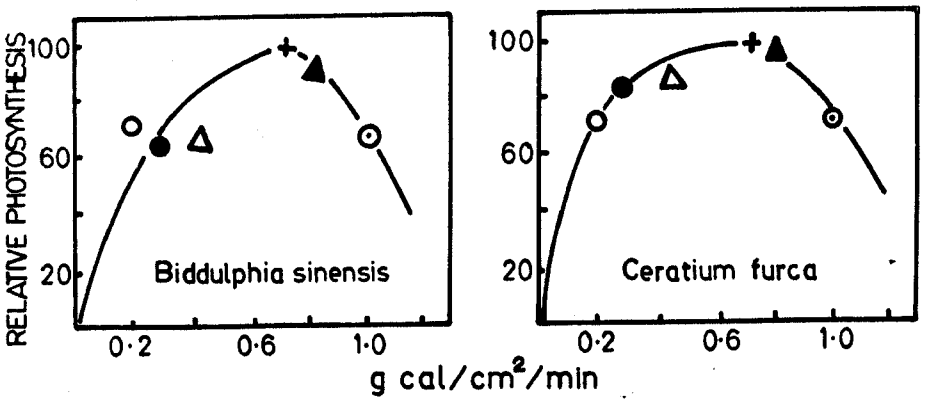


Fig 4. Photosynthesis in two organisms in relation to total energy available at different wavelengths of the spectrum. ○, 700-615 mμ; ●, 700-586 mμ; △, 700-538; +, 700-430 mμ; ▲ 700-402 mμ; ⊙, 700-400 mμ.

Photosynthetic response shown by the different organisms in response to quality of light indicates that phytoplankton quickly adapt themselves to changing light conditions. Such a chromatic adaptation is of distinct advantage to marine phytoplankton which have a floating existence. With rapid changes in depth, the light conditions also change, but the photosynthesis would not be affected much, even when a portion of the spectrum is cut-off.

Influence of salinity

The rates of photosynthesis in *Biddulphia* and *Ceratium* at different salinities have been shown in Fig. 5. In *Biddulphia,* the highest rates were obtained at salinities 10-20‰, but in *Ceratium* maximum photosynthesis occurred at still lower salinities, 6–10‰.

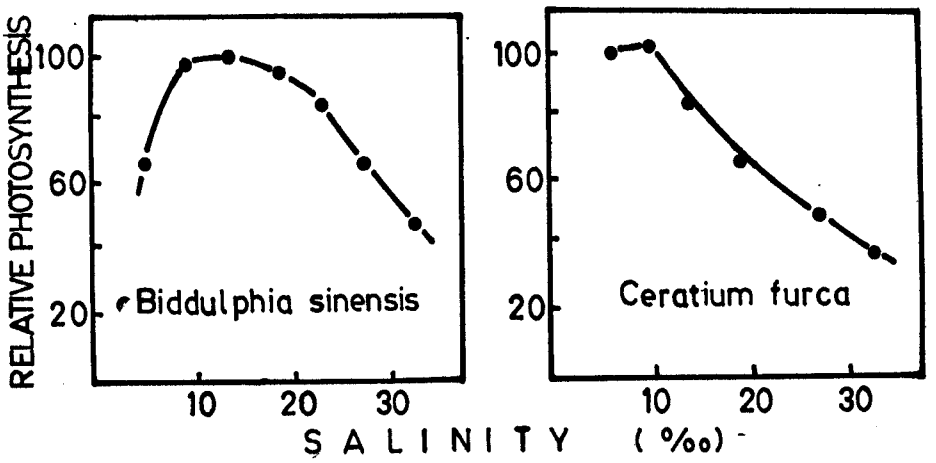


Fig. 5. Photosynthesis in two organisms as a function of salinity.

Ecological significance of salinity effect

The reduction in salinity along the south-west coast of India, induced by the heavy rainfall during the monsoon months, is very well marked and occurs every year. Along the south-east coast also, changes in salinity are brought about by the discharge of fresh water by many large rivers into the Bay of Bengal. This would mean that reduction in salinity in the coastal waters of India is associated with the enrichment of water with nutrients. The adaptation in phytoplankton for maximum photosynthesis in response to low salinity, is therefore so adjusted as to ensure their peak production during a time when high concentrations of nutrients are available in the environment. In the Cochin Backwater, where changes in salinity are very wide, many organisms have been found to bloom successively at exceptionally low salinities (Qasim *et al.*, 1972 b). These observations confirm that waters of low salinity support a greater abundance of phytoplankton in nature.

Influence of nutrients

Growth rates of *Biddulphia* and *Ceratium* as a function of nutrients followed the enzyme kinetics similar to that of Michaelis-Menten equation of bacterial growth (see Dugdale, 1967; Eppley and Thomas, 1969; Thomas, 1970). This equation has the form

$$\mu = {}^{\mu}\max \left(\frac{S}{K_s + S}\right)$$

where μ is the specific growth rate of algae, ${}^{\mu}\max$ is the maximum growth unlimited by low nutrient concentration, S is the nutrient concentration and K_s is the half saturation constant, which is equal to ${}^{\mu}\max/2$

Specific growth rate μ when plotted against μ/s gave the values of K_s and ${}^{\mu}\max$ graphically (see Qasim *et al.*, 1973). Table 1 gives the values of K_s and ${}^{\mu}\max$ of *Biddulphia* and *Ceratium*. Both the organisms have low K_s for phosphate and a high K_s for nitrate. When the two nutrients are used in combination, the K_s for *Biddulphia* becomes still lower but in *Ceratium* the K_s obtained is almost average of those for phosphate and nitrate. The ${}^{\mu}\max$ values in both the organisms were independent of high or low values of K_s (Table 1).

Ecological significance of nutrient effect

Both the organisms, *Biddulphia* and *Ceratium* are neritic species and are found in estuaries and inshore waters, where nutrients normally occur in high

TABLE 1. *Values of half saturation constant* (K_s) *and maximum growth rate* (μmax) *obtained for Biddulphia sinensis and Ceratium furca in enrichment experiments*

	Biddulphia sinensis			*Ceratium furca*		
	Phosphate	Nitrate	Phosphate + Nitrate	Phosphate	Nitrate	Phosphate + Nitrate
K_s	0.17	0.74	0.10	0.15	0.44	0.24
μmax	0.65	1.05	0.87	1.38	1.87	1.38

concentrations. In the Cochin Backwater, *Ceratium* is found in fairly large concentrations during the premonsoon months (March-April) when the nutrients are low. *Biddulphia,* on the other hand, becomes abundant during the monsoon months when nutrients reach maximum concentrations. *Ceratium* has a low K_s and therefore it is a better competitor at low concentrations of nutrients. When the nutrients become high, *Ceratium,* despite its lower salinity tolerance, is unable to compete with *Biddulphia* which has a higher K_s. The growth kinetics of the two organisms thus provide an explanation of the observed seasonal succession of the two species.

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CASSIDELLA PANIKKARI N. SP. (FORAM.) FROM THE KERALA SHELF

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ABSTRACT

A new species of the genus *Cassidella* Hofker 1951 is described and discussed.

INTRODUCTION

During a stay in Cochin in the months of January/February 1965, a series of bottom-samples from the lagoon of Cochin and the nearshore region off Cochin were taken with the kind assistance of the colleagues from the National Institute of Oceanography and the Oceanographic Department of Kerala University. In the nearshore region, a species of the genus *Cassidella* which is obviously a new one, occurs abundantly. We describe it here under the name *Cassidella panikkari* to express our thanks for the kind and prompt assistance given to our studies by Dr. Panikkar and his staff.

Genus Cassidella Hofker 1951

Cassidella panikkari n. sp.
Fig. 1 a—e

Holotype : Coll. Geol. Inst. University Kiel Catal. Nr UKG. 2583 Fig. 1

Paratype : 20 specimens, Coll. Geol. Inst. University Kiel, Catal. Nr. UKG. 2584.

Type locality: Sample Nr. 41, 9°57.7' N, 76° 4.4'E, water depth 29 m.

Diagnosis : A slender, twisted *Cassidella* with a small, depressed aperture

Description : The long and slender, often somewhat fusiform, test consists of up to 17 chambers, mostly 14-15 with the initial triserial part increasing rapidly in size, reaching its maximum width in the biserial position, in the middle or upper part of the test. The thin-walled test is smooth and hyaline, finely perforate, with a nonperforate area around the aperture.

In our Stereoscan-microphotographs the wall structure seems to be radial rather than granular, as has been stated for this genus. The sutures are distinct. The loop-like aperture is depressed, with the toothplate, which may be slightly denticulate, protruding from inside. In nearly all studied specimens, the aperture is partially filled by secondary layers of calcite. The tooth-plate is U-shaped and simple, as described by Hofker (1951, p. 264) for this genus. It starts at the upper end of the septal foramen, winding up the chamber wall and becoming U-shaped before the next formed aperture (Fig. 1 d, e).

Measurements: Length—from 0.21 mm. to 0.35 mm; max. breadth—0.07 mm to 0.10 mm; max. thickness—0.05 to 0.07 mm; diameter of proloculus—0.02 mm.

Occurrence: The species is abundant (most living specimens are found in the shelf samples (Nr. 38—42 and Nr. 57—59) with a peak in the depth of about 20—25 meters, where it ranges second or third among the living forms, contributing up to 19.4% to the whole population. The number of living forms in sample 39 i. g. is 57 specimens 10 cm^3 sediment. The rate for the empty tests is 19% with a number of 473/10 cm^3 sediment in the same sample.
The species is very rare in the lagoon samples. Only one sample (Nr. 4) contained 2 living specimens which may have been transported into the lagoon by currents. The number of dead specimens is also very small.

Remarks: *Virgulina fijiensis* Cushman, 1936, p. 49, pl. 7 fig. 9 a—c, is similar, but much bigger (with up to 19 chambers) and more robust. The variation in the outer shape of our species is great. There are long and very slender forms as well as those with broader and lower chambers, resulting in the more fusiform type. The twisting too, is variable. Some specimens are highly twisted in the initial part, later becoming more regularly biserial, whereas others may be twisted throughout (Fig. 1 c).

The species is very interesting, because it resembles closely the forms referred to *Fursenkoina* by Loeblich and Tappan (1961) after the abandonment of *Virgulina* as a foraminiferal genus. It has the same twisted chamber arrangement with the free part of a similar tooth-plate protruding from the aperture. But since Loeblich and Tappan point out that the type species of *Fursenkoina, F. squamosa* (d'Orbigny-, definitely has no initial, triserial stage, we cannot include our species in this genus.

The type species of *Cassidella, Cassidella tegulata* (Reuss), which has an initial triserial chamber arrangement, is much less twisted and the tooth-plate

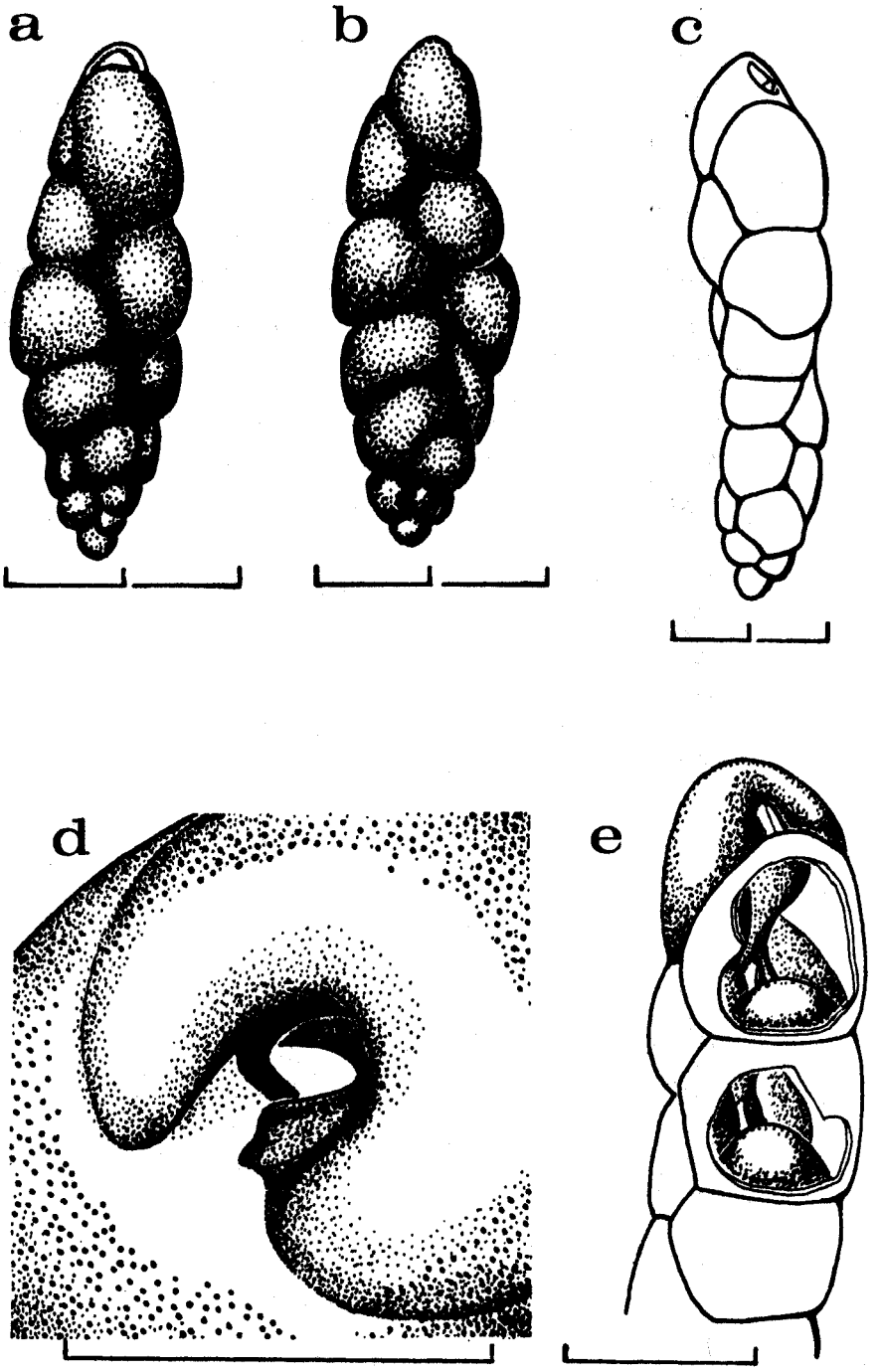


Fig. 1. a–e *Cassidella panikkari* n. sp. Scale: Each part = 50 micron.
a, b. Holotype, both sides. c. Long and very twisted form. d. Aperture with tooth-plate. Specimen with broken chambers, showing the tooth-plates winding up from the septal foramens.

does not protrude from the aperture. But other species, for example *Cassidella-pacifica* Hofker (p. 273, pl. 174 e, pl. 181), how these features clearly. Both genera are obviously very closely related and need much more detailed investigation than can be given on the basis of a single species.

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BIOCHEMICAL STUDIES ON MARINE ZOOPLANKTON THE AMINO ACID COMPOSITION OF SOME LOCAL SPECIES.

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ABSTRACT

Further analyses of the amino acid composition of protein hydrolysates of *Neomysis integer* has confirmed the importance of glutamic, aspartic, lysine, leucine and arginine (in that descending order) in both ovigerous females and less mature animals. *Mesopodopsis slabberi* closely resembles *Neomysis* in its amino acid composition. *Sagitta setosa* shows considerable similarity to the mysids in its protein amino, acids but alanine replaces leucine in importance. There is a somewhat larger concentration of glycine ($\sim$ 7%) and of histidine ($\sim$ 5%) among the less important amino acids. Despite the low level of protein in *Pleurobrachia pileus*, the pattern of amino acids shows considerable resemblance to the other planktonic species but glycine occurs in greater concentration than leucine or arginine.

In both mysid species glycine, taurine and arginine are the dominant free amino acids. No taurine is found in *Sagitta setosa;* glutamic is the major amino acid followed by aspartic, lysine, glycine and arginine.

INTRODUCTION

Relatively few studies have been made on the amino acid composition of species of marine zooplankton. Cowey and Corner (1963) investigated the amino acid composition, including the free amino acids, of *Calanus finmarchicus.* Jeffries (1969) dealt with the free amino acids in some zooplankton, especially *Acartia* species, though these were not "pure" samples. Several authors, Suyama, Nakajima and Nonaka (1965); Sidhu *et al.* (1970); Burkholder *et al.* (1967); Moiseev (1970) and Srinivasagam *et al.* (1971) have examined the composition of the body protein in *Euphausia superba.* The latter authors also compared the composition of *E. superba* with that of the euphausiid, *Meganyctiphanes norvegica,* and included an analysis for a marine mysid, *Neomysis integer.* In the present work the amino acid composition of *Neomysis* has been re-investigated using ovigerous females as well as less mature specimens. The composition of this mysid has also been compared with that of three other local zooplankton species. Of these species *Neomysis* occurs highest up the estuary in fluctuating but generally rather low salinity (mean $\sim$ 9‰). The other species rarely encounter salinities less than 30‰.

We are grateful to Miss Janet Redmond for assistance with the analyses. This work was supported by a grant from the Natural Envirnoment Research Council.

Material and Methods

Two different groups of animals were compared in the case of *Neomysis*. One set consisted of large ovigerous females which were analysed fresh immediately after capture in the field. The other group consisted of more or less full grown individuals of both sexes, but the marsupium in the females was little developed. These animals also differed in that they had been maintained in the laboratory before analysis for ~10 days in 9‰ seawater. This approximates to the average salinity in their natural habitat.

Both the *Sagitta setosa* material and that of *Mesopodopsis slabberi* after sorting was deep frozen in the laboratory (–20°C approximately) before analysis. As a test of the possible use of freeze dried material for analysis, some *Mesopodopsis* taken from the same haul were freeze dried in the laboratory and used subsequently. The results reported concern only the deep frozen material, but tests showed that there was exceptionally good agreement between the results for amino acid composition for protein hydrolysates of the deep frozen and freeze dried material. Some discrepancies were noted in the analysis of free amino acids from the freeze dried material; the concentrations of many of the amino acids were considerably reduced especially those occurring in smaller quantities. This has been encountered before in unpublished work on freeze dried material of *Sagitta enflata* and *Calanus plumchrus*.

Pleurobrachia pileus material was also freeze dried. As there seemed to be some doubt about the validity of concentrations of free amino acids in freeze dried material, only the protein hydrolysate analysis has been reported for *Pleurobrachia*.

For all analyses, the lipid was first removed from the tissue according to the method of Folch *et al.* (1957), except that in the case of freeze dried material a small quantity of distilled water was first added to the dried tissue so that the material was allowed partly to hydrate. It was inconvenient, however, to hydrate the tissues completely; this was particularly true of *Pleurobrachia*. Following the lipid removal, the free amino acids were extracted from the lipid free tissues with hot distilled water. Proteins were then precipitated with hot trichloroacetic acid and the hydrolysates prepared by refluxing with 6N hydrochloric acid.

Standard methods were used for obtaining 21 hour chromatograms of both free amino acids and protein hydrolysates, employing a Technicon auto analyser and using external norleucine standards at the beginning and end of the chromatogram run. An internal norleucine standard (0.1 μmols) was used in both sample and the standard amino acid solutions.

Results and Discussion

Neomysis integer (Leach)

Although the precise values of the individual protein amino acids reckoned as mg/gram dry weight are different in the ovigerous females and the less mature animals (Table 1), when reckoned as a percentage of the total amino acids, there is good agreement between the two groups of mysids (Table 2). The pattern of relative importance of the amino acids is generally similar in the two groups, and the percentage of individual amino acids never disagrees by more than 0.3%, except for methionine and cystine. These amino acids occurred in both groups in very small amounts and were the lowest in order of concentration (Table 1). They were however slightly higher in concentration in the large ovigerous females than in the less mature specimens. There is also very good agreement between these analyses and the data on amino acid composition of protein hydrolysates of *Neomysis* reported earlier by Srinivasagam *et al.* (1971). This good agreement suggests as might be expected that only relatively very minor changes occur in the composition of the protein of the body with age and maturity.

TABLE 1. *The amino acid composition of protein hydrolysates in the four species (Values as mg/g dry wt.)*

Amino Acids	*Neomysis integer*		*Mesopodopsis slabberi*	*Sagitta setosa*	*Pleurobrachia pileus*
	Ovigerous females	Less mature			
Aspartic acid ..	51.9	54.1	60.4	40.1	4.6
Threonine ..	19.1	19.8	24.4	16.0	2.1
Serine ..	17.5	18.1	25.2	18.1	2.2
Glutamic acid ..	79.9	97.5	81.2	54.6	4.8
Proline ..	13.9	12.4	17.4	16.2	2.0
Glycine ..	16.8	20.9	22.0	30.9	3.0
Alanine ..	24.3	27.7	31.9	38.6	2.3
Valine ..	24.2	27.7	30.8	26.8	2.2
Cystine ..	5.0	3.7	7.5	8.3	0.2
Methionine ..	10.7	8.7	12.9	12.4	0.2
Isoleucine ..	24.5	27.2	29.2	24.6	1.9
Leucine ..	36.0	42.6	42.6	27.1	2.9
Tyrosine ..	18.8	19.9	23.7	14.8	1.1
Phenylalanine ..	23.5	25.3	25.1	21.2	1.7
Lysine ..	47.5	51.8	56.8	42.6	3.4
Histidine ..	16.2	12.2	19.6	22.7	1.3
Arginine ..	34.0	39.6	36.5	38.3	2.8
Taurine ..	—	—	—	—	—
Ornithine ..	1.1	0.9	1.2	1.4	—
Total ..	464.9	510.1	548.4	454.7	39.4

TABLE 2. *The amino acid composition of protein hydrolysates in the four species expressed as percentages*

Amino Acids	*Neomysis integer*		*Mesopodopsis slabberi*	*Sagitta setosa*	*Pleurobrachia pileus*
	Ovigerous females	Less mature			
Aspartic acid ..	11.2	10.6	11.0	8.8	11.7
Threonine ..	4.1	3.9	4.4	3.5	5.3
Serine ..	3.8	3.5	4.6	4.5	5.6
Glutamic acid ..	17.2	19.1	14.8	12.0	12.2
Proline ..	3.0	2.4	3.2	3.6	5.0
Glycine ..	3.6	4.1	4.0	6.8	7.6
Alanine ..	5.2	5.4	5.8	8.4	5.8
Valine ..	5.2	5.4	5.6	5.9	5.6
Cystine ..	1.1	0.7	1.4	1.8	0.5
Methionine ..	2.3	1.7	2.4	2.7	0.5
Isoleucine ..	5.3	5.3	5.3	5.4	4.8
Leucine ..	7.7	8.4	7.8	6.0	7.4
Tyrosine ..	4.0	3.9	4.3	3.2	2.8
Phenylalanine ..	5.1	5.0	4.6	4.7	4.3
Lysine ..	10.2	10.2	10.4	9.4	8.6
Histidine ..	3.5	2.4	3.6	5.0	3.3
Arginine ..	7.3	7.8	6.7	8.4	7.1
Taurine ..	—	—	—	—	—
Ornithine ..	0.2	0.2	0.2	0.3	—

If the amino acids of protein hydrolysates reckoned on a dry weight basis are totalled, the large ovigerous females show a lower amount (465 mg/g dry wt.) as compared with the less mature animals (510 mg/g dry wt). This may reflect a total lower protein content for the large ovigerous females and this may be associated with an increased lipid content, as suggested by Linford (1965). But it will be remembered that the less mature animals had been maintained in the laboratory in constant diluted seawater; their total amino acids (510 mg/g) show some decrease when compared with the fresh non-ovigerous females, previously analysed by Srinivasagam *et al.* (1971), where the total was 585 mg/g. However, if the free and protein hydrolysate amino acids are totalled together, the animals kept in diluted seawater in the laboratory show relatively little difference from the total amino acids for fresh mysids (655 and 681 mg/g respectively). The reduction in protein amino acids and the raised concentration of free amino acids in those mysids maintained in 9‰ seawater may be associated with osmotic regulation in a constant salinity. In their natural environment the mysids are subject to salinities varying with the tide. It is perhaps significant that the total of protein and free amino acids approximates reasonably well to that of animals obtained fresh from the natural habitat.

Since the percentage composition of amino acids in protein hydrolysates is so similar for ovigerous females and the less mature animals, the results may be reported together. Glutamic acid is overwhelmingly predominant of the amino acids; then in descending order of importance follow aspartic, lysine, leucine and arginine, these five amino acids together equalling 54% and 56% respectively for the two groups. In the earlier work reported by Srinivasagam *et al.* (1971) these five amino acids totalled 54%. Moreover, in all three crustaceans previously analysed (*Neomysis, Euphausia* and *Meganyctiphanes*), the five dominant protein amino acids were identical and occurred in the same order of importance.

Cowey and Corner (1963) quote results for the amino acid composition of *Calanus finmarchicus*. On the basis of g. amino acid N/100 g total amino N, the order in descending importance is arginine, lysine, glycine, glutamic, alanine, aspartic and leucine. For the closely related species, *C. helgolandicus,* Corner and Cowey (1964) list arginine, glycine, lysine, alanine, glutamic, aspartic and leucine. While the data are not strictly comparable with values quoted as percentages, the same important amino acids appear as in other planktonic crustaceans, but the order is not identical and glycine occurs in larger concentrations in *Calanus*.

In *Neomysis,* following the five major amino acids, a group occurs with only relatively minor differences: valine, alanine, isoleucine and phenylalanine, each amounting to approximately 5% of the total (Table 2.) This result shows again very good agreement with our earlier findings.

As regards the free amino acids, the comparison of the two groups of mysids shows general agreement in the proportions of the major free acids. They also confirm the earlier report that, glycine, taurine, and to a lesser extent arginine, are the chief constituents. Together they account for 68% and 71% respectively for the immature mysids and the large ovigerous females. This may be compared with the earlier finding of 73% for *Neomysis*.

TABLE 3. *A comparison of the major free amino acids in three planktonic species (Each concentration is expressed as a percentage of the total. Note that only eight of the major amino acids are listed)*

Amino Acids	*Neomysis integer*		*Mesopodopsis slabberi*	*Sagitta setosa*
	Ovigerous females	Less mature		
Aspartic	3.1	2.9	4.7	12.0
Glutamic	6.0	5.6	7.9	17.8
Proline	5.9	2.4	—	8.9
Glycine	27.4	29.6	22.5	10.0
Alanine	4.8	5.2	2.9	6.7
Lysine	1.3	2.2	9.0	11.0
Arginine	17.6	12.0	25.5	10.0
Taurine	26.4	26.6	14.7	—

Of the other free amino acids, glutamic, proline, aspartic and alanine are present in relatively significant quantities, together totalling 15% in the immature mysids as compared with 16% in the earlier investigation. Ovigerous females in the present study show slightly higher amounts of these four free amino acids especially proline; together they amount to 20% (Table 3).

Ornithine is omitted from discussion because, though usually present in small quantities, this amino acid may result in part from decomposition of arginine. Two amino acids, both sulphur containing, cystine and methionine, in addition to being invariably present in the lowest concentration of the protein hydrolysates (*vide supra*) are also present in very small amounts among the free amino acids.

Mesopodopsis slabberi (Van Beneden)

Results of analysis of the protein hydrolysates show a remarkable similarity to that of *Neomysis;* glutamic, aspartic, lysine, leucine and arginine are again the most important amino acids in that descending order. Together they account for 51% of the total protein hydrolysates. The same pattern of amino acids, valine, alanine and isoleucine each of the order of 5% of the total, follow as in the case of *Neomysis*. But in *Mesopodopsis* the concentration of phenylalanine approximates more closely to that of serine, threonine and tyrosine, all amounting to approximately 4.5% of the total. Cystine and methionine are again present in the lowest concentrations (Table 2).

Analysis of deep frozen material showed the same three major free amino acids, glycine, taurine and arginine, as in *Neomysis*. Together they reached some 63% of the total free amino acids, a value somewhat lower than for *Neomysis*. But more significantly, arginine is the major free amino acid being slightly greater in amount than glycine (Table 3).

Mesopodopsis lives in relatively more saline conditions and inhabits lower reaches of Southampton water. It occurs in the deeper water layers where fluctuations in salinity with tide are comparatively small. This habitat difference may be associated with the relatively small amounts of glycine and taurine which are recognised as important in osmoregulation. Arginine is well known on the other hand as an energy reserve in crustaceans. Proline is another amino acid often participating in osmoregulatory functions in crustaceans. While occurring in *Neomysis* to a small extent (*circa.* 5%), it has not been recognised in the analysis of free amino acids in *Mesopodopsis*. Apart from proline, as in *Neomysis,* the quantities of glutamic, aspartic and alanine are also significant among the free amino acids of *Mesopodopsis*. Lysine apparently accounted for 9% of the free amino acids (Table 3); there is some suspicion, however, that this may be an artefact.

Earlier investigations by Srinivasagam *et al.* (1971) involved an examination of the free amino acids of two euphausiids, *Euphausia superba* and *Meganyctiphanes norvegica*, as well as of *Neomysis*. Although the concentrations of the free amino acids showed some differences between the three crustaceans, glycine, taurine and arginine were important in all the species; lysine occurred in fair quantity in the two euphausiids, and proline and alanine were found in moderate amounts in *Euphausia* and *Neomysis*. There is, therefore, some degree of agreement among these planktonic crustaceans as regards the more important free amino acids, though the lack of proline in *Mesopodopsis* is outstanding.

Some general agreement also appears from analyses by Jeffries (1969) of another planktonic crustacean group. For the copepods, *Acartia clausi* and *A. tonsa*, glycine is the major free amino acid; proline, taurine, alanine and arginine also occur in relatively large concentrations. Jeffries points out that the first four amino acids are subject to considerable and apparently fairly rapid changes in concentration. He believes that these may reflect the physiological condition and possibly productive capacity of the animals, apart from any osmoregulatory function. Cowey and Corner (1963) also report glycine, taurine, arginine, alanine, glutamic and proline as the most important of the free amino acids in *Calanus*.

Sagitta setosa J. Muller

There are considerable resemblances in the pattern of the dominant protein hydrolysate amino acids to those of the two mysid species. For instance, in *Sagitta* glutamic is the major acid, though it is slightly less prodominant than in the crustaceans. Lysine, aspartic and arginine are also important among the first five amino acids, but alanine has replaced leucine in order of importance (Table 1). The first five amino acids together from approximately 45% of the total.

The next grouping of amino acids shows some similarities to that found in the crustaceans in that valine and isoleucine are present in comparable concentrations. A significant difference is the relatively high amount of glycine (6.8%) (Table 2). Histidine, normally of minor importance in crustaceans is found in a concentration equal to 5% of the total and ranks tenth in descending order of importance. Once again the two sulphur containing amino acids, cystine and methionine, are present in lowest concentrations (Table 2).

Some comparison may be made with several analyses of samples of *Sagitta elegans* obtained earlier from the Millport Marine Station. These analyses are subject to slight suspicion since the material, deep frozen after collection, was maintained in the laboratory for a somewhat prolonged period. Nevertheless, the general order of importance of protein hydrolysate amino acids is very

similar to that in the related species, *Sagitta setosa.* Thus glutamic is again dominant; lysine, aspartic, leucine and arginine are next in importance, though in one or two analyses of *S. elegans* alanine replaced arginine in order of ranking. The first five amino acids total 50% as against 47% in *Sagitta setosa.* Valine and isoleucine are again in the next important group of amino acids, and with glycine occur in approximately the same amount (~ 5%).

Cystine is always in lowest concentration in the analyses of *Sagitta elegans.*

It is perhaps of interest that in another more typically oceanic and relatively warm water species, *Sagitta enflata,* preliminary analysis shows the same first six amino acids followed by glycine.

Some difficulty was experienced in estimating the free amino acid concentrations in *sagitta setosa* mainly owing to the relatively small amount of material available. However some differences between *Sagitta* and the two mysids are obvious. Glutamic, aspartic and lysine are the first three amino acids in *Sagitta,* followed fairly closely by glycine and arginine; there is also a fairly substantial amount (~ 9%) of proline. (Table 3). No taurine was recorded and the much decreased importance of glycine and arginine is in marked contrast not only to the present results for *Neomysis* and *Mesopodopsis,* but also to the data of Jeffries (1969) and Cowey and Corner (1963) for copepods. If these results are confirmed, they might suggest different metabolic pathways in Chaetognatha and Crustacea.

Pleurobrachia pileus (O. F. Muller)

Only freeze dried material has been used in these analyses (cf. Methods), largely on account of the very high water content of fresh tissue and owing to the brief seasonal appearance of the animal.

The concentration of total amino acids obtained from protein hydrolysates is relatively low (~ 40 mg/g dry tissue—Table 1). This is in accord with the very low protein and high ash content, reckoned on a dry weight basis, found in earlier proximal analyses of these ctenophores.

The relative importance of the individual amino acids obtained from protein hydrolysates shows, however, some considerable resemblance to that already recorded for other zooplankton species. Thus glutamic is again predominant, though aspartic is only slightly less abundant; leucine and lysine and arginine again are present in very significant amounts. A difference, however, is the relatively high concentration of glycine, which is more abundant than leucine and arginine (Table 1). These six amino acids tobether comprise ~ 55% of the total.

There is some resemblance to other zooplankton in the relative importance of alanine and valine, but isoleucine and phenylalanine are less abundant. Methionine and cystine are again in least concentration and indeed are barely detectable (0.5%—Table 2).

No data are included for free amino acids owing to the extremely small concentrations detected, mostly less than 0.1 mg/g.

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URANIUM SERIES INEQUILIBRIUM AND THE GEOCHEMICAL PROCESSES OCCURRING ON THE SURFACE OF COASTAL SEDIMENTS

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ABSTRACT

Remarkable anomaly has been observed between U^{238} and U^{234} in the marine environment by a mumber of workers in the field. But little information is available regarding the U^{238}, U^{235} and U^{234} activities in coastal sediments.

The present work deals with the ratio of the activities of U^{234}/U^{238} and U^{235}/U^{238} from the coastal sediments of the west coast of India from Bombay (19°N, 73°E) to the southern tip of India up to Kottilppad near Manavalakurichi (8°N, 77°E) in the monazite bearing area of Kerala State.

The sediment samples are leached with ammonium carbonate solution so as not to attack the mineral core of the sediment and to get the leachable uranium activities from the surface of the particles.

In all the sediment samples U^{234} activity is about 12 to 14% higher than the equilibrium value indicating that there is disequilibrium between U^{238} and U^{234}. The U^{235}/U^{238} activity ratios lie in the range of 0.045 to 0.048 thereby showing that there is no significant fractionation between U^{238} and U^{235}.

INTRODUCTION

U^{238} and U^{234} are separated in the uranium series by Th^{234} and Pa^{234}. The uranium series is given below :

$$_{92}U^{238} \xrightarrow[4.51 \times 10^9 Y]{\alpha} {}_{90}Th^{234} \xrightarrow[24.1d]{\beta} {}_{91}Pa^{234} \xrightarrow[1.18m]{\beta}$$

$$_{92}U^{234} \xrightarrow[2.48 \times 10^5 Y]{\alpha} {}_{90}Th^{230} \xrightarrow[8.0 \times 10^4 Y]{\alpha}$$

Masurements carried by earlier workers (Veeh, 1966) have shown radioactive disequilibrium between U^{238} and U^{234} in total deep sea sediment samples, corals etc. In water samples from the Pacific Ocean, Thurber (1962), Koide

and Goldberg (1965) have obtained a value of 1.15 for U^{234}/U^{238} activity ratio. Moore and Sackett (1964) have obtained a value of 1.14 for the above ratio in waters of North Atlantic. Miyake *et al.* (1970) have obtained values in the range of 1.07 to 1.18 at different depths in the North Pacific waters. Kazachevskii *et al.* (1964) have obtained a value of 1.15 for the Black Sea. Joshi and Ganguly (1972*a*) have obtained a value of 1.151 in the coastal waters of Bombay.

There has not been much systematic work on the ratio of the activities of U^{234}/U^{238} and U^{235}/U^{238} in coastal marine sediments. Blanchard (1965) obtained values of 0.93 to 0.96 for the ratio of U^{234}/U^{238} in estuarine sediments, while the shells from the estuary gave ratios of 1.10 to 1.11. All the values cited above, which were obtained by the earlier workers, are by attacking the mineral body of the sediment samples. In the present work, coastal sediment samples are leached with ammonium carbonate solution, an efficient leaching agent for uranium and which does not attack the mineral core of the sediment particles. In the dynamic processes in the marine environment, the sediment and the water interface are the most important and the equilibrium is expected only to be established between the chemical occurring on the surface of the sediments and the condition in the ambient medium.

Sample Collection

Fine fractions of the sediment samples were collected from the west coast of India, from Bombay (19°N, 73°E) to Kottilppad near Manavalakurichi (8°N, 77°E) in Kerala State. Figure 1 gives the location of the sampling points in the Bombay region, while Fig. 2 indicates the collection sites along the west coast of India.

Experimental Methods

The method is based on the simultaneous removal from the coastal sediments of the three isotopes of uranium, U^{238}, U^{235} and U^{234}.

In the surface leaching processes, 300 gm of the uncrushed, dried sediment was taken with 800 ml of saturated ammonium carbonate solution for seven to eight hours. The sediment particles were allowed to settle down overnight and the supernate was filtered through 0.22 μ membrane filter. The procedure was repeated with two more instalments, 800 ml of ammonium carbonate solution and filtered. The pooled carbonate filtrates were evaporated to dryness and the residue was heated each time with 5 ml instalments of concentrated hydrochloric acid till all the carbonates were destroyed. The final

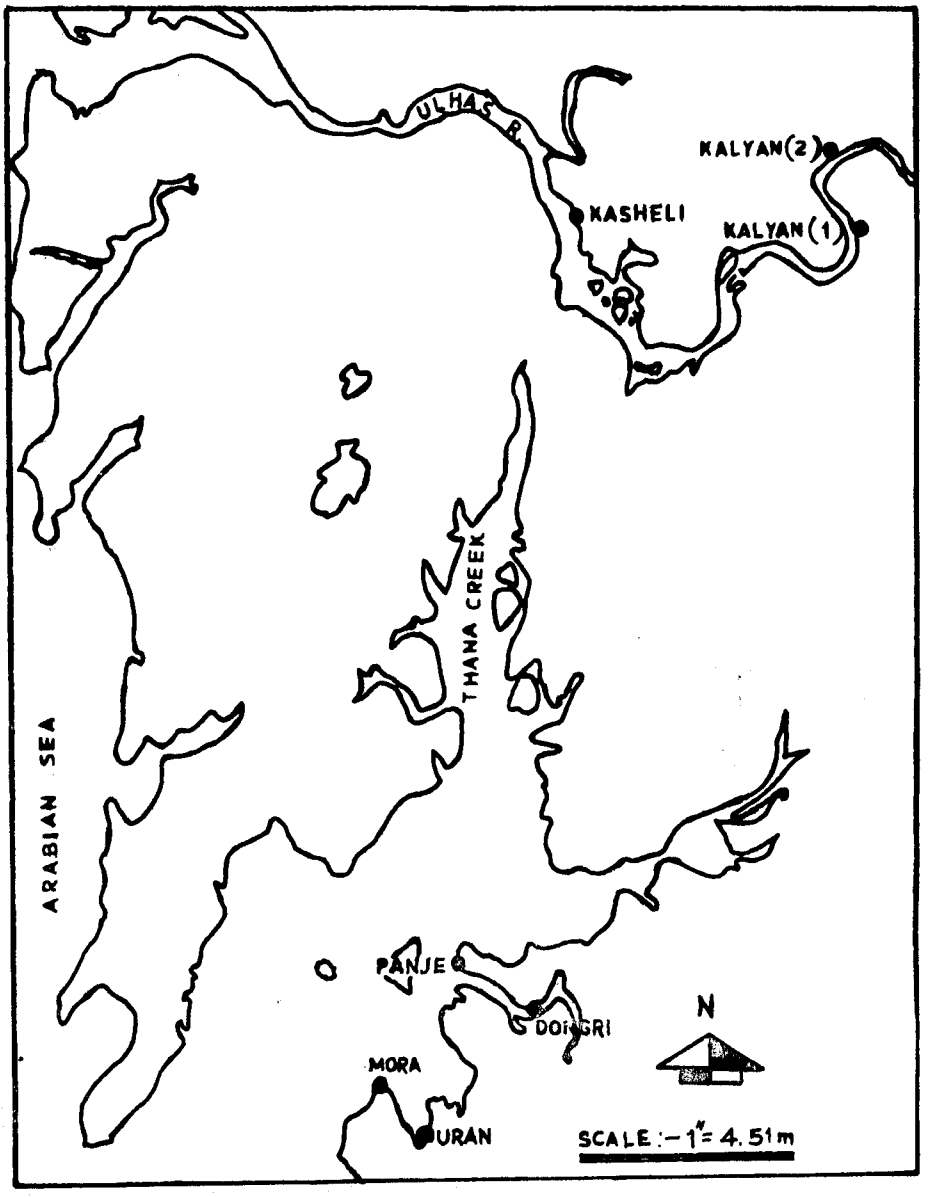


Fig. 1. Map of Bombay region showing the sampling points.

residue was ignited in a platinum dish at 450°C. The residue was then taken in 10 ml of 8 M hydrochloric acid. Removal of trace amounts of iron present in the sample was done by shaking the above hydrochloric acid solution with 10 ml of di-isopropyl ether for about five minutes.

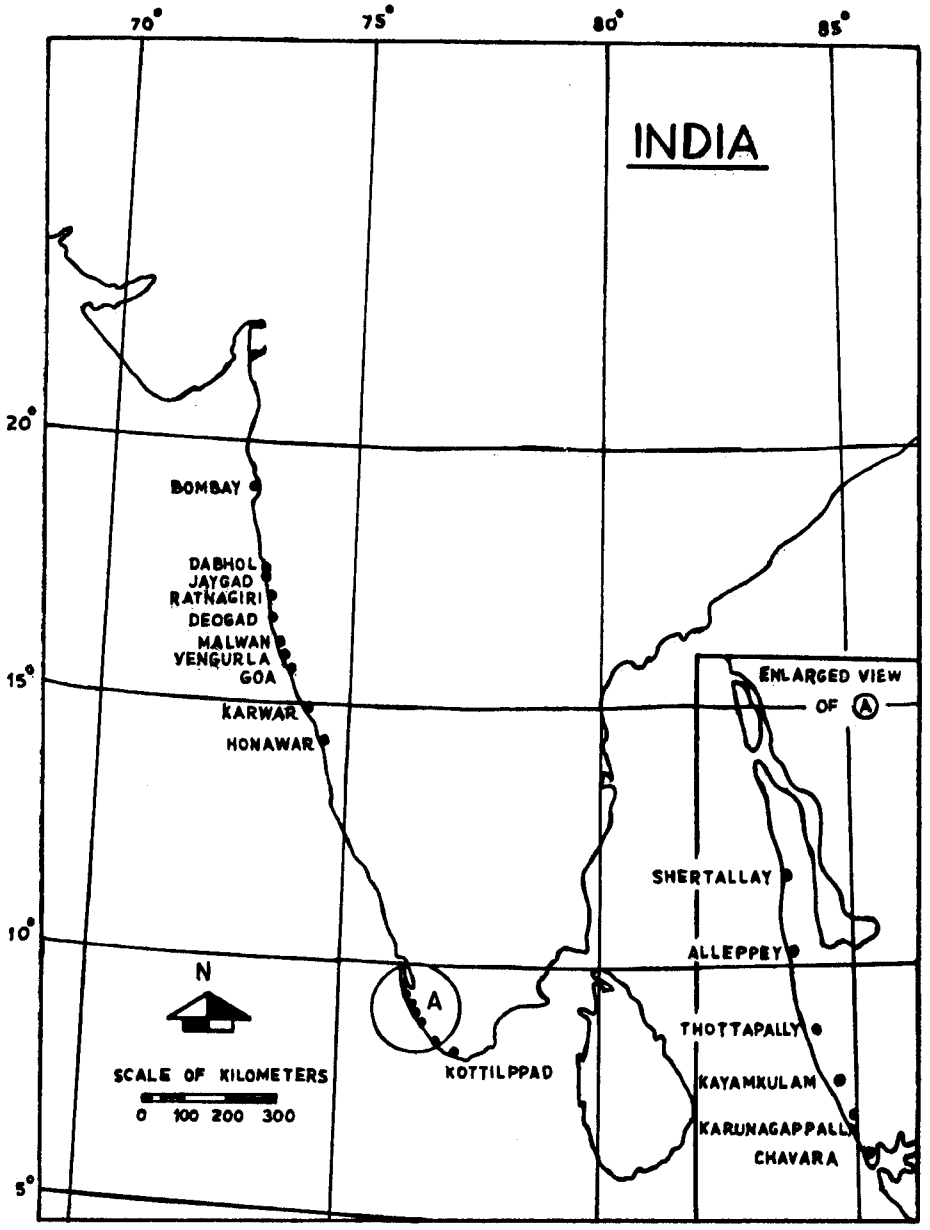


Fig. 2. Map of the west coast of India showing the sampling points.

Ion-exchange method for the separation of uranium

The aqueous layer after removal of iron was evaporated to dryness and then taken in 10 ml of 8 M hydrochloric acid and passed through anion-exchange column (1 x 15 cms), Dowex-1 x 8% (50-100 mesh) in chloride form. The

flow-rate was adjusted to 0.5 ml/min. Uranium was adsorbed on the column. The anion-exchange column was washed with 50 ml of 8 M hydrochloric acid with a flow rate of 1.0 ml/min. Protactinium was washed from the column with 10 ml of 3.8 M hydrochloric acid (flow rate 1.0 ml/min) and then the adsorbed uranium was desorbed from the column with 50 ml of 1.0 M hydrochloric acid with a flow rate of 0.5 ml/min. The chemically pure uranium obtained by this method was converted into nitrate form and plated on stainless steel planchet following the procedure of Cohen and Hull (1944).

Counting

Activities of U^{238}, U^{235} and U^{234} were obtained from the plated sample using a partially depleted silicon surface barrier detector (active area 200 mm^2) coupled to a well stabilised 256 channel pulse height analyser. The samples were counted for 1000 minutes to give a standard deviation $\pm$ 1.1% for U^{238} and U^{234} counts under the respective peaks and the standard deviation for U^{235} counts was obtained as $\pm$ 5.3%. The counting efficiency was 24% and the resolution of the detector was 43.4 Kev at 5.108 Mev alphas (Joshi and Ganguly, 1970; 1972 *b* and MS).

Results and Discussions

No significant alpha activity has been observed for the reagent blank.

Figures 3 and 4 show typical disequilibrium between U^{238} and U^{234} in coastal sediment samples from Dabhol and Karwar. Table 1 gives the activities of U^{238}, U^{235}, U^{234} and the activity ratios of U^{234} U^{238} and $U^{235}U^{238}$ From the table, it is seen that though U^{234}/U^{238} activity ratio indicates the existence of disequilibrium in U^{238} radioactive series, there is no significant fractionation between U^{238} and U^{235}

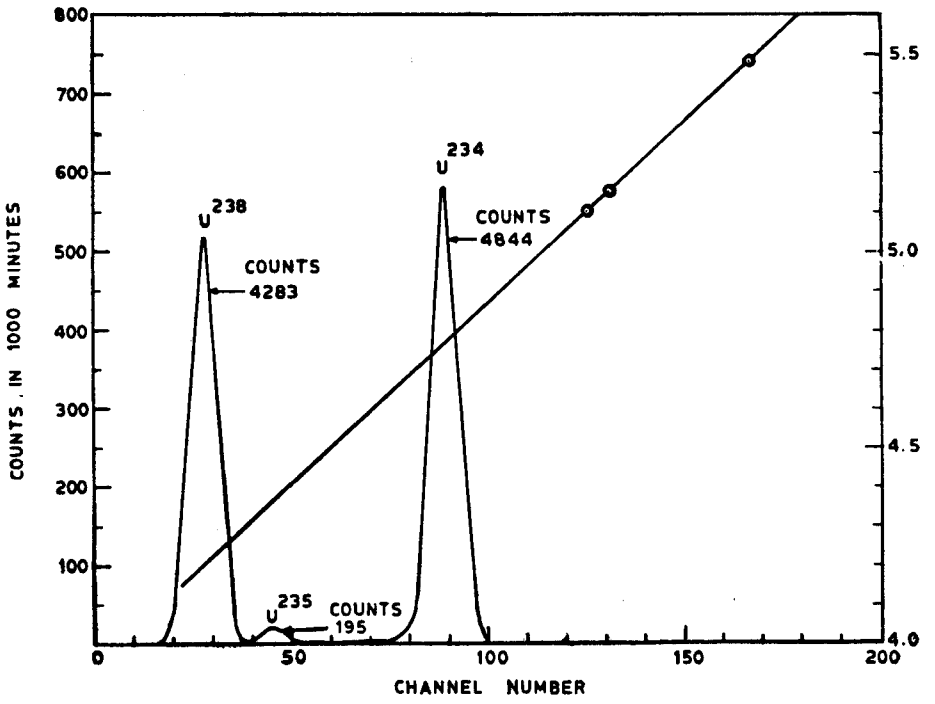


Fig. 3. Disequilibirum between U^{238} and U^{234} in sediment sample from Dabhol.

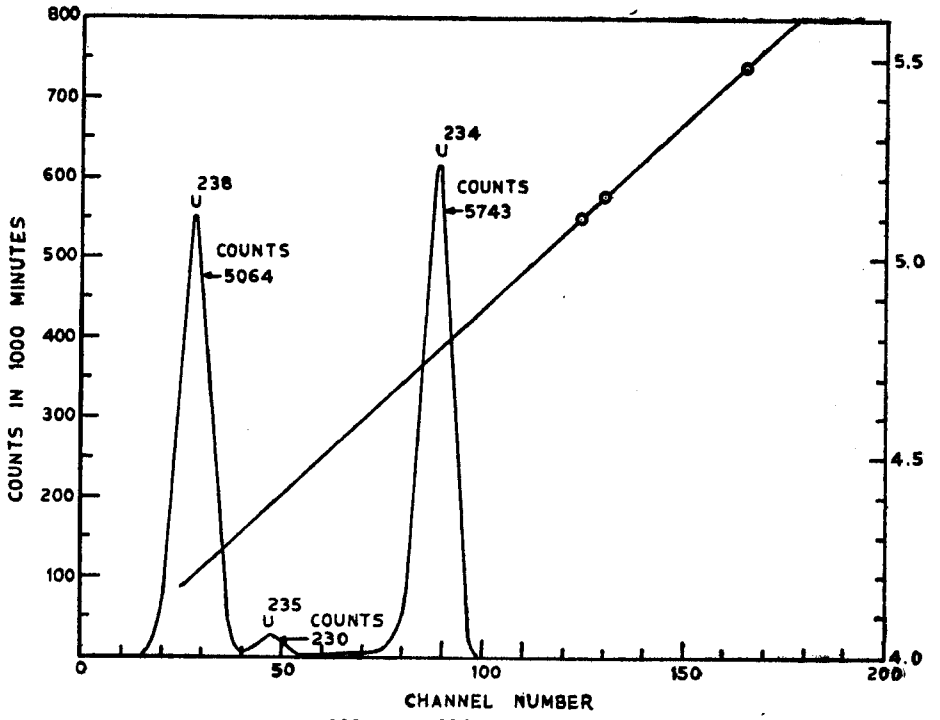


Fig. 4. Disequilibrium between U^{238} and U^{234} in sediment sample from Karwar.

Aliquots of Goa and Ratnagiri sediment samples were treated with 0.05 M hydrochloric acid and phosphate-free hydrogen peroxide in order to cleanse the particles of the surface organic matter and to obtain an acid extract of the uranium in the surface layer of the sediments. The acid extract after the above treatment was filtered and the filtrates were processed for column treatment for the chemical separation of uranium (Joshi and Ganguly, 1972 *a*). The remaining sediment residue was treated the same way as the original sediment.

Figure 5 gives the disequilibrium between U^{238} and U^{234} in the acid and hydrogen peroxide extract of the Goa sample, while Fig. 6 shows the two isotopes of uranium i.e. U^{238} and U^{234} are in equilibrium in the cleansed residue. Table 2 gives the activities of U^{238}, U^{235}, U^{234} and the activity ratios of $U^{234}U/^{238}$ and U^{235}/U^{238} in acid hydrogen peroxide extract and the corresponding leachates from the residues from Ratnagiri and Goa.

It is seen from these data that the anomaly between U^{238} and U^{234} exists only on the sediment particle surface and on removal of the surface activities and subsequent leaching of the residue gives the ratio of one as one would expect

in the mineral core of the sediment. However, U^{235}/U^{238} activity ratio exhibits, the ratio obtained for natural uranium.

TABLE 1. *Activities of uranium isotopes and their ratios in coastal sediments*

Sr. No.	Place of collection	Location	U^{238} (dpm)	U^{235} (dpm)	U^{234} (dpm)	U^{234}/U^{238}	U^{235}/U^{238}
1.	Bombay	19°N, 73°E	31.02	1.48	35.05	1.13	0.048
2.	Bombay	-do-	29.97	1.36	33.87	1.13	0.045
3.	Bombay	-do-	29.98	1.37	33.88	1.13	0.046
4.	Bombay	-do-	17.87	0.81	20.19	1.13	0.045
5.	Bombay	-do-	16.58	0.75	18.74	1.13	0.045
6.	Dabhol	17.6°N, 73.25°E	13.78	0.62	15.56	1.13	0.045
7.	Dabhol	do-	17.85	0.81	20.18	1.13	0.045
8.	Jaygad	17.5°N, 73.5°E	19.60	0.89	22.17	1.13	0.045
9.	Jaygad	-do-	20.62	0.94	23.30	1.13	0.046
10.	Ratnagiri	17°N, 73.5°E	21.05	0.95	23.93	1.14	0.045
11.	Ratnagiri	-do-	15.06	0.68	17.16	1.14	0.045
12.	Ratnagiri	-do-	18.36	0.83	20.86	1.14	0.045
13.	Ratnagiri	-do-	30.46	1.38	34.70	1.14	0.045
14.	Malwan	16°N, 73.75°E	21.69	0.98	24.66	1.14	0.045
15.	Malwan	-do-	26.47	1.20	30.12	1.14	0.045
16.	Vengurla	15.75°N, 73.80°E	35.37	1.60	40.14	1.14	0.045
17.	Vengurla	-do-	33.87	1.54	38.44	1.13	0.045
18.	Goa	15.5°N, 74°E	15.26	0.71	17.33	1.14	0.047
19.	Goa	-do-	23.13	1.05	26.26	1.13	0.045
20.	Goa	-do-	19.68	0.89	22.39	1.14	0.045
21.	Goa	-do-	20.43	0.93	23.20	1.14	0.045
22.	Karwar	14.2°N, 74.75°E	29.86	1.35	33.80	1.13	0.045
23.	Karwar	-do-	16.39	0.75	18.60	1.13	0.046
24.	Karwar	-do-	21.10	0.96	23.93	1.13	0.046
25.	Honawar	14.2°N, 74.75°E	29.86	1.35	33.80	1.13	0.045

The inequilibrium between U^{238} and U^{234} is explained by Rosholt *et al.* (1963) to be due to the preferential leaching of U^{234} as compared to U^{238} and U^{235}. Rosholt and his co-workers explain that during the transition of U^{238} to U^{234} U^{234} gets oxidised right at the time of its formation by virtue of two election-stripping. Thurber (1963), Cherdyntsev and his co-workers suggested that during the transition of U^{238} to U^{234}, the U^{234} atoms get re-located into the micro-cracks and the crystal defects, where U^{234} is more likely to be oxidised compared to U^{238} atoms, thus forming more soluble uranyl ions.

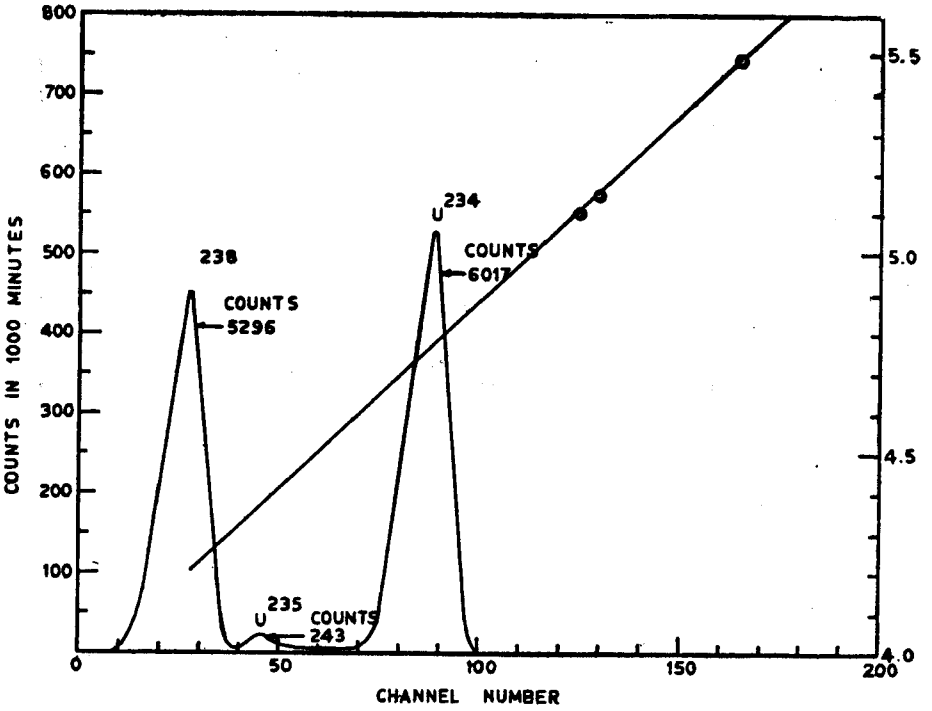


Fig. 5. Disequilibrium between U^{238} and U^{234} in the supernate attained after H_2O_2 + 0.05 M HCl treatment of the sediment from Goa.

TABLE 2. *Activities of uranium isotopes and their activity ratios in Ratnagiri and Goa sediments after hydrogen peroxide treatment*

Sr. No.	Place of collection	Location	U^{238} (dpm)	U^{235} (dpm)	U^{234} (dpm)	U^{234}/U^{238}	U^{235}/U^{238}
1.	Ratnagiri sediment residue	17°N, 73.5°E	20.99	0.96	20.99	1.00	0.046
2.	Ratnagiri acid + H_2O_2 extract	-do-	21.05	0.95	23.95	1.14	0.045
3.	Goa sediment residue	15.5°N, 74°E	21.60	0.99	21.60	1.00	0.046
4.	Goa acid+ H_2O_2 extract	-do-	22.07	1.01	25.07	1.14	0.046

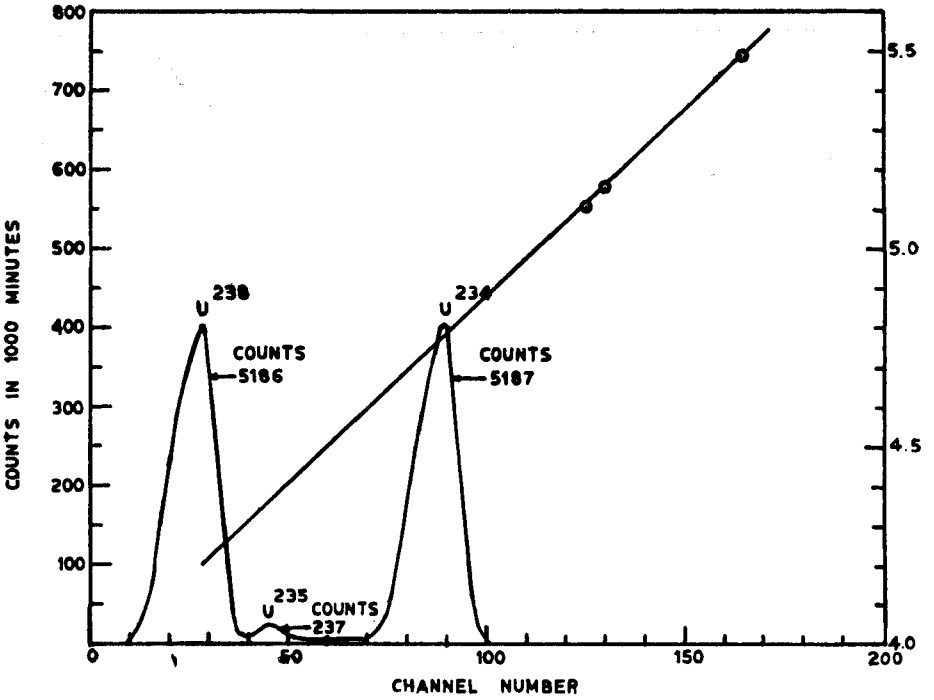


Fig. 6 Equilibrium between U238 and U234 in the sediment residue of Goa after removal of H_2O_2 and 0.05 M HCl Supernate.

From the above hypotheses one should get a ratio of U^{234}/U^{238} less than one in the uranium leachate from the sediment cleansed of surface organic matter. In the experiment performed (Table-2 in this laboratory Joshi and Ganguly, 1972*a*) the sediments was treatment with hydrogen peroxide and 0.05 M hydrochloric acid which removed quantitatively the surface layer of organic matter uranium complex which was in equilibrium with the ambient uranium in the sea water. The carbonate leachate of this organic matter (cleansed sediment) always gives a ratio 1 which throws doubts about the validity of the above hypotheses.

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PATTERNS OF DISTRIBUTION OF ARABIAN SEA HYDROMEDUSAE*

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ABSTRACT

A comparison between the surface and subsurface waters of the Arabian Sea and those of Bay of Bengal from the hydromedusan fauna point of view shows the following similarities and differences: In both the seas there is a marked difference between surface and subsurface waters as compared to intermediate and deep waters. In both the seas the surface and subsurface waters are under the monsoonal regime with biannual fluctuations of the amount of incoming solar radiation, rate of evaporation, pattern of circulation, convection currents and upwelling. Both seas are very deep. In the Arabian sea, evaporation is greater than what the total influx of fresh water could compensate. In the Bay of Bengal, the influx of fresh water is greater than the evaporation due to the enormous amount of fresh water contributed by the Ganga-Brahmaputra system and by the Irrawaddi.

Surface and subsurface waters in the oceanic area of the Arabian Sea have high salinity and high temperature and come very close inshore, practically up to the coast line in many areas, while in the Bay of Bengal, biologically speaking, the situation is reversed, "coastal waters" with low and seasonally fluctuating salinity remain at the surface and carry with them the "coastal water" fauna of hydromedusae that are mainly meroplanktonic species. Towards the centre of the Bay of Bengal are generally found mainly long-lived meroplanktonic species like the Pandeidae and large Leptomedusae. No such species are found in the centre of the Arabian sea, while some occasional Laodiceidae are found on the eastern side, where salinity is lowest, specially in the surface layers, and where the extent of the shelf is greater.

The situation, however, is entirely different in intermediate and deep layers, where both the western (Arabian Sea) and eastern (Bay of Bengal) monsoonal areas of the Indian ocean are similar and are in biological communication with one another and also with the Central waters of the Indian Ocean, with the Antarctic Intermediate Water and with the Antarctic plankton in deep layers.

The biological and ecological factors that determine the structure of the community of hydromedusae, in addition to the prime factor, which is their exclusive carnivorous habits, give them a high place in the trophic web.

* Contribution No. 340 of the Oceanographic Institute of the University of S. Paulo, Brazil.

INTRODUCTION

The hydromedusae are an interesting group for the study of the distribution of the plankton fauna, because they represent a homogeneous taxonomic group whose members are exclusively carnivorous throughout life. Furthermore, they are predators and kill their prey after capturing and paralysing it, with the poison contained in the nematocysts. Here we are concerned only with those species that have a planktonic stage throughout or during a part of their life history and therefore are members of the plankton community. They all have a gelatinous consistency and the diameter of the majority of the specimens is roughly between 200 μ to 3000 μ. Larger specimens of the large species are the Aequoridae (Leptomedusae), the Trachymedusae and a few Narcomedusae; these may reach a width of upto 5 cm, or rarely more, but are more frequently in the size range of approrimately 1-3 cm in diameter.

Because different species of hydromedusae have so may similarities, it is interesting to compare how the different details in their biology and ecology regulate the distribution and abundance of the species.

The biological and ecological factors that have been found to be decisive in determining the patters of distribution of this biologically speaking homogeneous group, are as follows: a) type of life cycle (whether holoplanktonic or meroplanktonic); b) type of reproduction (whether the medusa has or does not have vegetative reproductiion); c) longevity of the vagile phase (medusa); d) response to variation of environmental parameters of both the sessile phase (hydroid, when present) and the vagile phase (medusa, when present), i.e. the individuals adaptability; e) preferences for certain environmental factors.

The authors wish to express their thanks to Mr. J. Lupi for sorting the specimens from the samples. This work was partially supported by the National Science Foundation of the U.S.A. as a part of the U.S. Programme in Biology, International Indian Ocean Expedition; it was partially supported by the Office of Naval Research, U.S. Navy (NONR 4382; NR 104-185), by grants made to Drs. I. E. Wallen and M. Vannucci.

MATERIAL

This paper is a brief synopsis of the knowledge gained through the study of the hydromedusae contained in the plankton samples collected a) during the IIOE by the American ships; b) of the hydromedusae taken during the Antarctic

programme sponsored by the National Science Foundation of the U. S. and c) of the series of samples taken by the Indian Ocean Biological Centre (IOBC) of the National Institute of Oceanography, India.

The research materials is represented by a) the hydromedusae sorted at the Smithsonian Oceanographic Sorting Centre (SOSC) in Washington, D.C. (U.S.), which were determined and counted by the authors at the Oceanographic Institute of the University of S. Paulo, Brazil; b) by the environmental data of the station at which the hydromedusae were taken as found in cruise reports of the participating institutions and in computer printouts of the World Oceanographic Data Centre A, in Washington, D.C. and c) the material and data collected and processed at the Indian Ocean Biological Centre (IOBC) by Santhakumari and Vannucci.

Papers by Navas (1971), Santhakumari and Vannucci (in press), Vannucci and Navas (1971, 1972), Vannucci and Santhakumari (1971) and Vannucci *et al.* (1970), contain detailed information on the species and their occurrence.

The present paper is neither an inventory nor a description of the fauna of hydromedusae and its distribution in the Arabian sea, but rather an abridged summary of the knowledge gained through years of study of this material.

The antarctic material of the Smithsonian Institution, being studied at present by Navas in S. Paulo, is not strictly comparable to the Indian Ocean material collected during the IIOE, because of differences in the nets used. Most of the antarctic material was collected with the IKMT (IsaacsKidd midwater trawl) that had a mesh width larger than that of the plankton nets used during the IIOE. Thus, only the larger sized species were collected in antarctic waters and so far we have no information on the smaller species and young stages of the larger antarctic and subantarctic species; nevertheless, the wealth of information contained in these samples makes them extremely interesting for comparison.

Ecological Distribution of Hydromedusae

The Arabian Sea environment

From the point of view of distribution of plankton species, the more important features of the Arabian sea are the following:

a) The water mass to be found from the surface to a depth of 100 to 150 m is Arabian sea surface water (ASSW) with salinity higher than 35.8‰ throughout its geographic range and higher than 36.5‰ in the western part.

Temperature is everywhere higher than 20 to 21°C, upto 30°C in the northern part in August. The dissolved oxygen content drops steadily below 50 m depth down to 1.13 ml/1. It is because of intense evaporation due to heating by solar radiation with relatively little fresh water input.

b) From 100 to 150 m depth down to 400 m, there is Arabian sea subsurface water (ASSSW). It has temperature from 10 to 19°C and salinity ranging from 35 to 36‰, higher towards the Red Sea and the Persian Gulf, with values upto 39.7‰, oxygen content is lower than 2 ml/l and falls very low or down to nil in the oxygen minimum layer. Anoxic conditions may occur mainly off the Indian coast and may at times reach the surface through process of upwelling or through upward tilting of the thermocline. It is formed by the input of the Red Sea and Persian Gulf waters, and is mixed by convection currents. Red Sea and Persian Gulf water may be traced down to 600 and 1000 m depth and as far south as Madagascar.

c) From 400 m depth down to about 1500 m, there is Arabian sea intermediate water (ASIW) with temperature ranging from 4 to 13°C and salinity between 35.0 and 35.5‰. At places where there is admixture of Red Sea water or Persian Gulf water, the salinity may be as high as 36.5‰; the dissolved oxygen content may vary from 0.4 to 1.43 ml/1. It is originated in the same manner as the ASSSW, but here convection plays no part.

d) At depths between 1500 and 3000 m there is Arabian sea deep water (ASDW) with temperature of 2°C or higher, salinity from 34.68 to 34.79‰ and about 3 ml/1 dissolved oxygen content. It results from the mixing of ASIW, south Indian Ocean intermediate water and Indian Ocean bottom water.

e) Depths greater than 3000 m are occupied by the Indian Ocean bottom water (IOBW) that results from mixing of antarctic bottom water and north Indian deep water. It is characterised by 0.2 to 1.47°C temperature, 34.69 to 34.77‰ salinity and 4.03 to 4.68 ml/1 dissolved oxygen content.

The Arabian sea may best be looked upon as the northwestern monsoon area of the Indian Ocean; it is under the influence of the monsoons, that cause a bi-annual reversal of the surface gyral with the associated phenomena of periodical upwellings specially intense during the SW monsoon in different areas; they also contribute to generating one of swiftest currents in the world, the seasonal Somali Current. Below surface layers, however, the water masses are not influenced directly by the monsoonal regime and are rather under direct or

indirect influence of the antarctic system. The Arabian sea has two large embayments of oceanographic importance, the Persian Gulf that contributes a certain amount of dense, highly saline, high temperature water, through the Gulf of Oman and the Red Sea that contributes a considerable amount of high density, highly saline and hot water through the Gulf of Aden. Both Persian Gulf and Red Sea Water are formed locally by evaporation.

Biologically speaking, the Suez Canel has added a new dimension to the Indian Ocean and Arabian Sea in particular, by opening a passage way to species migrating to or, more rarely, from the Mediterranean. All the migrants must withstand the extreme conditions of salinity and temperature of the Great Bitter Lakes, either in an active or resting stage, in their crossing through the Suez Canal.

Finally, although many of the coastal areas bordering the Arabian sea have a high salinity and border hot, arid lands, there are also many estuaries and lagoons, with brackish waters or salinity gradients ranging from sea water to fresh water along the Indian coast. All, however, have high to very high temperatures. Finally, the upwelling areas on the western side of the Arabian sea are intense seasonal phenomena of biological importance towards determining the patterns of distribution and the abundance of species.

Distribution of the hydromedusae

In surface and subsurface waters and at their boundary, in the high seas far from land masses, the most abundant species are three Trachymedusae and one Narcomedusa that represent 70% or more of the total catch. All of them are holoplanktonic and are independent of the bottom for completing their life cycle. The species, in decreasing order of abundance are: *Aglaura hemistoma, Liriopa tetraphylla, Rhopalonema velatum* and *Solmundella bitentaculata.*. Next in abundance, although much more rare, are the Narcomedusae *Pegantha martagon, Cunina octonaria, Panthachogon haeckeli,* (a Trachymedusa), *Cunina peregrina, C. frugifera* and *Pegantha triloba.* Many of the Narcomedusae of the genera *Cunina* and *Pegantha* have sessile larval stages, very small actinulae in their life cycles, but nevertheless they are independent of the bottom as a substratum, since the larvae when present live as commensals or parasites in the gastral cavity of other Narco—or Trachymedusae (rarely in Anthomedusae) and in *Tomopteris helgolandica* (Vannucci, unpublished). All of them are holoplanktonic and eurytopic for both salinity and temperature. Also the trachymedusa *Amphogona apicata,* that may also be found in ASSW and ASSSW, is found far from land masses and is eurytopic for both salinity and temperature.

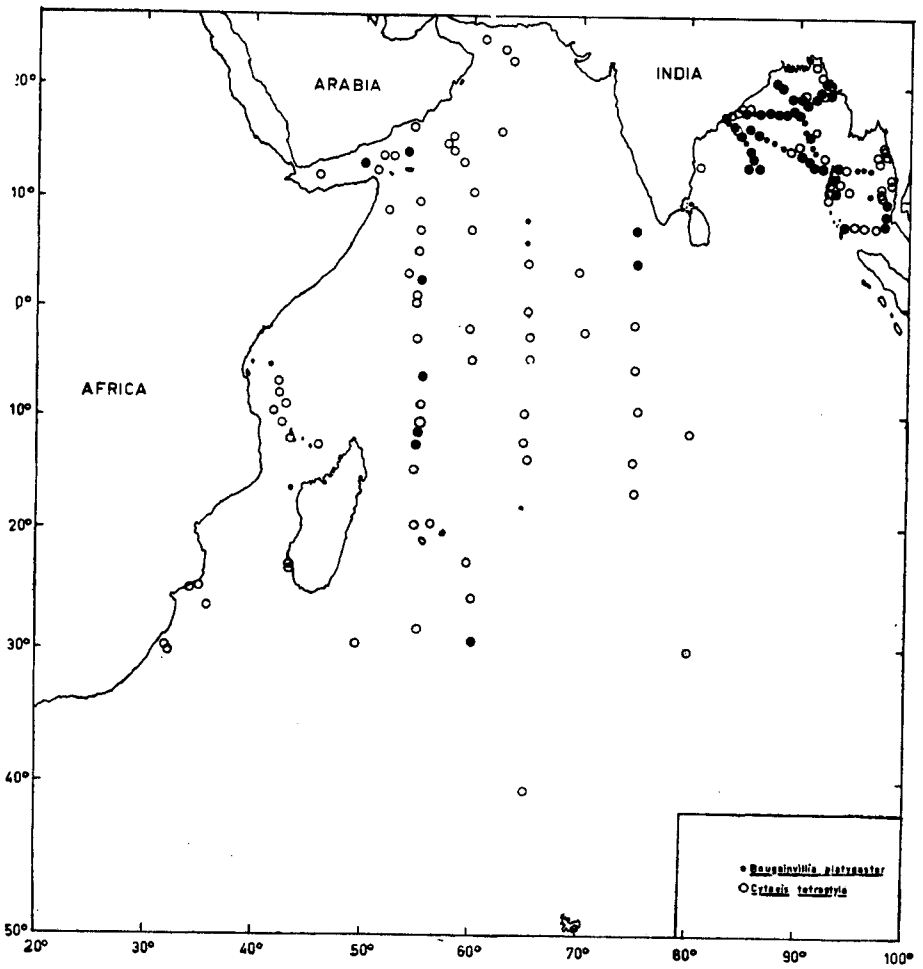


Fig. 1. Geographic distribution of *Cytaeis tetrastyla* and *Bougainvillia platygaster*. The overlap in distribution is relatively small.

The most frequent and abundant meroplanktonic species is *Cytaeis tetrastyla,* that is the fourth most abundant of all the species. It is an Anthomedusa that presumably may have a sessile hydroid stage in its life cycle but which normally multiplies through intensive vegetative reproduction of the medusa and thus becomes independent of the bottom to increase its numbers.

Bougainvillia platygaster is another Anthomedusa comparable to C. *tetrastyla* because it also has intensive vegetative reproduction of the medusa, and also most probably has a hydroid in its life cycle. They both have approximately the same size and are surface species (infrequently found in intermediate or deep waters), high temperature, eurythermal and euryhaline with high oxygen

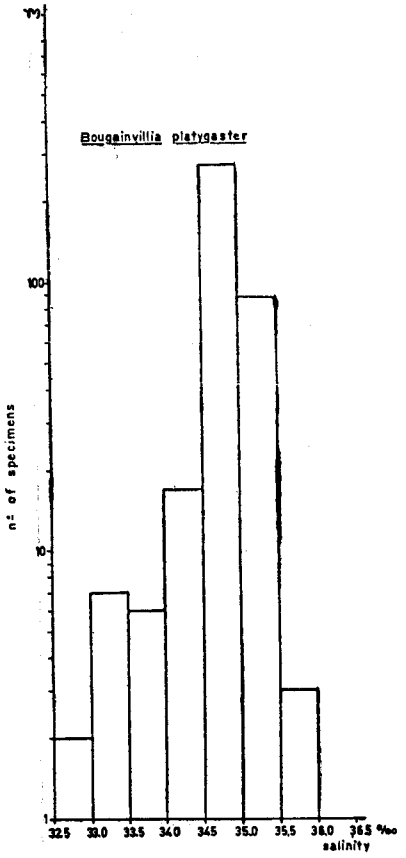


Fig. 2. Frequency distribution of *Bougainvillia platygaster* for salinity. A well marked mode is evident at the 34.5 to 35.0°/oo interval and virtual absence above 36.0°/oo.

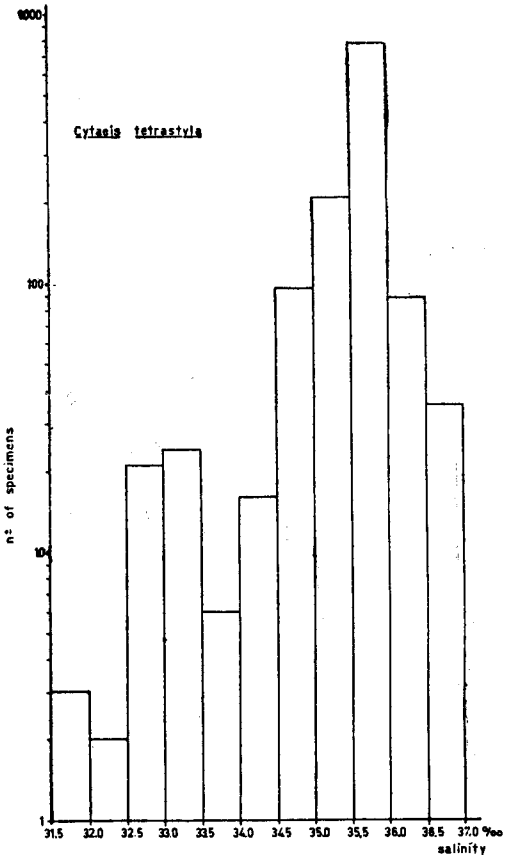
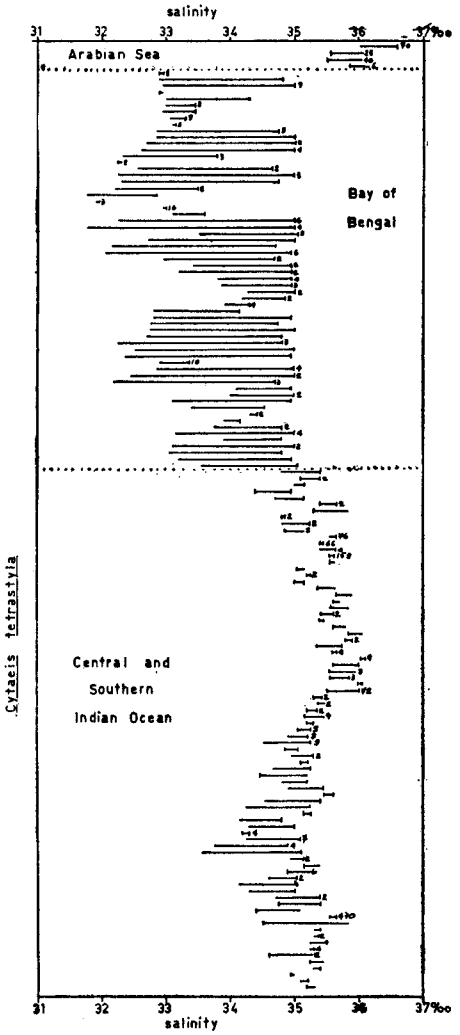


Fig. 3. Frequency distribution of *Cytaeis tetrastyla* for salinity. It was found on a wider range than *B. platygaster* with a mode at the 35.5 to 36.0°/oo interval.

requirements. Accordingly both have a wide geographic distribution. The salinity preferences of *B. platygaster,* however, are lower than those of *C. terastyla* (Figs. 2 and 3) and thus it is very frequent and abundant in the Bay of Bengal, while *C. tetrastyla* replaces it in frequency and abundance in the Arabian Sea (Fig. 1). The optima of *C. tetrastyla* appear to be around 35.5 to 35.6‰ salinity, 17 to 21°C temperature and 5.3 to 5.5 ml/1 dissolved oxygen, while the optima for *B. platygaster* seem to be 34.5 to 35.5‰ salinity, temperature higher than 23°C and high dissolved oxygen content (Figs. 4 and 5).



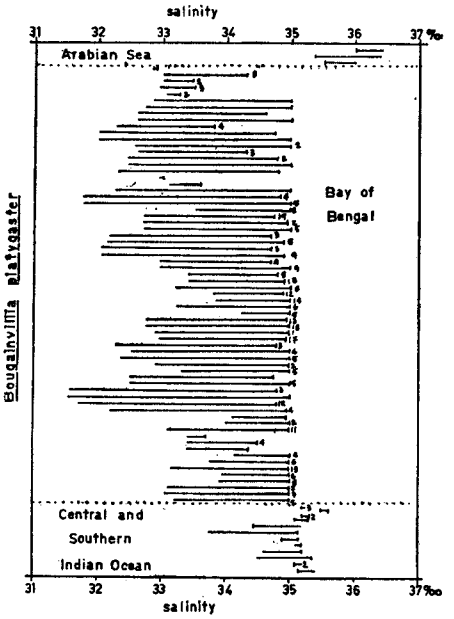


Fig. 5. Distribution of *Bongainvillia platygaster* in different water masses. Explanation of symbols as in Fig. 4. It shows that this species, differently from *C. tetrastyla* is to be found almost exclusively in the Bay of Bengal.

Fig. 4. Distribution of *Cytaeis tetrastyla* in different water masses. Salinity is show on abscissae. Each line corresponds to a haul and shows the salinity interval through which the net fished. The bar at the end of the line shows the maximum value that was reached, the open end indicates surface. When both ends are barred it indicates that a closing net was used, enclosing the salinity values shown. Numbers at the end of each line indicate the numbers of specimens caught; no number indicates that the sample had only one specimen.

No other species of hydromedusae were found to be well represented in ASSW, ASSSW and the boundary between the two, in the Arabian sea, away from the bordering coasts. Specimens of the other species were found occasionally and mostly they represent long-lived species, tolerant of high salinity. These are the Anthomedusae: *Heterotiara anonyma* and *Calycopsis papillata,* presumably they are both meroplanktonic; and another very long-lived Anthomedusa, *Koellikernia fasciculata,* that is a Mediterranean immigrant.

Summing up the hydromedusan fauna of the ASSW and ASSSW far from land is essentially made of Trachymedusae, then Narcomedusae and *Cyteais tetrastyla* (Anthomedusa with vegetative reproduction of the medusa) and other occasional species. High salinity, high temperature, distance from land and therefore a suitable substratum for the hydroids as well as an extensive oxygen poor layer are the most important environmental factors that act as a selective force for many species in these waters.

The hydromedusae of the Arabian Sea intermediate waters cannot be considered separate apart from the system of antarctic intermediate water (AIW). Although AIW as a water mass cannot be traced as such north of 10°S lat in the Indian Ocean (Wyrtki, 1971), the hydromedusae and, most probably, other plankton animals as well, have spread north and colonized the ASIW where conditions are comparable although temperature and salinity are higher and oxygen content may be lower than those of the AIW. Salinity of AIW is 34.2 to 34.8‰ (35.0 to 35.5‰ in ASIW), oxygen content ranges from 1.41 to 4.40 ml/l (0.4 to 1.43 ml/l in ASIW), and temperature about 4°C (4 to 13°C in ASIW). For these three parameters the equatorial intermediate water is in between AIW and ASIW and probably offer a passage for plankton species. Thus the medusae relatively abundant in the ASIW have also been found in AIW. They are all holoplanktonic Trachymedusae and Narcomedusae, with the exception of the long-lived Anthomedusa *Euphysora furcata.* They are the following species : *Botrynema brucei, Halicreas minimum, Solmissus marshalli, Aegina citrea, Aeginura grimaldi, Panthachogon haeckeli, Colobonema sericeum.*

Curiously enough, the deep sea widely distributed *Panthachogon haeckeli* and the antarctic congeneric species *P. scotti* have not been found in the intermediate layers of the Bay of Bengal, that are comparable to those of the Arabian Sea and support a similar fauna.

Furthermore, there are some AIW species that apparently do not enter in the Arabian Sea, for instance *Crossota brunnea,* a strict AIW water form which stops at lat. 10°S and is not to be seen in the Bay of Bengal either. Other antarctic species also were not recorded so far from the Arabian Sea.

There is a group of species that can be found in the lower range of ASSSW that were found only north of the subtropical convergence at 40°S lat. These are all holoplanktonic; *Sminthea eurygaster, Pegantha triloba* and *Amphogona apicata* that form a group of species distinct from the ASIW group of species. They are warmer water species and do not extend south of the subtropical con-

vergence at 40°S lat; they belong to the Indian Ocean Central Water System. Some were found in the Bay of Bengal subsurface waters and AIW but not in the Arabian Sea.

The salient feature of the ASIW species is that they are essentially holoplanktonic, stenothermal and with high oxygen requirements.

We do not have sufficient information on the hydromedusae of the deep and bottom waters of the Arabian Sea.

What precedes refers to the hydromedusae of the open ocean in the Arabian Sea. The distribution and abundance of the neritic fauna are more difficult to describe on a general basis, because of the varied conditions of the peripheral areas of the Arabian Sea. Furthermore, we do not have samples from the Persian Gulf nor from the Red Sea and only a few from the Gulf of Oman and from the Gulf of Aden. Red Sea samples taken by the "Meteor" during the IIOE are being studied by Eckardt-Schmidt.

In a general way, however, in near shore waters there is a reversal in relative abundance, with increase of meroplanktonic forms, and decrease of holoplanktonic species. In neritic waters of the western side of the Arabian Sea. the selective factors of major importance are temperature and salinity and a holoplanktonic life cycle is not the selective factor of much importance. Only those species that tolerate or prefer higher ranges of both these parameters are present, along with high salinity and high temperature holoplanktonic species like *Cunina peregrina, C. octonaria* and *C. frugifera.* Some holoplanktonic species may also be found in the western Arabian Sea, such are *Solmissus marshalli, Panthachogon haeckeli, P. scotti, pegantha clara, P. triloba, P. martagon* and *Amphogona apicata.* These species are eurytopic to a large extent, for both temperature and salinity, excepting *Panthachogon scotti* which was taken in temperature not higher than 14.5°C and about 35.5‰ salinity.

They are mainly found at Shallower depths only in regions of intensive upwelling, such as along the Arabian Peninsula.

Other holoplanktonic forms were captured near the coast, but in subsurface or intermediate (ASSSW or in ASIW) waters only. These are: *Sminthea eurygaster, Aegina citrea, Halicreas minimum, Colobonema sericeum.* The meroplanktonic species which were more abundant in the western and northern Arabian Sea were: *Eirene viridula* (rare), *Bougainvillia fulva, Aequorea aequorea, A. pensilis, Heterotiara minor, H. anonyma, Laodicea fijiana, Vannuccia*

forbesi, Zanclea orientalis, Z. costala, Euphysora bigelowi. In no place they were as abundant as the holoplanktonic off shore medusae, and most of them were concentrated in the Gulf of Aden, where total zooplankton volume per unit of water was among the highest from the Arabian sea.

We have no knowledge of the hydromedusae of special environments along the coast of western Arabian sea.

The eastern Arabian sea is entirely different from the western side. But not much is known of the hydromedusae of the coasts of Pakistan and India and most of our knowledge centres on samples taken in the bays of Goa and in the backwaters of Kerala. These are strongly dominated by meroplanktonic medusae although some of the eurytopic holoplanktonic species may be found frequently and sometimes in swarms such a *Liriope tetraphylla,* quite near the shore. The rather rare Trachymedusa *Petasiella asymmetrica* may perhaps occur with relative abundance (Vannucci and Santhakumari, 1971).

The influx of fresh water from land into the Arabian sea apart from the water contributed by the Indus river, does not extend far out into the sea, except in the surface layer and at specific places and seasons, where warm low density water may be found for miles in the sea as a thin layer mainly during and after the SW monsoon. Thus everywhere in the Arabian sea, (Ramamirtham and Jayaraman, 1963), high salinity and high temperature waters come very close inshore and also along the eastern side of the Arabian sea. These carry with them holoplanktonic species that are often brought to relatively shallow depths during the upwelling.

The major mass of meroplanktonic fauna of hydromedusae is to be found in estuaries, embayments and backwaters. These show the typical association of species of such environments, for they are euryhaline, warm water forms and tolerant of abrupt and sometimes drastic environmental changes. They are the same species as found all over the tropical belt in such environments and are often present in swarms (density of up to 50 specimens/m^3). Such are: *Blackfordia virginica* and its sibling species *Phialucium carolinae,* species of the Eirenidae, Eutimidae and Lovenellidae.

To sum up, it seems that the coastal, estuarine and backwaters of the Arbian sea are characterized by the usual association of meroplanktonic euryhaline warm species as are found under such conditions in all the tropical belt. They are also characterized by their occurrence along the coast line, at places where the shelf is very narrow, or at times or upwelling. Thus *Cytaeis tetrastyla,* Rhop-

palonematidae, Geryonidae and Cuninidae are found very near the shore. This is due to the peculiar conditions of very high temperature and salinity of the Arbian sea waters that come to the edge of the land even when dilution occurs at the surface due to rains or runoff from land. As in other tropical, subtropical and temperate areas, certain species of the Aequoridae are found at the boundary area between marine and brackish water species.

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MIGRATORY BEHAVIOURS IN MARINE ANIMALS AND THEIR PHYSIOLOGICAL REGULATIONS.

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ABSTRACT

The author has gathered a variety of factual informations to show that the variations in physiological properties such as the alteration in the osmo and ionic regulatory mechanisms in response to the environment in which the animals live, can condition, at least in part, certain stages of migration both in amphihaline and holohaline animals. This happens in conjunction with the temperature of the water. Such a modification cannot, however, account for the different types of migration in animals. It is, therefore, necessary to determine the changes in physiological mechanism which develop before and during migration, particularly in the neuroendocrine and sensorial systems. This has been clearly demonstrated in some cases where evidence on the sympathicotony is available. The author believes that the exact cause of migration is extremely complex, for it includes different stimuli and receptors. The author puts forward a hypothesis that in some holohaline migratory fishes such as *Thynnus thynnus* and certain large sharks, fluctuations in the thermoregulatory capacity may be responsible for their largescale movement in water masses having different temperatures.

Numerous examples tend to prove that physiological adjustments in animals are necessary before an animal can change its environment. Claude Bernard considered such an adjustment as the very essence of life. It would perhaps be necessary here to try and gather some experimental evidence on marine animals so as to demonstrate the physiological regulation and then to speculate the possible mechanism underlying this behaviour. That external factors play an important role in the migration cannot be doubted; but these can only act as stimuli if the animals are to respond to them by modifying their behaviour. This sensitivity to the external factors varies according to the physiological state of the animal. Indeed, in certain rivers in my country, salmon and eels have been observed to migrate simultaneously, both upstream and downstream, particularly the eels which are found in certain canals adjoing

the coastal ponds and the sea. Although the fish belonging to the same species present two different types of behaviour they are actually subjected to the same environmental conditions but certainly their physiological state does not remain the same. This is the reason why they respond to environmental conditions in a very different manner.

Let us now take a look at the physiological regulations which have been shown to play an important role in the migratory behaviour of marine animals, and let us first of all consider the term "amphihalines", which I have coined to designate animals which normally, in the course of their life cycle, pass from sea water to brackish or freshwater and vice versa. The salmon, the eel, the alosa are the best examples. Similarly the "euryhalines" are those animals which are able to tolerate wide salinity variations but these need not necessarily face a very wide variations during their life cycle. All amphihalines are necessarily euryhaline, at least during certain periods of their life, but not all euryhalines are amphihaline, e. g. certain sticklebacks. As opposed to amphihalines, we find other holohaline animals which constantly live in an environment approximately uniform from the point of view of salinity, but these are able to carry out vast migrations, such as the tuna.

As far as the amphihalines are concerned, it appeared to me in 1930 that a change in the osmoregulatory mechanism must be one of the important factors underlying their migratory behaviours. While attempting to enlarge the idea already given on Elasmobranchii and Selachii, regarding the modifications of "milieu interieur"[1] in relation to the variation in salinity of the surrounding, I went down to the banks of the Loire, where sea lampreys were being caught in the springtime during their anadromous migration. At this season, having left the sea where a greater part of their growth had been accomplished, these cyclostomes ascended the rivers into their spawning grounds. I observed that if these lampreys are caught some days after they leave the sea, they soon die if any attempt is made to expose them to sea water, even if the acclimatization is done gradually. A study of the freezing point of their blood and its molecular concentration showed that the molecular concentration of blood increases rapidly with an increase in the molecular concentration of the water. The freezing point which averaged — 0.54° for lampreys caught and kept in freshwater descended to 0.77°, within 24 hours after the environment attained a $\triangle$ of – 1.00° by progressively adding sea water. When this $\triangle$ reached – 1.96°, the blood of the lamprey which was collected only 4 hours after its capture, as

1 The term "milieu interieur" introduced by Claude Bernard is literally translated as "body fluid".

it was dying, showed a Δ of $-1.08°$. This was obviously incompatible for survival (Fontaine, 1930). When these data were compared with those of Burian (1910) who gives $-0.586°$ as freezing point for sea lamprey caught in the Mediterranean, in an environment with a Δ of approximately $-2.3°$ (Krogh, 1939) it appeared that the sea lampreys we studied at the beginning of their anadromous migration, when placed in hypertonic environments, presented a much less effective osmoregulation than those which were caught from the sea. From these considerations the idea arose that a modification in the osmoregulatory ability appearing at a precise stage in the life cycle may be the factor, or one of the factors, leading to their migration. Possibly the decline in the osmoregulatory mechanism in response to a hypertonic sea water environment was particularly severe and thus the animal was no longer capable of adapting itself to this condition. However, this phenomenon is not so serious in the other species, for the elver caught in our rivers at the beginning of their anadromous migration can be transplanted into the sea water environment which these have just left, without any obvious ill-effect. However, it is important to note that unlike the sea lamprey, in the elver migration is not associated with the gonad maturation.

Later studies confirmed the above idea. We have in particular studied the stage just before the catadromous migration in the young Atlantic salmon (*Salmo salar* L.). This stage is very important because a series of striking morphological transformations occur in salmon. The young salmon now acquires a silvery appearance, so different from its colour during the preceding sedentary stage which led the Englishmen to give salmon two different names. The first when the fish has a spotted coat very similar to that of the common trout was termed as 'parr' and the second, when the fish takes on a bright silvery appearance with their scales full of guanine and flaking off easily, termed as 'smolt'. The transformation from parr into smolt was called 'smoltification' and the intermediary stage was termed as 'parr-smolt'. The question now arose as to whether the catadromous migration of the amphihalines, such as salmon, could be attributed, at least in part, to a change in the osmoregulatory or ionoregulatory capacities of the fish when it was faced with hypotonic environments. This was actually the case, for as early as 1951, we pointed out an important fall in the Cl ion content in the muscular tissue of the smolt in comparison with that of the parr (Fontaine, 1951). Moreover, by regular determinations of the Cl ion exchange between the young salmon and its environment, it was demonstrated in my laboratory that the sedentary parr salmon, which lives and passed its first stage of growth in the very pure waters of the steams, shows a capacity for absorbing Cl ions from very slightly mineralized freshwater (the water of its

biotope) more satisfactory than the smolt. The latter loses these ions from its body whereas the former gains them (Chartier-Baraduc, 1959). It appears (Chartier-Baraduc, unpublished data) that the loss in sodium ions increases with smoltification. Everything occurs as though, the fish is getting conditioned to avoid too large fluctuations in its "milieu interieur" in response to certain ions. This results in the decline if its ionoregulatory mechanism when faced with a hypotonic environment. The muscular tissue of the smolt gives an index of "milieu interieur" with reference to certain salts, particularly sodium chloride.

The salt regulation however does not always follow, the same pattern during the premigratory phase. Thus Kubo (1955) pointed out that during smoltification of the *Oncorhynchus masou*, two successive stages occur, one shows a rise and the other, a fall in the freezing point of blood, just before migration, Houston and Threadgold (1963), while working on the *Salmo salar,* noticed a fall in the plasma-chlorine at the beginning of smoltification, but this value rises when the silvery parr stage is reached. A rather similar fluctuation in the osmotic pressure, would appear to result from Parry's data (1961) on the same species. Miles and Smith (1968), while making a similar study on *Oncorhynchus kisutch* did not observe any notable change in the plasma chloride concentration during the immediate premigratory phase and find the relationship (weight-plasma chloride concentration) quite contrary to that pointed out by Houston (1959) in the premigratory development of the steelhead trout. Differences in the chloride concentrations of the blood of yellow and silvery eels has been obtained both in the written reports and in our own observations (Callamand and Fontaine, 1940*a*, 1940*b*; Callamand, 1943; Fontaine and Callamand, 1948; Koch, 1949; Sharrat *et al.,* 1964). Nevertheless, the weakest chloremia has been observed in the silvery eels from which muscular demineralization becomes evident (Fontaine and Koch, 1950). These differences seem to be related to the more or less rapid development of branchial chloride secreting cells, which appears during smoltification of the salmon (Hoar, 1951) whereas, according to Colombo (1961), the chloride cells of the gills of silvery eel do not absorb chlorides from freshwater, unlike the yellow eels, but these could excrete them in sea water. These differences may also be related to the variations in the temperature of water, the influence of which on osmoregulation has been fully demonstrated (this will be discussed later) and in eels, to the duration of the fast, preceding the downstream migration (which probably lasts longer in the silvery eels caught during their downstream migration at the end of the winter than in those caught at the beginning of the autumn). As a rule, when we take into consideration the different biochemical constants of the parr during smolti-

fication and similar constants of the smolt or silvery eel, we notice that the range in the values is very large. This indicates that the adjustment in the homeostasic processes is very meaningful and has a direct relation with the start of migratory behaviour, although, in my opinion, it may not always have a direct influence (this will be shown later).

The modification of the osmoregulatory processes during smoltification is not only in Cl and Na ions, but also in others. My assistant Chartier-Baraduc (1960), has demonstrated that during smoltification, the potassium content in the muscle and brain increases, probably causing excitability to the tissues which may lead to migratory behaviour. Changes have also been observed in the calcium ions a greater decrease in calcemia occurs in the smolt as compared to the parr (Fontaine *et al.*, 1969), although the decrease in the calcium content of the muscle is a general feature. Variations of this type certainly affect the permeability and excitability of the membranes. These modifications in the hydromineral balance are associated with the neuroendocrine balance, either directly or indirectly, and give rise to behaviour modifications under the action of certain hormones.

Thus the increase in thyroid activity observed during smoltification played an important role in the triggering off this migration (Fontaine, 1960). It led to a greater loss of Cl ions (Baraduc, 1957) and Ca ions (Chartier-Baraduc, 1968). It also increased the motor activity which in turn, as has been shown from the experiments in which trouts were placed in an artificial current and were thus forced to swim hard, resulted in a loss of Cl and sodium ions from the muscle and this stimulated the thyroid and interrenal activity (Fontaine and Leloup, 1959; Fontaine and Leloup-Hatey, 1960). Thus we find an extremely complex interaction between osmoregulatory process, integration mechanism and the behaviour of fish. The interrenal tissues, were found to be very active in the smolt (Fontaine and Olivereau, 1957) and the introduction of suitable dosage of corticosteroid (Fontaine and Hatey, 1954), changed the osmoregulatory function, just as the activated Stannius corpuscles did during smoltification (Fontaine and Lopez, 1965) and which affected the calcium metabolism (Fontaine, 1964, 1967; Fontaine *et al.*, 1972).

The hypothalamo-pituitary axis (Arvy *et al.*, 1959) and several pituitary hormones (stimulins and general metabolism hormones and growth hormone) also affect and these not only produce an interaction which induces the animal to leave freshwater, but also ensures its adaptation to sea water. Indeed, the smolt has been observed to be more euryhaline than the parr and it seems clear

that the growth hormone (Smith, 1956) and the thyroid hormones (Fontaine and Baraduc, 1954) increase its euryhalinity.

Moreover, I have pointed out earlier that in the course of smoltification, a hypertrophy of the anterior interrenal occurs. This gives rise to the activation of the glandular tissue which probably correspondence to the corticosurrenal of higher vertebrates leads to a considerable increase in the 17-hydroxycorticosteroid content of the blood. The cortisol (a corticosteroid) which remains predominant in the blood of the salmon at all stages (cortisone appears in large quantities in the course of smoltification) seems connected with the branchial excretion of sodium in sea water (Mayer *et al.*, 1967). This may, to some extent, lead to the development of euryhalinity which appears during the smoltification and which helps the smolt to adapt to its new environment. Other observations give reasons to think that in amphihaline fish, a change in the osmoregulatory mechanism in response to the environment in which they find themselves, is in preparation for the fish to leave the environment. The diagram given by Kubo (1960), which shows variations in the molecular concentration of the blood of the Pacific salmon, *Oncorhynchus mason,* during its life cycle, indicates a clear rise in the molecular concentration of the blood at the time when the salmon approaches the sea coasts and begins its anadromous fluvial migration. The observations indicate a change in the osmoregulatory mechanism because of the hypertonic environment and this can be compared with that of the lamprey when it is at a similar stage in its migratory cycle.

Before looking for the significance of these observed changes in the osmoregulatory processes in response to migratory behaviour it seems necessary to see the effect of amino acids (free or incorporated in the proteins). The intracellular osmotic regulation also gets modified and this is associated with a significant decrease in the free amino acids of the muscle of young salmon during smoltification, whereas no change occurs in the total amino acid content (Fontaine and Marchelidon, 1971). However, the decrease in the free amino acid concentration does not seem to be a mechanism which compensates for an osmotic imbalance. It is probably a result of an accelerated growth in which free amino acids is used for the biosynthesis of proteins. Undoubtedly it contributes to the imbalance which characterizes the premigratory phase and the start of catadromous migration.

These changes in osmoregulation play an important role in determining the course of migration. Thus it has been observed that certain young Pacific salmon, caught in freshwater at the beginning of their catadromous migration, show a positive halotropism (Baggerman, 1960). This results from the chan-

ges in osmoregulation, in the vicinity of hypotonic freshwater environment, and serves as a guide in the estuarine zones. Thus distances of thousands of kilometers covered either by the *Salmo salar* L. in the Adour Basin in France to reach the waters west of Greenland, or by the European eel to reach the Atlantic shores during the course of its life cycle, seems a search for the salinity which is compatible to their changed osmoregulatory mechanisms and these changed physiological conditions seem to guide them. We have also shown that at the beginning and during a greater part of its catadromous fluvial migration, the smolt in the Adour Basin, does not follow a regularly increasing salinity gradient (Fontaine and Vibert, 1952). This also seems to be true for the long Atlantic migrators which migrates from our sea coasts to the waters off the west coast of Greenland. I believe that the determination of the routes of these migrations is very complex phenomenon and may involve, at different stage, different stimuli and receptors (Fontaine, 1965). In particular, in my opinion, the start of the migration of the smolt may be attributed to a change in behaviour resulting from a neuroendocrine evolution which brings the smolt to a sympathicotonic state very different from that of the parr (an increase of thyroid and interenal activity and adrenalinemia) in such a way that when the parr is looking for stones at the bottom and swimming close to the river bed, the smolt leaves the pebbles, rises to the surface, swims energetically and frequently even jumps out of the water and finally reaches the entrance to the sea. This does not mean that the changes in ionic regulation observed during smoltification play no role in setting off migration. As I have already pointed out, these changes are accompanied with changes in the K and Ca contents in certain muscular and brain tissues. These are also associated with endocrine activities (interrenal, for example). However, it is not the search for a new environment for which the changed osmoregulatory mechanism is better-adopted, which sets off the migration in the fish. We believe, that the search comes at a later stage, when the passage from fresh to sea water in the neighbourhood of the estuary begins to be identified.

As in the case of fish, the osmoregulatory mechanisms plays an important role in the amphihaline invertebrates at certain stages of their migration.

Already in 1939, Panikkar demonstrated the homeosmotic behaviour in the shrimp, *Palaemonetes varians* and pointed out the importance of this feature in the understanding of the distribution of the species (Panikkar, 1939). In 1940, with similar data on *Leander serratus,* he drew attention to the relationships between the migratory habits of certain *Leander* in waters of differing salinities and their osmoregulatory mechanisms (Panikkar, 1940*a*). Furthermore,

Panikkar (1940*b*) underlined the importance of temperature on the osmoregulation and favoured the idea that the correlation between the two influenced the geographical distribution of several species of crustacea.

Broekema (1941) offered an explanation of the migrations of *Crangon crangon* L. by saying that it is necessary for ensuring a satisfactory osmoregulation. Indeed, these shrimps live in sea water during the winter, and in brackish water during spring and summer. Broekema has shown that for a two year-old shrimps, the optimal salinity is approximately 33‰ at a temperature range 3—5°C and 28—29‰ at a temperature range 20—22°C. For the yearlings the optimum salinity is 18 to 19‰ at a temperature of 22°C. Thus, for the same temperature, the optimum salinity become higher with age.

In salinities below 21 to 23‰, *Crangon crangon* is hypertonic to its surrounding milieu. In salinities above 21 to 23‰, it is hypotonic towards the "milieu exterieur" and the difference between the "milieu exterieur" and the "milieu interieur" is greater at high temperature than at low temperature. Thus Broekema speculates that shrimps leave the coastal waters in autumn because at this time the fall in temperature corresponnds to a higher salinity optimum which they find in the open sea. However, during the warm season, Broekema noticed that a large proportion of shrimps negotiates such waters where the salinity is lower than that of the optimum. Thus it seems that with these populations we cannot attribute their choice of migration solely to osmoregulation. On the other hand, Verwey (1957) points out that the other Crustacea on the coasts of Holland perform migration in the reverse manner, i. e. they reach the open sea in summer and arriving in the coastal waters in autumn. These are *Hyas araneus, Crangon allmanni* and *Pandalus montagui.* Does it mean that the temperature-salinity relationship for these species is different from that of *Crangon crangon*? This question can be answered from what Panikkar (1940*b*) already emphasized that the ecological observations made on several crustaceans showed an inverse correlation between temperature and salinity.

Since then, numerous studies, and in particular by Flugel (1959), Kinne (1963-1964), Panikkar (1968) have given important details and have suggested explanations of the above mentioned phenomena. These leave hardly any doubt that the temperature-salinity interactions intervening in the processes of osmo and ionoregulation play a role in the migration of amphihaline Crustacea. This has been confirmed from the studies carried out on *Eriocheir sinensis,* whose eggs are fixed to the female's pleopod and these hatch in salt water during the spring. After, the development proceeds, the last larval stages return

to freshwater. They spend some years of their growth period in the freshwater and at the approach of sexual maturity, the crabs return to the sea. Mating takes place in brackish water and this is soon followed by the journey of the females to the open sea after spawning. Several biologists (Schwabe, 1933; Scholles, 1933; Widman, 1936) have pointed out that the ovigerous females suffer adversely from a sudden transfer from salt water to freshwater. Kamps (1937) added the fact that sexually mature females cannot tolerate the sudden change from freshwater to sea water whereas immature adult crabs can do so perfectly well. This would mean that maturation of gonads brings about a change in the osmoregulatory process and incites the *Eriocheir* to leave freshwater gradually. This hypothesis has been verified by Koch and Heuts (1944) who showed that except for the periods of sexual maturity, the Chinese crab is homeosmotic from freshwater to saltwater having a concentration of about 23‰ of NaCl. But in the ovigerous females this homeosmotic zone moves towards higher concentrations. The minimal salinity compatible with the normal physiological value for the stage has been found to be arount 6‰ NaCl. Even at this high concentration of the "milleu exterieur", the individual values have been found to differ widely. This shows that we are close to the limit of adjustment. Thus the migration of *Eriocheir* from freshwater to higher salinity water seems to be brought about by a decrease in the osmoregulatory capacities as a result of hypotonic environment.

These examples I have taken from among the amphihaline migratory animals which justify the hypothesis of a change in their physiological regulations (osmo and ionoregulation) leading to their migration. However, we may question whether the intervention of such a phenomenon can really be envisaged in the case of holohaline migrators living in sea water of almost constant salinity. In fact, all oceanographers know that some of these migrators can be found in water masses of different salinity and temperature and that these two factors influence densities, osmotic pressures, viscosities, speeds of sound propagation, coefficients of the absorption of gases, speeds of the diffusibility of ions, etc. These are some of the important factors to be considered while attempting to know the physiology and behaviour of marine animals in general. Some of these considerations led Sakamoto (1962) to speak of the T-Cl character of oceanic water masses which affect the movements of shoals marine fishes. Butt (1938) has also shown that some teleosts are capable of distinguishing very slight differences in salinity, of the order of 0.06‰. In the light of this it does not seem impossible to believe that the holohaline migrators may be even more sensitive during their migratory cycle to the concomitant variation of temperature and salinity rather than to the variation in salinity alone.

This is why Woodhead and Woodhead (1958) and Woodhead (1959) attempted to explain the migration of cod from the Barents Sea. During summer the cod is found in shallow waters in the northern part of the Barents Sea where it feeds intensively. In the autumn, it leaves these fishing banks and travels south. The mature individuals migrate to the spawning zone in the Lofoten Islands, off the north coast of Norway. Spawning takes place in March and April and the spent fish move northwards and return to deeper waters where they find their food. The eggs and young larvae are gradually transported to the same zones by the surface currents.

Woodhead and Woodhead (1965*a* and 1965*b*) have shown that a seasonal thyroid cycle exists in all individuals whether mature or immature. The thyroid becomes active towards the end of September and this state continues until March, when the gland enters into a resting phase till the following autumn. A study of the thyreotrope power of the pituitary (Woodhead and Fontaine, 1959) did not reveal important variations in the pituitary-thyreotrope power during this cycle. In adult individuals, the highest values are observed in the month of June (the hormone's stocking phase) and the lowest during the autumn. The activity of the thyroid gland at this time would lead to a greater secretion of TSH by the pituitary. It is also known that the cod is hardly ever caught at a temperature lower than 2°C, except in summer, (July and September), when the fish enter the cold Arctic waters for feeding on krill (*Euphasia superba*) and capelan (*Mallotus vilosus*). It therefore seems that the cod finds a temperature of 2°C as a physiological limit, except during summer when it eats influsively and also gets more light. Taking inspiration from Doudoroff's research (1945) on *Fundulus* which shows that a fall in temperature dislocates the osmoregulation and results in death, Woodhead believed that too low a temperatures cause either and excessive influx of ions in the "milieu interieur", or a deficiency in the elimination of ions, or both. Thus, a threat to such a change in osmotic and ionic imbalance begins to act as a limiting factor. The temperature limit varies according to the physiological state of the fish. It could be lower in summer when it takes more nourishment and when it is probably in a better condition to defend itself against the threat that a hypertonic environment may present. Adopting these results as a working hypothesis, P. M. J. Woodhead and A. D. Woodhead thought that at a temperature lower than 2°C, the ionic and osmotic balance of the body gets disturbed. These authors measured the freezing point of blood plasma and the Cl, Na and K contents of blood plasma. They then found that cod caught during the fishing expeditions, of winter and spring in waters having a temperature of 2°, 4° and 5°C showed relatively well-grouped values which can no doubt be considered physiologically as normal values. But cod caught in water lower than 2°C gave a significant percentage of values above the normal. The diffe-

rence normally existed in molecular and ionic concentrations, between the blood plasma and the sea water. This indicated that osmoregulatory capacities would diminish in a hypertonic environment. On the other hand, in the cod caught during the summer expeditions, no difference of this kind was found. These authors made a histological study of the gills and observed, that in individuals with disturbed osmotic regulation there was a depletion of mucus followed by an increase in the number and size of the chloride secreting cells. According to them, the mucus depletion allows salts to enter the body more rapidly and consequently the change seen in the chloride cells suggest an increase in the secretory activity probably meant for compensating a rise in the salt concentration of the blood.

What physiological modifications can really explain the changes in the tolerance limits of temperature observed during the annual cycle, we do not know, as no sufficient knowledge of the endocrine or interrenal cycles of the cod is yet available. However, we can suppose that the thyroid gland plays an important role as it becomes active in autumn and rests in spring.

However, it must be noted that the thyroid activity has been determined by the histological method, and that this technique reveals only the cellular activity and not its hormonal output. Further researches are needed by injecting dosages of thyroid hormones into the blood and perhaps, then, the knowledge of the thyroid hormone levels would make it possible to establish a closer link between ultimate temperature tolerance limits and the activity of this gland. However, feeding may also plays, an important role in determining the ability of cod to arrive in large shoals in waters where the temperature has fallen to 0°C. These problems are of utmost importance for the fishery scientists because only then we can understand the heavy mortality of cod observed in particularly severe winters, when they are attacked by the cold currents of the Arctic. At that time they seem to succumb before the physiololgical mechanism is able to make any adjustments. From these observations it is possible to explain the changes in the distribution of cod and in their size, for when a penetration of cod occurs—as was observed some years back—into the Arctic waters from the Atlantic, this permits a geographical expansion of the cod northward, affecting the size of fish also by providing an abundant nourishment leading to a faster growth.

But we have so far discussed the effects of temperature in confirmation with salinity on osmoregulation. Possibly it also affects the migratory behaviour directly in all poikilotherms and also of the marine homeothermal animals which have thermoregulatory mechanism. It has been an accepted fact in the case of Cetacea which are homeothermal. We know for example that the blue

whales are found, in the Arctic and Antarctic waters during summer because in polar zones plankton is abundant only during summer. In winter, they leave for the Equator and this movement is interpreted in the following manner. Water has a very high calorific capacity and homeothermous Cetacea can live in very cold water, thanks only to their thick layer of fat. Now, during the period preceding the birth of the young, this fatty layer diminishes considerably, so that we may reasonably suppose that the whales move to warmer waters because their physical thermoregulation does not remain sufficiently effective. From a finalist point of view, it has been remarked that the younger whales having a larger surface in relation to their weight than the adults are more exposed to a heat loss than their parents. It is therefore necessary for the females to reach warmer seas. Otherwise they would drop their young ones.

Objections have been put forward because these same explanation (migrations depending on the thickness of the fatty layer) does not hold good for the other species of Cetacea. Only a comparative study of the physical and chemical thermo-regulatory capacities of different species during the course of their life cycles could possibly explain these discrepancies.

However, recent researches show that certain highly migratory fishes (Tuna, sharks) give evidence of a veritable thermoregulation. Already in 1835, Davy had pointed out that the temperature of the bonito, *Thynnus pelamis* could rise 10°C higher than that of the water in which it lived. Measurements carried out by Carey and Teal (1966, 1969) using much more precise techniques have revealed that thermoregulatory capacities differ greatly in different species of tuna. The largest difference has been found in the red tuna, *Thynnus thynnus,* which is capable of maintaining its body temperature within a margin of 5°C (between 25° and 30°) in waters with a temperature range of 10°—30°C. Thus this tuna with a mean body temperature of 25° may be observed in water of 10°C. This difference of 15° is quite considerable for a poikilotherm, but it is even more marked because the tuna with a temperature of 28.8° has been found in waters of 7.3°C. This represents a considerable thermogenetic power. This is one of the physiological characteristics explaining the extensive migration of this species. Indeed this tuna can go, in less than 50 days, from the waters of Bahamas which is about 30°C to those off the coasts of Norway which is approximately 6°C. Undoubtably there are advantages for a fish having a high temperature, especially when it is a migratory fish, for the conduction of the nerve-impulses and the speed of muscular contraction, are then, also greater. But most fish are unable to have a body temperature appreciably higher than that of the environment, for the blood passes through the gills before reaching

the tissues. Since the equilibrium between gas, water and blood occurs at the level of the gill, the temperature equilibrium also develops at about the same level, because thermic diffusion is faster than the molecular diffusion. After leaving the gills, the blood attains almost the same temperature as the water and the metabolic heat, heats the blood by the same it reaches the tissues. The intensity of metabolism gets itself limited by the rate of oxygen transported by the blood, and calculations made show that the fish is not able to maintain its body temperature greater than 1 °C from that of the environment, by the metabolic processes alone. Since tuna can have a body temperature several degrees higher than that of the sea, it is likely that it must possess some mechanism to preserve its metabolic heat. This mechanism probably operates in part, at least by the inner heat exchange, called cross-current. This is developed through a system of parallel arteries and veins and this system which acts as a barrier and prevents the loss of heat and allows the temperature to reach a much higher level than that of the environment. May I point out that the principle of this cross-current system is very complex and involves too many closely linked small veins and arteries through which blood circulates in the opposite directions and hence the term cross-current. The arterial blood comes from the gills, but it receives the heat of the venous blood which returns from the tissues and is warm. Hence the arterial blood, as it moves through the blood-vessels gets a progressively increasing venous temperature-gradient. The heat produced at the tissue level, particularly in the muscles, gets carried by the venous blood and is not lost simply at the level of the gills into in the surrounding water. This is the explanation for the accumulation of heat in the body which is traversed by a well-developed cross-current system, particularly in the red muscles.

Specific variations in the ability to preserve heat, do seem to occur in a species during its life cycle and this should account for the differences that exist between the migrations of different species and also within the same species. For example, in the red tuna, this differences in temperature between water and the muscle become less pronounced in graved fishes as than the immature adults which have largely somatic growth. This decline in the thermoregulatory mechanism in maturing fishes could be what directs the tuna to seek for relatively warm waters. The ability to do so indeed does not depend only on the anatomical peculiarity, but on the nature and magnitude of the biochemical processes that take place at the level of muscles and certain organs which possess their own characteristic blood-flow (volume, speed, etc.). It is easy to imagine that these characteristics can change in the course of the life cycle and particularly at the time of breeding. Recent advances in the devices for measuring body temperature which can be attached to fish continues to trans-

mit the internal body temperature and the external temperature of water and the possibility, which now exists, to keep tuna in captivity for long periods in large salt water tanks should permit us to verify this hypothesis.

It is with the hope that the young Indian scientists, while following the example of Dr. Panikkar, would add their important contributions to the study of the relationship between the changes in certain physiological properties and the migrations of marine animals, that I take the liberty of formulating this hypothesis.

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OCEANIC PARTICULATE MATTER: SIZE DISTRIBUTION IN WATER AND IN SEDIMENTS

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ABSTRACT

Estimates are made of the rate of sedimentation of particulate matter on the ocean floor using the experimentally measured size distribution of particles in the Pacific Ocean. The calculations are based on a simple Stokes' settling model which does not take tnto account any creation or loss of particles in the sea water column. The expected deposition rate is at least an order of magnitude higher than that observed in open occean areas. The expected particle size distribution in sediments is also markedly different from that observed. The implications of these discrepancies are pointed out breifly in terms of the dissolution and recycling of the particulate matter.

INTRODUCTION

It is well known that the vertical and areal distribution of several trace elements in sea water is governed mainly by the interaction of oceanic suspended matter with sea water. Hence in the study of the marine geochemistry of trace elements it is important to have a knowledge of the chemical composition, concentration and size distribution of particulate matter in sea water (Lal, 1971). Until recently the data available on the size distribution of oceanic particulates had been very meagre and hence no attempts were made to understand quantitatively the relation between the size distribution of particles in the various marine reservoirs viz. sea water, sediments and particulate input sources (eolian dust and river suspended matter). Such a comparative study is essential for understanding contemporary processes of marine sedimentation and the regulatory effect of oceanic suspended matter on the marine geochemistry of several trace elements.

In this paper we discuss the available data on the size distribution of particles the Pacific Ocean waters at depths upto 1000 m. We then make an attempt to deduce theoretically their absolute rate of sedimentation as well as

the size distribution of particles in sediments based on a simple particle settling model. This is compared with the experimental results reported here for the particle size distribution in open ocean Pacific sediments. The results are found to be very discordant. The implications of the discrepancy are discussed in terms of various physico-chemical and biogenic processes operative in marine environment.

It is a pleasure to acknowledge Mr. S. K. Bhattacharya for stimulating discussions and Miss Nanda Prabhu for help in sediment analyses. Four of the cores used in the presest study were collected by Dr. B. L. K. Somayajulu during the NOVA expedition of Scripps Institution of Oceanography, during 1967.

Particle Size Distribution in Sea Water and in Sediments

Nomenclature:

In the following discussions, we will adopt the following symbols :

D Diameter of particles in cms.

Density of particulate matter (g/cc)

F_S Flux of particles settling on the ocean floor (number/cm^2 time)

V Stokes' settling velocity of particles (cms/time)

A Constant in Stokes' velocity relation: $V = AR^2$

S Sedimentation rate (g/cm^2 time)

Subscripts s and w will be used to for sediments and sea water respectively.

Experimental data on particle size distribution in sediments and in sea water:

Several techniques (Krumbein and Pettijohn, 1938) have been discussed for the size measurement of distribution of particles in sediments. Also a great deal of work has been reported (Sverdrup *et al.*, 1942; Goldberg and Arrhenius, 1958; Delany *et al.*, 1967; Goldberg and Griffin, 1970; Goldberg *et al.*, 1963) for the size distribution of deep sea sediments. However, many of the published results cannot be used directly for the present analyses since the size frequency measurements were made for larger size intervals. We have therefore measured, using the pipette method the size distribution of particles in five radiometrically dated red clay sediments from Pacific Ocean. The Pacific Ocean sediments were chosen for the present studies since the data on particle size distribution in sea water are abundant for the Pacific Ocean only.

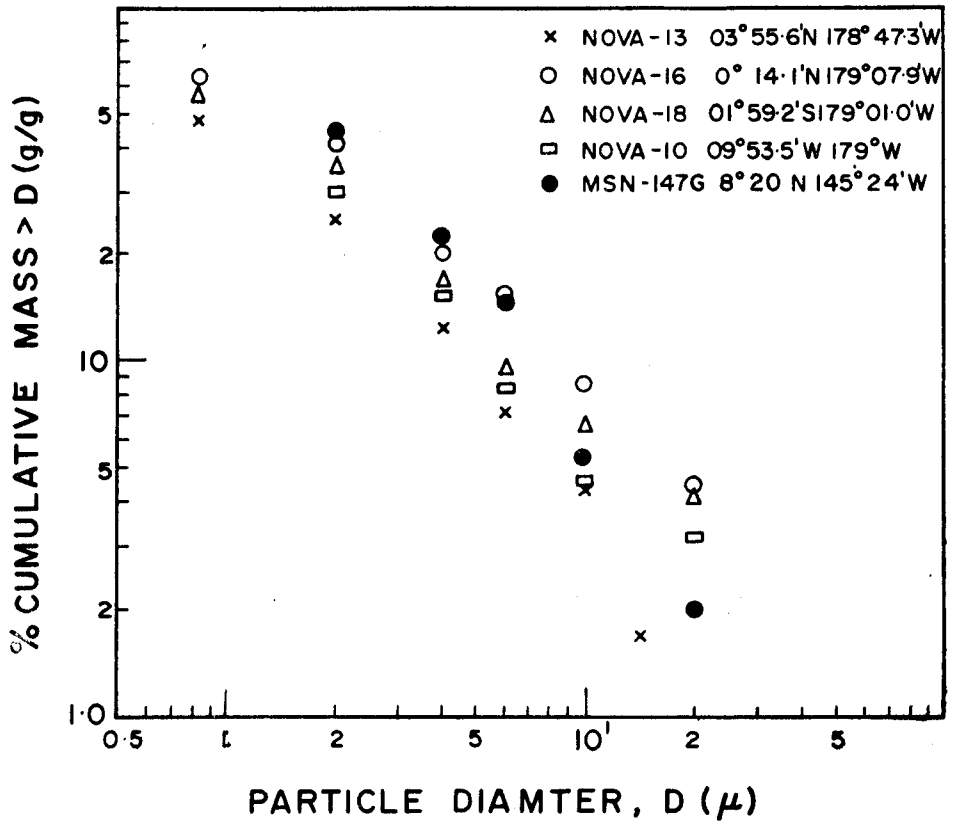


Fig. 1. Measured cumulative mass-size distribution of particles in radiometrically dated red clay sediments collected from Pacific Ocean. For sample locations and other relevant details see Table 1. The size distribution has been measured using the " pipette method ".

The results of our measurements are given in Table 1 and in Fig. 1 In few of these samples the size distribution measurements were made at different depths in the core. The distribution was found to be similar within experimental errors implying that the size distribution of particles in the source has remained the same during the past several thousands of years. Fig. 2 gives the average size distribution of five Pacific red clay samples reported by Revelle *et al.* (Sverdrup *et al.*, 1942).

It is evident from Figs. 1 and 2 that the size distribution of particles in deep sea sediments in the range 2-15 microns can be approximately expressed (Bader, 1970) as a power law spectrum of the type:

$$M_S\ (>D) = KD^{-\delta} \qquad \text{.....(1)}$$

where M_S in the fractional mass (g/g sediment) of sediment due to particles of

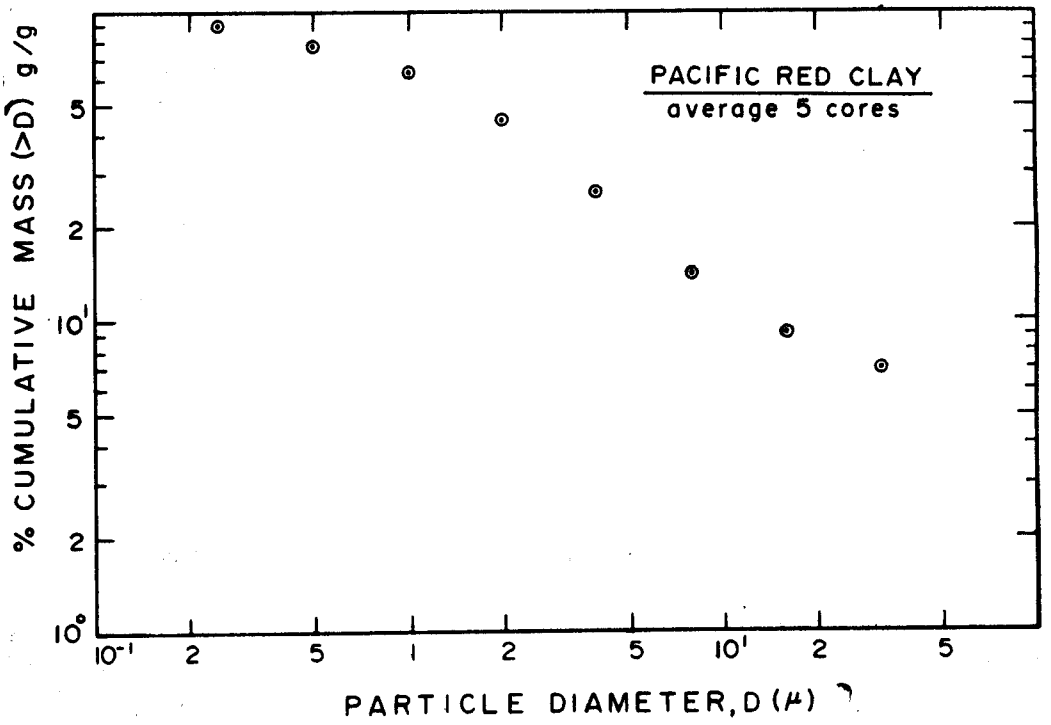


Fig. 2. Average cumulative mass-size distribution of particles in five red clay samples from the Pacific. For sample locations and data, see Sverdrup *et al* (1942).

size (diameter) greater than D cms. K and ϑ are constants. The average value of K and ϑ for the Pacific sediments measured by us and those by Revelle *et al.* (Sverdrup *et al.*, 1942) are summarised in Table 2. These values are applicable for particles of size 2-15 microns only. The value of ϑ for the five cores measured are similar, 1.0-1.26 a result not unexpected since they are collected from nearby locations, the results of Revelle *et al.* correspond to a smaller value; 0.66 is the average for five cores.

In the case of ocean water, several measurements are available (Carder *et al.*, 1971; Beardsley *et al.*, 1970) which can be considered as representative for open ocean Pacific waters. Fig. 3 shows an illustration the data of Cadrer *et al.* (1971) for the measured size distribution of particles in sea water collected from Eastern Equatorial Pacific. These measurements have been made by the recently developed Coulter counter technique (Sheldon and Parsons, 1967) which

TABLE 1. *Relevant details of the Pacific sediment cores studied and the measured mass-size distribution*

	Location	Water depth (meters)	In-situ Density* (g/cc)	Cumulative mass (%)					
				$>0.8\mu$	$>2\mu$	$>4\mu$	$>6\mu$	$>10\mu$	$>20\mu$
NOVA-III-10	09°53.5'N 179°00'W	6105	0.49	—	30.5	15.7	8.5	4.6	3.2
MSN-147G	8°20'N 145°24'W	5110	0.38	—	44.3	22.3	15.0	5.4	2.0
NOVA-III-13	03°55.6'N 178°47.3W	5331	0.38	48.4	25.1	12.5	7.3	4.3	—
NOVA-III-16	0°14.1'N 179°7.9N	5430	0.37	64.2	41.0	20.6	15.2	8.6	4.5
NOVA-III-18	1°59.2'S 179°91'W	5585	0.36	56.1	35.2	16.5	9.7	6.5	4.3

*Data from Amin (1970)

is known to be more precise (Sheldon and Sutcliffe, 1969) compared to the optical methods (Jerlov, 1953, 1968; Burt, 1958) or the filtration technique (Mullin, 1965; Saijo, 1964). Since we would like to restrict our discussions to Pacific Ocean waters the data of Brun-Cottan and Ivanoff (1971) have not been included.

TABLE 2. *Measured values of sedimentation rates and parametric constants and K for Pacific Ocean sediments*

Core	Sedimentation rate a)			$K \times 10^5$
	$cm/10^3y$	$g/cm^2 \cdot 10^3y$		(cm^{δ})
NOVA-III-10	—	—	1.18	1.3
MSN-147G	0.19	0.072	1.26	1.0
NOVA-III-13	0.14	0.053	1.06	3.2
NOVA-III-16	0.15	0.056	0.95	13.0
NOVA-III-18	—	—	1.02	6.0
Average	0.16	0.06	1.1	4.9
Mean of five *b*) Pacific cores	—	—	0.66	0.64

a) Data from Amin (1970)

b) Data from Revelle (1936) (see Sverdrup *et al.*, 1942)

Carder *et al.* (1971) have used Weibull function to fit the observed particle size distribution in sea water. We have reanalysed their data in terms of a power spectrum for particle diameters in the rage 2-10 microns. Analogous to the case of equation (1), we represent particle size distribution as:

$$N_W (> D) = Kw\ D^{-\delta} \qquad \text{.....(2)}$$

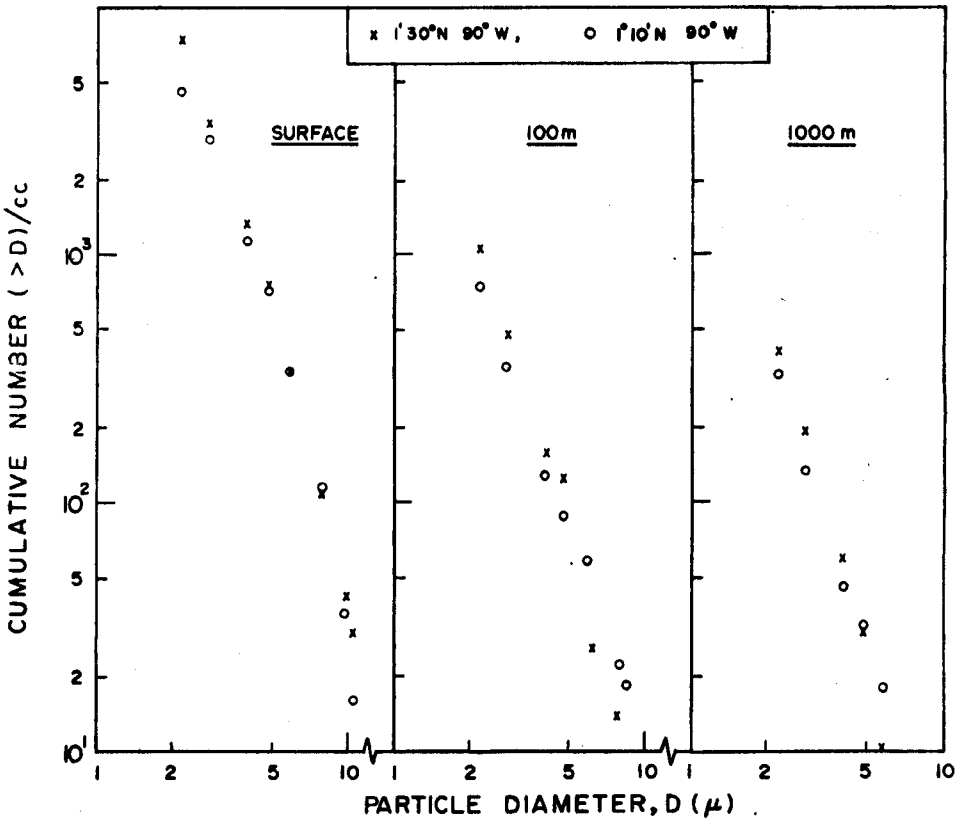


Fig. 3. Size distribution of particles in sea water collected from Eastern Equatorial Pacific. Measurements have been made using Coulter Counter. Data are from Carder *et al.* (1971).

where N_W is the cumulative number of particles of size greater than D cms per cc of water. K_W and δ are constants. The calculated values of these constants for the data of Carder *et al.* (1971) are given in Table 3.

TABLE 3. *Station locations and measured values of K_W and δ for particle size distribution in Pacific waters* a)

Station	Location	Values of K_W and δ					
		Surface		100 m		1000 m	
		$K_W x10^8$	δ	$K_W x10^8$	δ	$K_W x10^8$	δ
YPT 41, 52, 53	0°10'S-0°45'N 90°W-91°W	2.5	3.15	10.4	2.7	1.9	2.84
YPT 39, 40	1°10'N-1°30'N 90°W	3.0	3.1	5.3	2.79	0.34	3.02
YPT 34, 36, 37	2°30'N-4°N 87°40'W-89°W	0.21	3.3	10.5	2.72	7.9x10-4	3.5

a) Data are from Carder *et al.* (1971)

The maximum number of particle are found in surface waters (Fig. 3) which can be explained in terms of high organic productivity occurring at or near the surface waters. The values of the various profile samples range between 2.7 and 3.5. However no distinct systematic correlation seems to exist between S values and sampling depth.

Comparison of particle size distributions in sea water and in sediments:

In the following treatment, based on the measured size distribution of particles in water, we will calculate the expected size frequency distribution of particles in sediments and also the absolute rate of sedimentation. We make these calculations on the assumption that a steady state equilibrium exists between particle input to the ocean and subsequent deposition to the deep sea floor. The size distribution of the particles will be assumed to have remained the same in the sea-water, over the last several thousand years. As will be discussed later, these assumptions seem to be generally valid since the measured sedimentation rates (Amin, 1970) and the size distribution of particles at various depths are found to have remained constant over the past hundreds of thousands of years.

Essentially, our model simplifies to gravitational settling of particles from sea-water to sediments, with no physical or chemical changes occurring during settling or in the course of its preservation in the sediments. These considerations are expected to apply to norganic particles, at best. We now seek a relation between the expressions (2) and (1).

The expected number of particles settling on the ocean floor, per unit area and time is

$$dF_s = dN_w \; V \qquad \text{.....(3)}$$

where dF_s and dN_w are the flux (number/cm^2 time) and the number of particles/cc in water respectively having diameter between D and D+dD, and V is the settling velocity (cms/time) of a particle of diameter D.

As an approximation, we assume that the average sedimentation velocity can be estimated fairly well using Stokes' formula. The Stokes' settling velocity of a particle of radius R cms is given by

$$V = AR^2 = \frac{A}{4} D^2 \qquad \text{.....(4)}$$

where A is a constant. Hence

$$dF_s = \frac{AK_w\delta - (\delta-1)}{4} D \qquad \text{.....(5)}$$

The corresponding (differential) mass influx to sediments is given by

$$dM_s = \frac{\pi AK_w\delta - (\delta - 4)\, dD}{24} D \qquad \text{.....(6)}$$

The rate of sedimentation, S ($>$D) of particles of diameter exceeding D is then obtained on integration of (6):

$$S\ (>\ D) = \frac{\pi AK_w}{24\ (\delta - 5)} D^{-(\delta - 5)} \qquad \text{.....(7)}$$

Equation (7) predicts that the cumulative mass size distribution in sediments will also be power law if the steady state distribution in sea water is a power law. The slope in sediments is flatter by 5 powers, compared to the slope in cumulative number size distribution in sea water; c.f. equations 2 and 7. The observed value of slope, γ in sediments is of the order of 1.0 which would correspond to range of $\delta \simeq 6$. The experimental range of values of δ is however only 2.7-3.5.

We may also estimate the absolute value of S for particles of 2-10 microns on the basis of equation (7) the observed number size distribution at 1000 m in sea water (Table 3). The calculated value of S. (2-10 microns) is found to be between (2-3.5) $\times$ 10^{-3} g.cm^{-2}yr^{-1}, based on the following constants

$$\rho = 2.5 \text{ g. cm}^{-3}$$
$$A = 1.2 \times 10^{12} \text{ cm}^{-1}\text{yr}^{-1}$$

The experimentally determined value of S (2-10 microns) is 2×10^{-5} g. cm^{-2} yr^{-1} (see Table 2 and Fig. 1) which is at least one order of magnitude lower than that theoretically estimated based on suspended particles in sea water at 1000 m depth.

Thus it becomes clear that majority ($\sim 99\%$) of the particles in suspension at 1000 m depth do not reach the sediments as such: they dissolve and break-up en-route to sendiments—both the processes must be operative in order to result in the two discrepancies noted above.

Conclusions

In summary, the observed lack of a direct Stokes' transformation correlation between observed particle size distribution in sea water and in sediments indicates that only a small part about 1% of the particles suspended in the sea water at 1000 m depth reach the ocean floor. This can be understood if one postulates that a great majority of these particles are biogenic, for example, calcareous particles (c.f. Somayajulu *et al.* (1969) which dissolve en route to sediments. On dissolution of biogenic particles, reference is made to some recent calculations made by Lal and Lerman (1972) and Pond *et al.* (1971).

Break-up of particles in transit is also indicated from the data. Additionally, one should consider processes such as formation due to bacteorological action of organic particle of 2-6 microns as postulated by Sheldon *et al.* (1967) on the basis of laboratory experiments.

A more detailed study is now under way—both theoretically as well as experimentally to understand the details of processes happening as particles go through the water column.

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SEA-FLOOR INTERFACE STUDIES IN SAN PEDRO BASIN

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Abstract

The submersible *Deepstar* 4000 has proved useful in providing information on the chemical and physical processes taking place at the sea-floor interface, a region where collection of data is difficult. Although it might be expected that vertical chemical gradients would occur adjacent to the sea floor as a result of accumulated detritus, in the San Pedro Basin the chemical properties of the water in the layer adjacent to the bottom were found to exhibit very small gradients. The average concentration of salt, oxygen, phosphate and nitrate increased slightly and that of silicate decreased slightly.

On the basis of five measurements the heat flux from the earth to the water was found to average 1.81μ cal/cm^2 sec. It was concluded that this heat flow is partly responsible for the development of positive temperature gradients measured near the sea floor and that when the water is sufficiently heated, vertical convection cells may be created that extend from the sea floor to a minimum temperature level a few meters above.

Introduction

One of the most valuable uses of a submersible is for deep-water investigations of environmental dynamics, geological features and living organisms. A primary advantage is the ability to see geological structures and living organisms in their natural ecological habitat and photograph them at close range. Quantitative physical and chemical oceanographic measurements are afforded when specialized sampling and measuring instruments are mounted on the craft or used in conjunction with it. The ability to position such instruments exactly, whether on the sea floor or in the sediment or at a distance from the bottom, and observe their proper operation is an additional advantage.

One of the first such uniquely instrumented series of dives by the submersible *Deepstar* 4000 was concerned with the water-sediment interface in the San Pedro Basin located off the Southern California Coast (LaFond, 1971). Data were gathered specifically on the chemistry of the water column, with emphasis on the near-bottom microchemistry, and the heat flux across the water-sediment interface.

Vehicle

Deepstar 4000 is a 9-ton, 3-man submersible 19 feet long, 7 feet high, 11-½ feet wide over the fairing, and capable of descending to 4000 feet (hence its name). It has been described by Shenton (1972).

A spherical pressure chamber composed of two steel hemispheres with a hatch for entrance and exit serves as the crew's compartment. Other penetrations through the sphere are 2 viewing ports, a camera port, 2 passages for electrical control and sensor wires, and 5 bushing for mechanical linkages used for the manual dropping of weights. Batteries, motors, weights, pumps, hydraulic system, and other auxiliary equipment are located in a free-flooded area outside the pressure sphere and surrounded by metal structural members for protection.

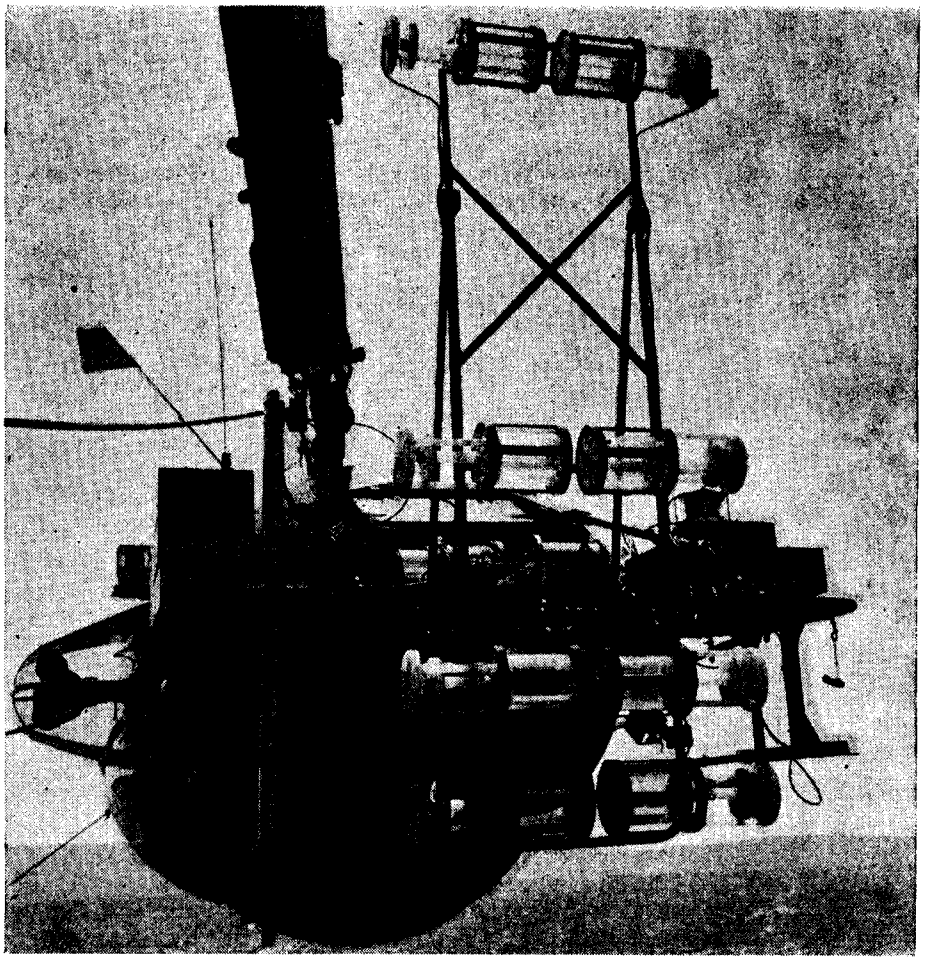


Fig. 1. *Deepstar* suspended from ship's crane, showing brow fitted with sampling bottles, sensing devices, and ballast modules.

Deepstar with its attached brow (Fig. 1) is designed to carry a 570-pound scientific payload of external instrumentation packages and recording

instruments. A mechanical arm-and-claw assembly, fitted externally on the sphere and operated hydraulically, permits the gathering of samples. Modules of syntactic foam provide buoyancy for the brow and keep the instruments within the viewing area without greatly affecting the submersible's stability in the water. The instrumented brow is readily removable, so that *Deepstar* can also be used as a bare boat for geological or biological observations.

The vertical movement of *Deepstar* is controlled by the pilot through a system of expendable weights and floodable cylinders. Fine buoyancy is attained by dropping small lead trim weights and flooding a series of floatation cylinders. Power for the vehicle is provided by lead-acid batteries. Air is purified by a method similar to the one used in Cousteau's diving saucer.

Communication devices include an underwater telephone with a range of 7 km and a two-way radio with a range of 17 km. A precision echo sounder permits examination of the bottom terrain beyond the crew's normal underwater viewing range. The camera port accommodates a 16-mm movie camera; a 70-mm still camera is mounted outside the hull. A tape recorder functions as a log book. Lights for running, observation, and still and movie photography are grouped at the forward end of the vehicle.

Deepstar's surface ship, *Burchitide,* functions as a "mother" ship; its clear deck space, low freeboard, and crane for vehicle transport between deck and water afford ample handling and storage facilities.

San Pedro Basin

Basins are well suited to the study of sea floor interface conditions because of the decreased water circulation below the sill depth and the somewhat stagnant conditions that thus prevail. During spring tides, however, it is possible that tidal oscillations cause some spill over the sill.

The area chosen for the dives upon which this report is based was the San Pedro Basin, located between the Southern California coast and the offshore Channel Islands in the vicinity of Long Beach (Fig. 2). The bottom is fairly flat, although low undulations were observed on one dive. The maximum depth is 913 m. and the sill is 175 m above the bottom (Emery, 1960). The three dives (nos. 446, 448, 450) upon which most of this report is based were made in August 1968. Two previous dives (nos. 186, 187) were made in December 1966.

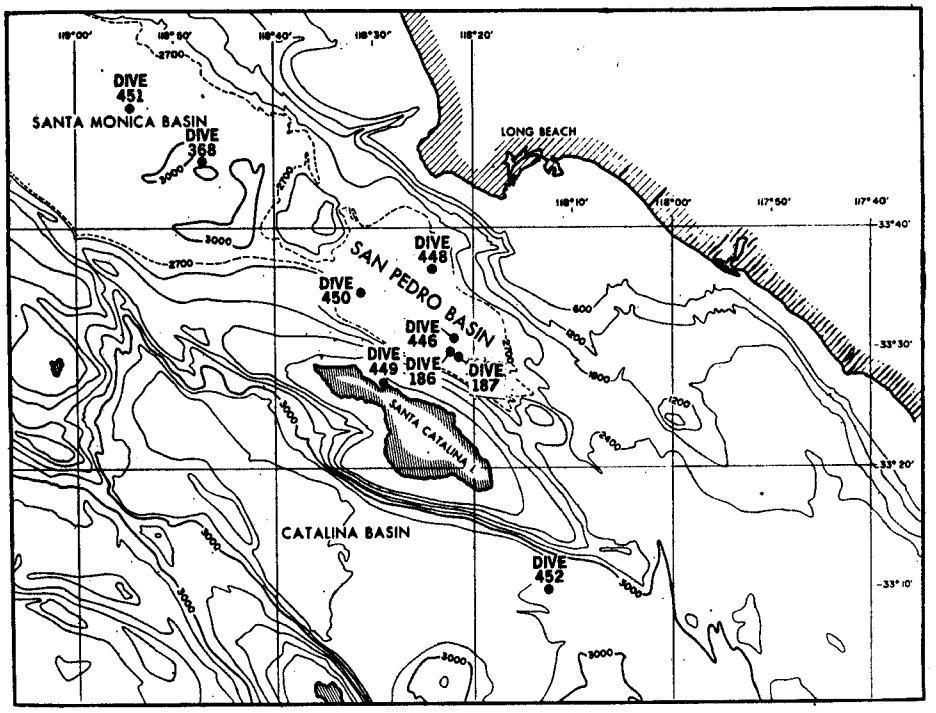


Fig. 2. Location of *Deepstar* dives in the vicinity of San Pedro Basin.

NEAR-BOTTOM CHEMISTRY

It was expected that in a basin where the horizontal water circulation was restricted by a sill, the chemistry of the water would be affected by the sea-floor sediments and that there would be an increased tendency for detritus to accumulate and dissolve at the bottom. *Deepstar,* provided the opportunity to make measurements and collect undisturbed water samples close to the sea floor and at precisely known distances from it. Analyses provided vertical distributions of the various nutrient constituents as well as of salinity and oxygen.

Equipment

The *Deepstar* equipment for this series of physical and chemical studies included water sampling bottles, thermal probes for measuring water and bottom temperatures, and motion picture and still cameras.

A major innovation was the use of a new kind of water sampling bottle called the Barker Bottle (Fig. 3; LaFond, 1967; Good, 1968). It consists of a plastic tube fittted with a piston-like plunger and 0-ring seals. In the cocked position the bottle is open, ready for actuation by a rubber spring released by a fine brass wire. When a switch within the craft is closed, an electrical current

melts the wire and allows the bottle to close. Each bottle holds two liters of securely sealed sea water, collected at a known position with reference to the bottom.



Fig. 3. Barker Bottles used to sample near-bottom water for chemical content; bottles are shown mounted on vertical frame attached to *Deepstar*.

Procedures

Four rows of Barker Bottles were mounted horizontally in a frame attached to the side of the submersible (Figs. 1, 3). When the craft was resting on the sea floor, the rows were 0.15, 0.45, 1.05, and 2.25m from the bottom. Any combination of bottlles could be tripped and closed simultaneously.

The extend upward the vertical range of data collected by *Deepstar* in San Pedro Basin, Nansen bottle casts were made from a surface vessel. In order to approach the level of *Deepstar* sampling, an acoustic pinger was utilized on the Nansen cast cable in such a way that the first sampling bottle could be positioned at a height about 8 m above the sea floor.

Chemical Analysis

Data on the chemical structure of the water column in the region off Southern California have been previously reported by Emery (1960) and Holm-

Hansen *et al.* (1966). The current Nansen casts stressed deeper sampling and corresponded more closely in space and time with the *Deepstar* data. Five aliquots of water from each sample were placed in individual bottles. Oxygen was analyzed on shipboard; the nutrients phosphate, nitrate, silicate (after freezing), and salinity were subsequently analyzed ashore, following the procedures

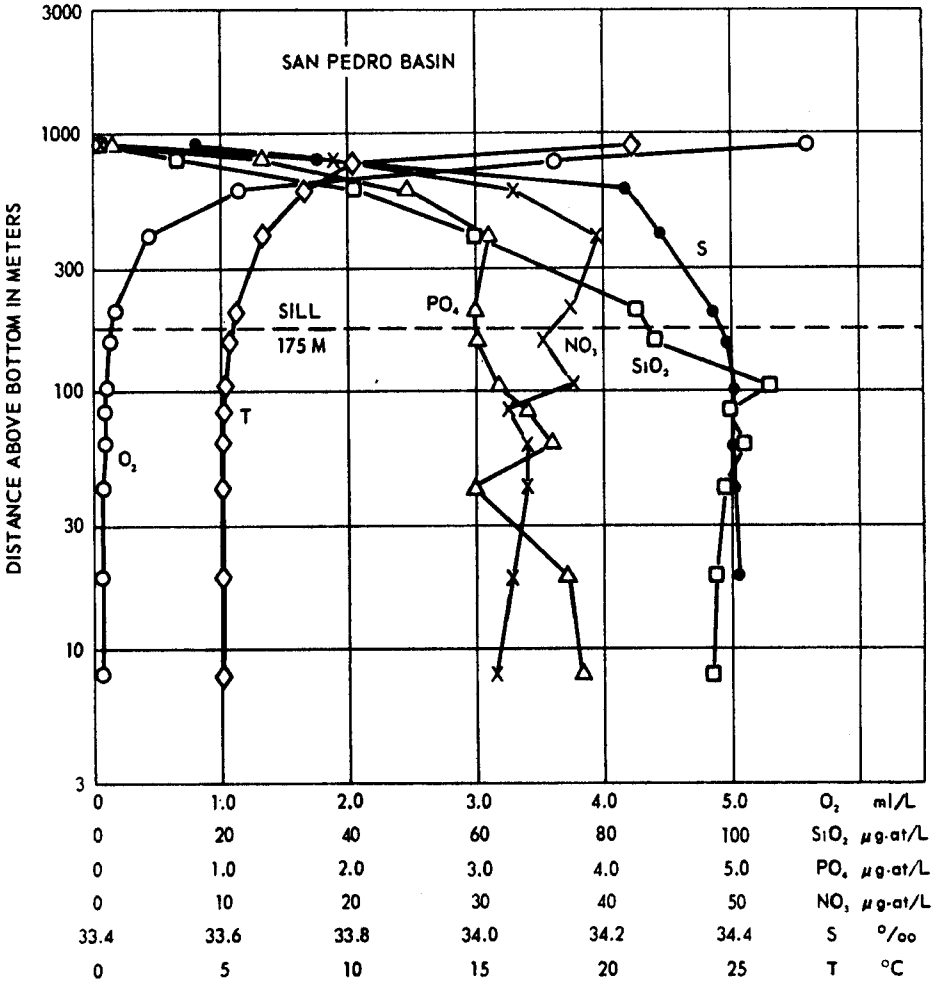


Fig. 4. Chemical structure of the column in San Pedro Basin.

described by Strickland and Parsons (1968). Data from both the Nansen casts and *Deepstar* dives are presented in graphic form (Figs. 4, 5). Values for each of the three dives in the basin (nos. 446, 448, 450) were linearly interpolated and averages were made for the same height (distance from the bottom) up to the highest common depth Z. Above this height the curves were extrapolated by differences.

Salinity : The entire water column was sampled from a surface ship, with the Nansen bottles so placed that the vertical spacing became closer with increasing depth. The chemical results, shown in Fig. 4, reveal an increase in salinity from 33.5‰ near the surface to 34.37‰ at the sill depth (175 m from the bottom); below this depth the change is only 0.04‰.

The details of the salinity structure near the sea floor is shown in Fig. 5a on a greatly expanded scale. The values for dives 446, 448, and 450 are shown as fine lines. The average of the three dives is a heavier line; it shows a slight

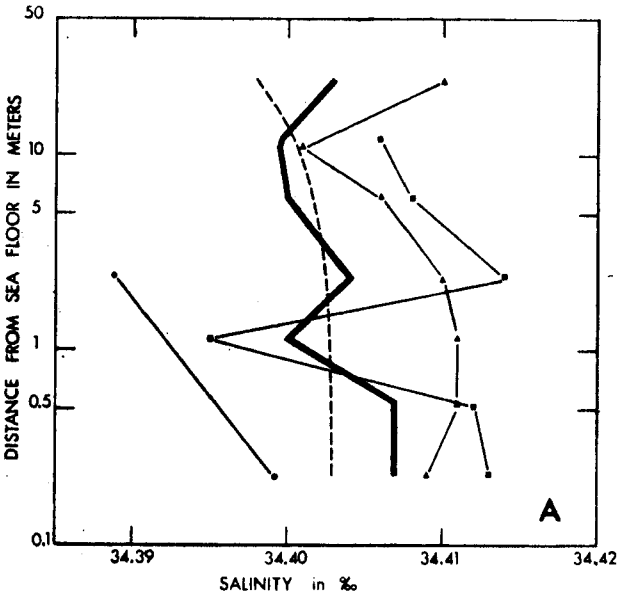


Fig. 5. a. Chemical structure of near-bottom water from dives 446 (•) 448 (■), and 450 (▲)—salinity.

increase toward the bottom. The least-squares fit of the three curves is represented by a dashed curve and can be expressed as

$$S=34.402-0.0002\ Z,$$

where Z is meters from the bottom.

Oxygen: The concentration of oxygen in San Pedro Basin (Fig. 4) shows a relatively rapid decrease from the surface to near the sill depth. Below the sill the values are extremely low, with changes approaching the limit of accuracy of the Winkler method used to determine the amount of dissolved oxygen in sea water. The detailed distribution near the bottom is shown in Fig. 5. b; the curve for the average of the three dives is nearly constant, varying

from only 0.26 to 0.32 ml/l in the lower 20 m. Another investigator reports 0.1 to 0.3 ml/l (Minard, 1968). The least squares fit can be expressed as

$$0_2=0.30-0.0024\ Z.$$

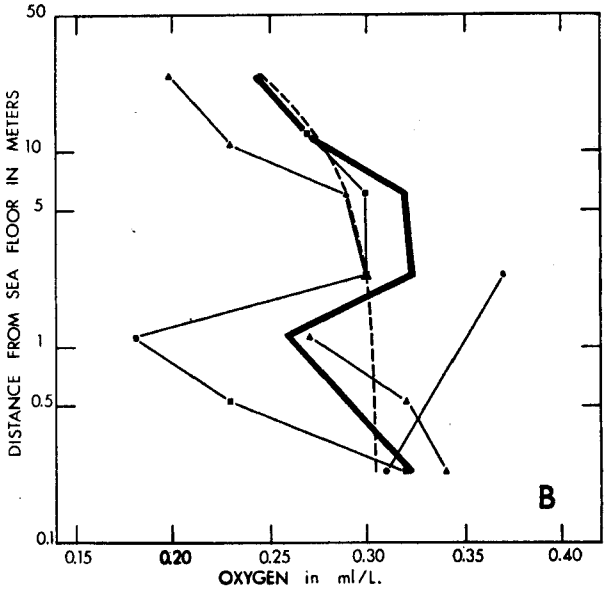


Fig. 5. b. Chemical structure of near-bottom water from dives 446 (•), 448 (▬) and 450 (▲)—oxygen.

Under these conditions any organic matter that sinks to the bottom soon uses up the available oxygen in decomposition and an anaerobic state then develops. This is evidenced by the black border around dead fish and other material on the sea floor (Figs. 6a, b, c). A white fungus (Fig. 6 d) observed in certain parts of the basin may also be related to decomposing organic matter. One white mound (Fig. 6e), collected with the mechanical claw and brought to the surface, turned out to be decomposing bananas.

Phosphate : The plant nutrients phosphate, nitrate, and silicate are used by phytoplankton in photosynthesis; thus the amount of phosphate below the euphotic zone normally increases with depth. The expected increase was generally observed and at 10 m above the bottom the phosphate value was 3.75 μg-at/1 (Fig. 4).

The distribution of near-bottom phosphate values and their average are shown in Fig. 5c. There is still a slight trend toward increasing values with depth but no large change. The least squares fit for the three sets of data is

$$P0_4=3.6-0.0066\ Z.$$

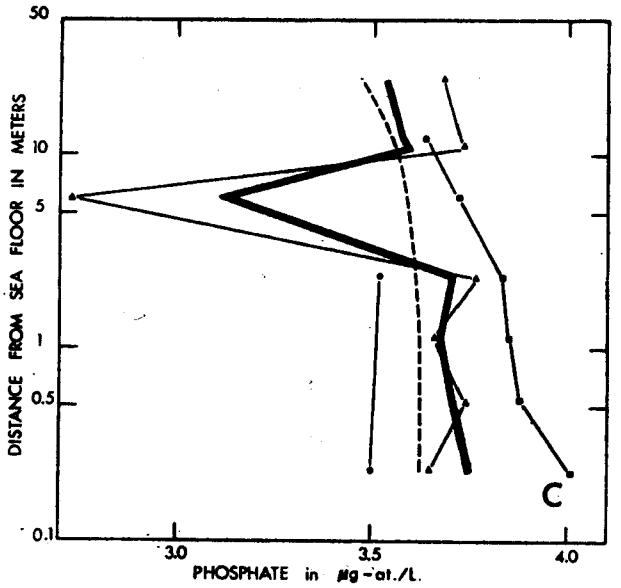


Fig. 5. c. Chemical structure of near-bottom water from dives 446 (•), 448 (▬), and 450 (▲)—phosphate.

Nitrate: The concentration of nitrate, like that of phosphate, is normally low in the surface layer. The data obtained show considerable variation; the maximum is at 400 m, below which values decrease to 25 m above the bottom. The near-bottom nitrate values (Fig. 5d) are irregular. The least squares fit is

$$NO_3 = 38.5 - 0.47\ Z.$$

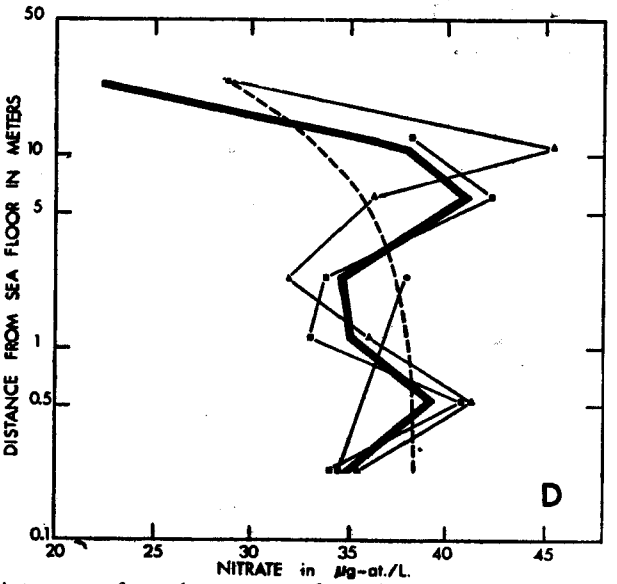


Fig. 5. d. Chemical structure of near-bottom water from dives 446 (•), 448 (▬) and 450 (▲)—nitrate.

Silicate: The last nutrient to be considered, silicate, shows higher values with increasing depth throughout most of the water column down to 100 m above the bottom; below this depth there is a slight decrease to the bottom

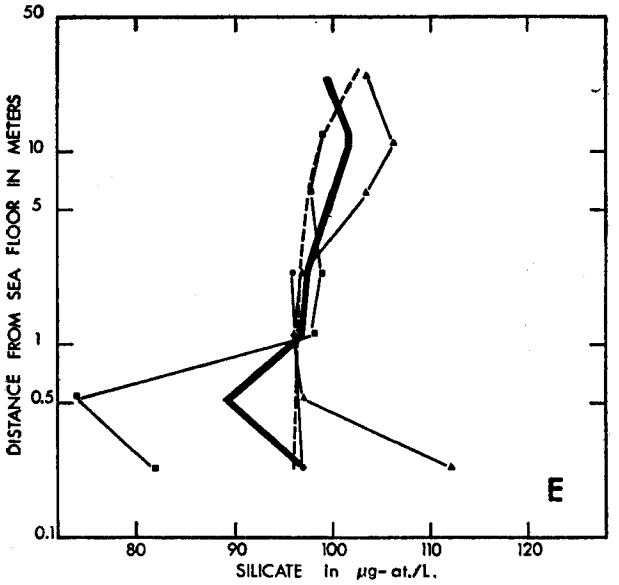


Fig. 5. e. Chemical structure of near-bottom water from drives 446(•), 448 (■) and 450 (▲)—silicate.

(Fig. 4). The decrease is confirmed by the *Deepstar* data (Fig. 5e). The least squares fit of the data is

$$SiO_2 = 96.1 + 0.27\ Z.$$



Fig. 6. a. Sea floor features. Dead squid outlined in black (approximately 40 cm long)

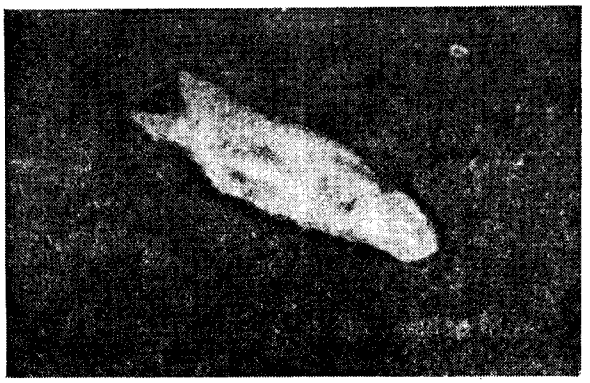


Fig. 6. b. Sea floor features

Dead fish (approximately 30 cm long)

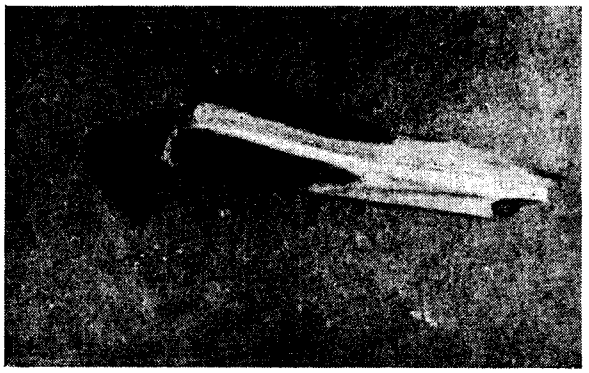


Fig. 6. c. Sea floor features

Newspaper showing black areas from contact with bottom.

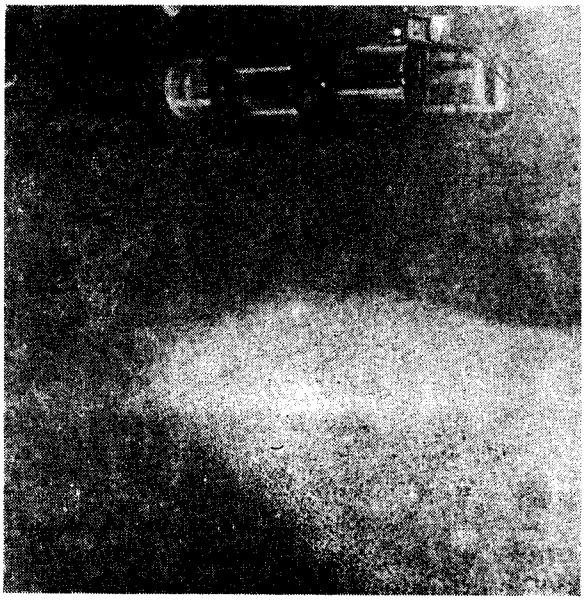


Fig. 6. d. Sea floor features

White patch believed to be a fungus (approximately 2 m in diameter)

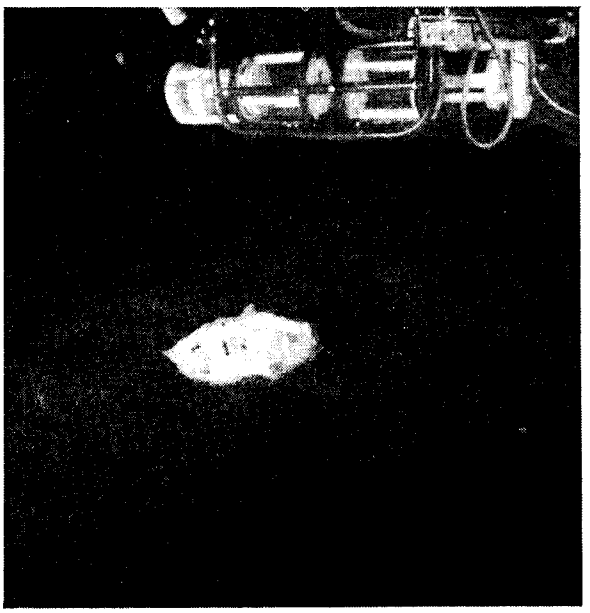


Fig. 6. e. Sea floor features
White coating on a stock of bananas (approximately 50 cm in diameter)

Chemical summary

The chemical structure of the water near the sea floor in San Pedro Basin showed no strong gradients or stratification; the variability observed in some cases was within the limit of accuracy of the analysis (0.003‰ for salinity, 0.03 ml/l for oxygen, 0.03 μg at/l for phosphate, $\pm$ 4% for nitrate, $\pm$ 2 1/2% for silicate). The water from sill depth to bottom was nearly uniform, and only slight trends could be ascertained from averages derived from all the chemical data. The lack of stratification may be attributed to vertical convective circulation and diffusion, which will be discussed later.

Water-sediment Temperatures

Besides the data on chemistry, data were obtained on temperature changes in the lower water column, across the sediment-water interface, and within the upper sediment layer.

Equipment

Temperatures in both water and sediment were acquired with thermistor beads mounted on the end of a plastic and aluminum shaft (Fig. 7; Good, 1968). Two probes were employed, one mounted horizontally on each side of the brow framework. Either could be released by firing an explosive bolt, which action



Fig. 7. Probe used to measure temperature in water and sediment; shown hinged on the submersible's brow.

permitted the probe to swing from a horizontal to vertical position. With two probes available the acquisition of a vertical temperature series in the water and the sediment was virtually assured. On dives 448 and 450 a single, hydraulically actuated temperature probe was used. This afforded remotely controlled penetration to a depth of over one meter.

Procedures

During the early dive series the temperature structure of the sediment was determined as follows. With the negatively buoyed sub-mersible resting on the sea floor, the thermistor probe was released, placing the tip containing the sensor very close to the bottom. *Deepstar's* mercury ballast was then pumped forward, causing the craft to tilt and force the probe into the sediment (Fig. 8). The progressive depth of insertion was increased in increments of 2 to 15 cm. The probe was held at each level until the recorded temperature remained constant (to within 0.0001°C relative), indicating equilibrium. The probe was thus inserted until its entire length (over one meter) was buried or until hard sediment was reached. During the later dives (Nos. 448 and 450), when the hydraulic probe was employed, it was not necessary to tilt the craft between readings, for the probe was forced out of the housing and into the sedi-

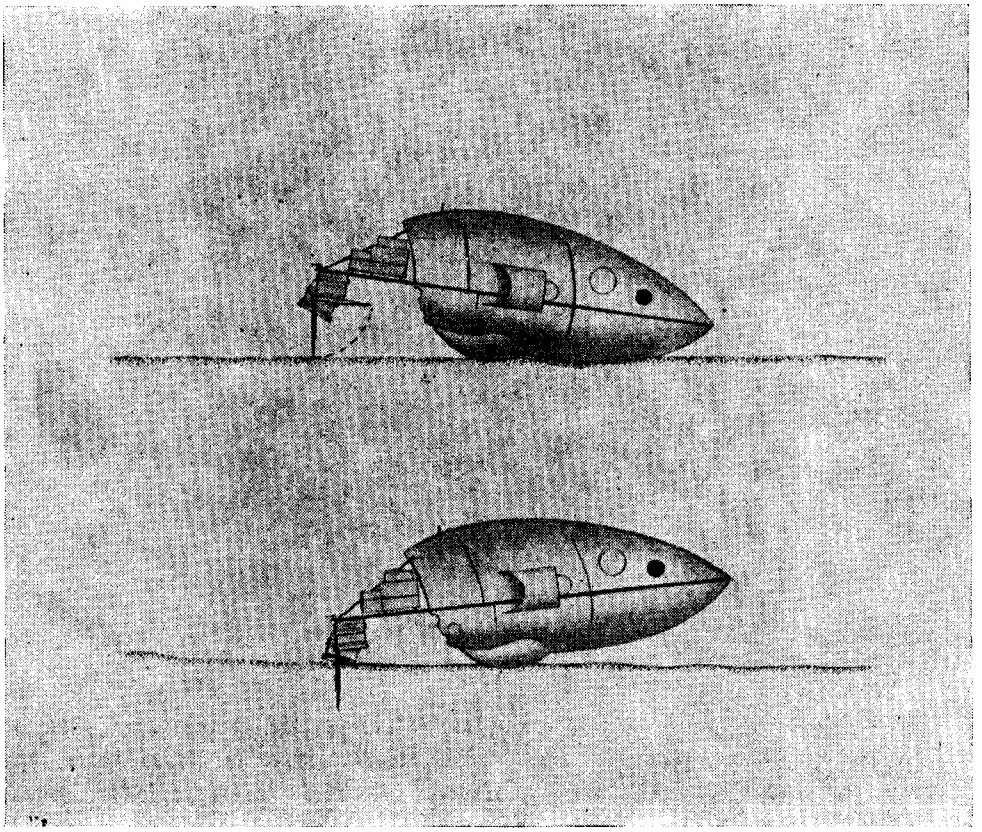


Fig. 8. Procedure for inserting temperature probe into sea floor.

ment by means of hydraulic pressure controlled from within the submersible. With either method it was sometimes possible to make two or more temperature profiles in the sediment on one dive.

The temperature of the lower layers of the water column was determined with the same probe used to measure the sediment or an adjacent probe. For these readings the craft cruised forward and up and down between the sea floor and a height of as much as 20 m above it.

Sediment temperature structure

Temperature in the soft sediment of San Pedro Basin was found to increase nearly linearly with depth (dives 187, 448, 450). Five examples of observed sediment temperatures are shown in Fig. 9. The least-squares fit of the positive temperature gradients, which range from 0.088 to 0.112°C/m, is given in Table 1.

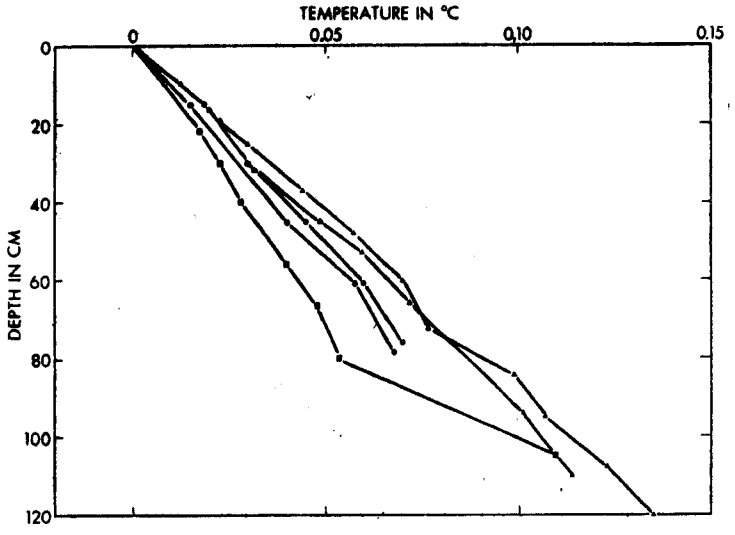


Fig. 9. Temperature structure in the sea-floor sediment from dives 187 (•), 448 (▲), and 450 (■)

Water temperature structure

With ballast properly adjusted and sufficient battery strength available, several traverses through the lower 20 m could be made on a single dive. It was found that the temperature of the water below the sill depth was nearly uniform. However, when the water temperature was measured to a relative accuracy of $\pm$ 0.0001°C, it was found that the temperature was a little higher near the sea floor, decreasing upward a few thousandths of a degree to a minimum of a few meters above (LaFond, 1969). On successive runs about 100 meters apart, the level of minimum temperature occurred at different heights above the bottom. The gradients approaching the minimum temperature level became very weak, and thus the exact depth of the minimum temperature should not be precisely determined. An example of the temperature structure near the bottom, made from data acquired on vertical excursions on dive 448, is shown in Fig. 10.

The depth of minimum temperature and the average gradient between the minimum temperature level and the bottom were determined for 16 near-bottom traverses and are listed in Table 2.

Heat flux

Some of the observed increase in temperature with depth can be attributed to the adiabatic effect, which is 0.87 x 10-4°C/m at this depth (Sverdrup, 1942). Most of the measured values, however, are above the adiabatic tem-

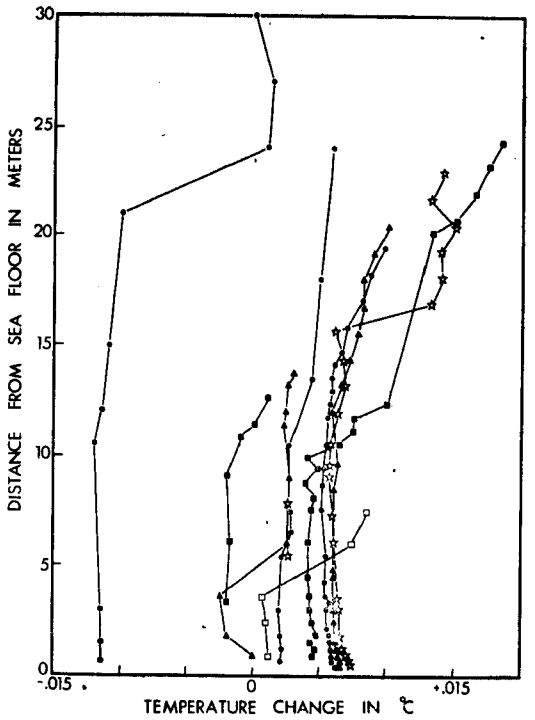


Fig. 10. Temperature structure in the water column adjacent to the sea floor from dive 448.

perature gradient, especially when the minimum temperature falls close to the bottom. The difference may possibly be due to the advection of warmer, more saline bottom water. It is more likely, however, that the near-bottom gradient indicates a state of equilibrium between the upward terrestrial heat flow and a boundary layer of low eddy viscosity (turbulent mixing).

If the earth's crust is warmer at one level than another, heat will flow from the region of higher to that of lower temperature. The heat flux is proportional to the temperature gradient in the sediment and can be determined as follows:

$$q_z = -K \frac{\partial \theta}{\partial z}, \qquad (1)$$

where

q_z = total heat flux (cal/cm² sec),
K = thermal conductivity (cal/cm sec°C),
θ = temperature,
z = vertical axis, positive upward.

Using this expression and the *Deepstar* temperature measurements it was possible to establish the heat flux from the sediment to the water (LaFond, 1968). The thermal conductivity of the sediment, which was not known, was determined from its porosity. Samples obtained from corings made close to the dive sites revealed the porosity to be 69.9 percent at 3-8 cm, 51.4 percent at 28-33 cm, and 59.6 percent at 89-94 cm. From a graph of the vertical distribution the mean vertical porosity was found to be 55.8 percent, corresponding to a thermal conductivity of 18.5 x 10^{-4} cal/cm sec °C (Bullard, 1963). The heat flux was found to range from 1.63 to 2.07 and average 1.81 with a standard deviation of 0.165 μcal/cm^2 sec (Table 1). This is slightly higher than the the world average of 1.2 μcal/cm^2 sec (Revelle and Maxwell, 1952).

TABLE 1. *Sediment heat flux, q_z*

Dive No.	Run No.	$\frac{\partial \theta}{\partial z}$ (°C/m)	q_z (μcal/cm^2 sec)
187	1	0.092	1.70
187	2	0.088	1.63
448	1	0.112	2.07
448	2	0.105	1.94
450	1	0.093	1.72
Average		0.098	1.81

Heat flux measurements in the deep ocean are normally made with temperature sensors and self-contained recorders attached to corers. In the San Pedro Basin, even though the depth is only 913 m, the presence of a sill produces an effect similar to that observed in deep lakes, reducing the horizontal circulation and preventing the water temperature from fluctuating (Lyubimova and Shelyagin, 1966). The slow penetration of the *Deepstar* thermal sensor, a few centimeters at a time, reduced the frictional heat more than is possible with a rapidly inserted corer. These factors, together with the more sensitive electronics that provided relative readings accurate to better than 0.0001°C, add credence to the value of 1.81 μcal/cm^2 sec. This addition of heat from the sea floor over long periods of time undoubtedly contributes to the slightly higher temperature layer at the sea floor.

Diffusion

Other physical properties can be obtained from the *Deepstar* data. For example, diffusing flow $\vec{Q}$ is proportional to the gradient of effective density p',

$$\vec{Q} = -a\nabla p', \qquad (2)$$

where a is called the diffusion constant (Morse and Feshbock, 1953). In the case of heat flow, equation (1), the effective density of heat is proportional to the temperature,

$$p' = C\theta = pc\theta, \qquad (3)$$

where

C = specific thermal capacity,
c = thermal capacity, and
p = density of substance.

If only the vertical component of the heat flow equation is considered, the vertical diffusivity is

$$a_z = q_z/pc\frac{\partial \theta}{\partial z}, \qquad (4)$$

where

$a_z pc$ = K of equation (1)

For water at 913 m with a salinity of 34.40‰ and a temperature of 5.11° C, the thermal capacity is 0.962 and the density is 1.028. The sediment heat flux is 1.81 μcal/cm^2 sec, and $\partial\theta/\partial z$ has values ranging from 0.38 to 12.5 x 10^{-4} °C/m, with an average of 2.31 x 10^{-4} °C/m. These values compare well with measurements made off the Oregon coast, which averaged 4.5 x 10^{-4} °C/m (Bodvarsson et al., 1967). The calculated vertical diffusivity ranges from –4.91 to –0.15 x 10^{-2} cm^{2}sec (Table 2).

TABLE 2. *Near-bottom water temperature*

Dive No.	Run No	Level of Minimum Temperature (meters from bottom)	$\frac{\partial\theta}{\partial z}$ (°C/m x 10^{-4})	Vertical Diffusivity (cm^2/sec x 10^{-2})
187	1	10	1.67	–1.10
	2	3	4.65	–0.39
	3	2	12.50	–0.15
448	1	10	0.77	–2.38
	2	4	6.34	–0.29
	3	7	0.99	–1.85
	4	9	1.05	–1.74
	5	9	0.98	–1.87
	6	9	1.02	–1.79
	7	11	0.61	–3.00
	8	3	1.03	–1.78
450	1	9	2.24	–0.82
	2	5	1.65	–1.11
	3	8	0.38	–4.82
	4	12	0.52	–3.52
	5	12	0.58	–3.16
Average		7.7	2.31	–1.86

Stability

Although the water at the sea floor is warmer, it is also denser because of the slightly higher salinity near the bottom. In a basin of very low eddy viscosity, near bottom stability could be upset periodically by the development of convection cells. Heat entering the bottom water at the rate of 1.81 μ cal/cm^2 sec can create such instability and cause the bottom water to mix with the layers above. It is believed that the observed variance of the boundary layer thermal gradients is related to convection cells induced by heat flow (Fig. 11). These can be of varying height, as shown by the minimum temperature depth in Fig. 10. The greatest instability occurs when the temperature minimum is nearest the bottom.

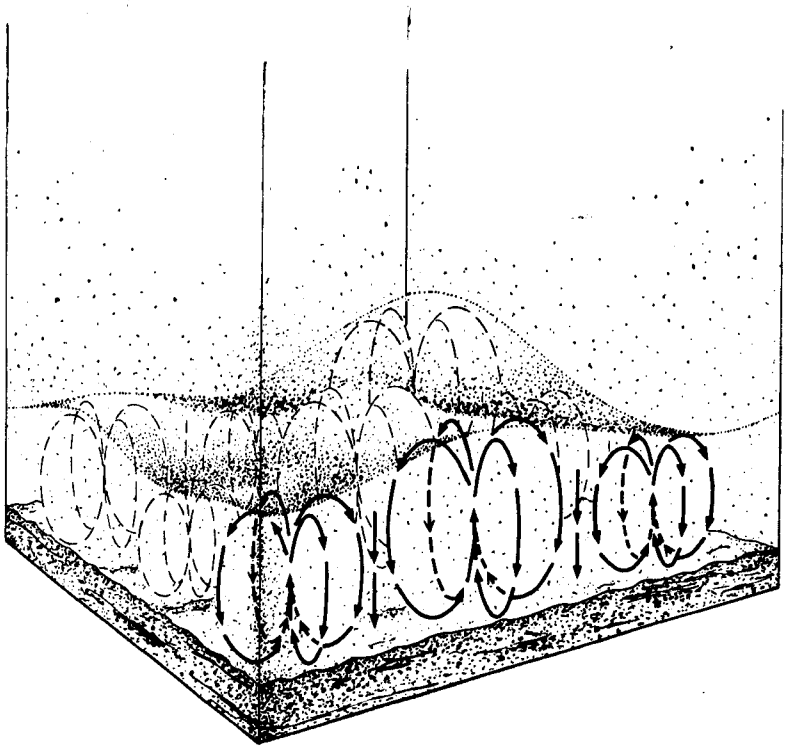


Fig. 11. Schematic diagram of water circulation near sea floor caused by convection cells.

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SOME TRENDS IN MARINE CHEMISTRY

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ABSTRACT

The role of the atmosphere in transferring materials from the continents to the oceans and from the oceans to the continents is one of the most exciting fields in marine chemistry today. New dimensions in this area have evolved from studies of the mobilization of metals, of carbon monoxide and other gases produced in the surface layers of the oceans, of pesticides, and of terrestrial plant volatiles.

Researches in marine chemistry are stimulated in a number of ways. Perhaps the most important thrusts come from the overwhelming curiosity to understand the environment. As a result, chemical models of the oceans have been fashioned continually over the past two centuries on the basis of prevailing concepts from the natural sciences. Much attention is now directed to the problems of chemical speciation. Sea waters can be described as solutions of a whole spectrum of chemical forms including complex ions, ion pairs, uncharged dissolved molecules, simple anions and cations, and gases.

Exploitation of the sea's living and mineral resources often demands knowledges about the composition of ocean waters. For example, in the early decades of this century much of chemical oceanography was dedicated to studies on the fertility of seawater. Definition of areas productive in fish and shellfish were sought using the distributions of nutrient chemicals and of the photosynthesizing microscopic plants which they supported and which formed the base of the food chain.

Today, the ability of man to alter the composition of ocean waters through his manipulations of matter and energy have presented the possibilities of undesirable effects upon living organisms, including man himself, and upon climate as well as of the restricted use or loss of marine resources. Such man-produced substances as DDT and PCB's are building up in the marine environments to levels which can damage ecosystems. The behaviors of such substances in our environment are needed to predict their impacts and to such ends many pre-

sent day investigations are aimed. These pollution directed studies are both increasing our knowledges about processes not involving man and are providing direction for the management of marine resources. In this presentation I will consider one aspect of marine chemistry that is developing as a part of our studies on man's inputs—the role of the atmosphere in transferring materials from the continents to the oceans and vice versa.

Atmospheric transport has gained greater recognition as a mechanism for the global distribution of such man-produced materials as DDT and the radionuclides from nuclear detonations. The role of terrestrial soil bacteria in destroying gaseous materials some of which have origins in the oceans, is gradually being understood. Also, the organic molecules, both natural and man-related materials accumulating as surfactants at the air-water interface, may be most effective in the uptake of non-polar molecules from the air. It is in these areas that most promising researches in marine chemistry may develop.

The Atmospheric Transport of Metals

The recent outbreaks of methyl mercury poisoning in Japan, resulting from the consumption of contaminated marine fish has focused attention on the environmental reactions of mercury. Unlike many other metals, it appears that the primary transport of mercury from the continents to the oceans takes place via the atmosphere rather than in rivers (Weiss *et al.*, 1971). The river and ice-cap runoff together bring in about 3.8 kilotons of mercury annually to the marine environment, while the continental flux to the atmosphere, from the degassing of the earth, is estimated to lie between 25 and 150 kilotons of mercury per year. This amount of mercury, computed from its contents in airs and in rainwaters, falls back to the earth's surface in precipitation with a substantial portion of it into the oceans. The total world production of mercury is about 8.8 kilotons per year, about a third of which escapes to the atmosphere, primarily up the stacks of electrolytic cells used in the production of caustic soda and chlorine. About 1.6 kilotons of mercury per year enter the atmosphere through the burning of fossil fuel. Thus, man's impact upon the global mercury budget is quite small.

The mobilization of mercury most probably results from the volatility of its elemental form and of its compounds. A new facet to its behavior was discovered in pollution studies—the bacterial formation of methyl mercury. The intensity of this production is not known but perhaps soil or water bacteria are making this highly volatile substance in large enough amounts to be responsible for a significant transfer of mercury from the earth's surface to the atmosphere. The analyses of the forms of mercury in rain and in air might produce some most startling results.

There may be other metals transferred to the oceans from the continents through the atmosphere, perhaps some mediated by bacterial reactions. Emission spectrographers through studies with the d. c. arc have noted that certain metals and their oxides, sulfates, carbonates, silicates and phosphates are selectively volatilized—As, Hg, Cd, Sn, Pb, Zn, Tl, Ag and Bi. It is conceivable that substantial amounts of such elements are escaping from the solid earth in volatile forms. Rewarding researches might be found in the speciation of such elements in the atmosphere and their fluxes from the earth's surface.

The Oceans as a Source of Atmospheric Gases

Until a few years ago the oceans were generally regarded as a sink or exchange reservoir for atmospheric gases, especially the man-introduced pollutants some of which occur naturally. This stance has been broken down with the observations that the oceans act as a source for the atmosphere of carbon monoxide and perhaps methane (Swinnerton *et al.,* 1970) and nitrous oxide (Junge and Hahn, 1971). The production of carbon monoxide in surface ocean waters appears to be light oriented—for biologically productive zones of equal intensity there is correlation between carbon monoxide production and light intensity. Whether simultaneous metabolic processes in living organisms are necessary or whether the carbon monoxide production is a result of the photochemical oxidation of organic matter is as yet unresolved. The methane appears to be a metabolite of living marine organisms. The nitrous oxide supersaturation in surface waters has been attributed to nitrate reduction through bacterial activity, similar to its production by soil bacteria. Recent work suggests that ethylene and propylene may be produced by light reactions on dissolved organic matter (Wilson *et al.,* 1970).

What are the fates of these ocean-produced gases? Laboratory experiments suggest that soils, through bacterial activity, are a major sink for CO (Inman et al., 1971). The soils of the United States alone, it is argued, can oxidize 6.5 times the annual estimated production in the U. S. or three times the estimated worldwide production due to man's activities. Photochemical decomposition in the atmosphere reduces the N_2O levels and Junge and Hahn (1971) suggest that the arid regions of the world like the Sahara desert may act as an additional sink. Soils, through microbial or chemical means, may have the ability to remove ethylene, other hydrocarbons, sulfur dioxide and nitrogen dioxide from air (Abeles *et al.,* 1971). Ethylene decomposition of soils requires oxygen and does not occur readily in autoclaved soils. On the other hand, soils more rapidly removed sulfur dioxide and nitrogen dioxide and only slight reductions in activity were noted with autoclaved samples.

This flow of materials from the oceans to the continents and to the atmosphere provides a dramatic new mood for marine chemists. A host of questions can be posed which can initiate future researches. Are there other gases similarly being transported? Are there any involvements with metals, such as the gaseous methyl mercury molecule? Could the atmosphere of past times have been substantially different with respect to the concentrations of these gases where the sources of sinks produced or decomposed the gases with differing intensities.

Natural Organics

The global dispersion of some synthetic organic chemicals has been attributed to an atmospheric transport from the continents to the oceans. The most extensive studies have been carried out with the pesticide DDT and its degradation products, but the behaviour patterns so far formulated for these materials appear to apply to other halogenated hydrocarbons such as the polychlorinated biphenyls (Woodwell *et al.*, 1971). This rather startling result from pollution studies suggests a re-evaluation of some past suggestions about the flow of land-formed organic phases to the oceans, materials that might contribute substantially to the oceanic burden of organic materials.

The widespread occurrences of DDT and its residues prompted considerations of a variety of transport processes. The materials have been found in both northern and southern hemispheric polar glaciers. Gray whales which graze upon benthic organisms in the Chukchi and Bering Seas and birds such as the petrels and shearwaters which feed upon planktonic organisms far from land were found to contain measurable, and often considerable, quantities of DDT family members. To make sense from these findings, a comparison was made of the river versus the atmospheric transport of these compounds. The water solubility is extremely small—one part per trillion, while there is the very low vapor pressure of DDT at 20°C, 10^{-7} mm of mercury. On the bases of analyses of DDT in both US and European rivers, it is estimated that about 100 tons per year are carried to the oceans which is about 0.1 percent of the annual production of a hundred thousand tons.

The DDT residues are removed from the atmosphere both by dry fallout and by rainfall. Concentrations of DDT in rain shows wide variations both with respect to location and time of year. Ranges go from tens to a thousand of parts per trillion. Using an average value of the order of 80 parts per trillion and a total annual precipitation of water over the oceans of 3.0×10^{20} cc, about 2.4×10^{10} grams of DDT residues would be yearly transported

to the oceans, about 25% of the annual production. Thus, it is plausible that DDT residues are entering the oceans at the surface-atmosphere interface. Enrichment in the surface films, which contain fatty acids and fatty alcohols, has been proposed. Such a path could allow ready entry to the food web through the bacteria and phytoplankton that live in the vicinity of these films.

The role of the atmosphere in the global dissemination of DDT recalls the rather provocative arguments made about a decade ago by Went (1960), who proposed that 200 megatons of volatile plant products are released annually into the atmosphere. Such substances may be responsible for some of the blue hazes in the atmosphere over vegetated areas and may be source materials for petroleum formation. Later, after the field measurements of some plant terpenes, alpha and beta pinenes, myrcene and isoprene (Rasmusen and Weni, 1965) he revised his figure upward to 438 megatons per year. The possibility that these plant volatiles may contribute substantially to the oceanic burden of organic matter has curiously escaped consideration by marine organic chemists. This attitude may reflect the smallness of this production compared to the thousandfold higher rate of plant productivity in the oceans, estimated to be about 50,000 megatons per year.

The fates of these terpene materials are not known. Degradation through photochemical oxidation or through microbial activity to other organics or even to CO_2 and water is possible. Went (1960) considers removal from the atmosphere with precipitation as a most feasible pathway. As a result a substantial portion of the original material or residues can enter the mixed layers of the world ocean.

It is tempting to relate these observations to the most unusual properties of organic materials in seawater. Both the dissolved and particulate components have near uniform vertical distributions below depths of 200 or 300 meters (Menzel and Ryther 1970). Above these depths, in the photic zones and the adjacent deeper waters, the particulate organic matter and the dissolved organic matter are directly and inversely proportional to the rate of primary productivity respectively. The homogenous concentrations of both phases in the water column suggest they are both old and highly resistant to decomposition. Perhaps, as Ryther and Menzel suggest, they have been accumulating over the entire history of the oceans. Only a small portion of the organic burden of the oceans has been qualitatively identified. Perhaps ten percent of the total includes the fatty acids, primarily saturated members. Smaller amounts of such materials as amino acids and hydrocarbons have been assayed.

An experimental approach to ascertain the validity of substantial contributions of plant volatiles to the dissolved or particulate load of organics in the deep seawater column involves analyses of the surface slick materials for terpenes or their photochemical degradation products. Using the revised rate figures of Went, 438 megatons/year, and assuming this rains out uniformly over the earth's surface of 5×10^{18} cm^2, 0.2 micrograms/cm^2 /day s expected. These amounts are readily accommodated in the surfactant layers and are measurable by such techniques as gas chromatography.

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PLANKTON, ECOLOGY, AND TERMINOLOGY

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ABSTRACT

The conceptual relationship between some common ecological terms is made more explicit so that they may be used with greater clarity. The unit ecosystem ('*cenosis*') has three essential parts: the '*biocenosis*', the '*geocenosis*' (physical environment), and their interaction. The relative importance of biological and physical components varies from one part of the biosphere ('*biotope*') to another; according to Sanders, this determines the diversity of species in the biocenotic community. These species share the resources of the cenosis, each share being termed a '*niche*'; the monoculture is the extreme where all resources are monopolized by a single species. The geocenosis may be pictured as the common physical environment where the various '*habitats*' of species in the biocenotic community overlap; '*fidelity*' is the extreme where the entire habitat of the species lies within the limits of the geocenosis.

The relationship of other ecological terms is explored within this context.

The term 'ecology was introduced into the scientific literature by Ernst Haeckel just over 100 years ago. "By *'ecology'* ", he wrote, "we mean the entire science which deals with the relationship of the organism with its environment, to which, in a broader sense, all the conditions of existence may oe considered to belong. These are partly of an organic and partly of an inorganic nature; both the former and the latter, as we have shown above, are extremely important with respect to the form of the organism, because they force it to adapt itself to them. The inorganic conditions of existence, to which every organism must adapt itself, first of all include the physical and chemical properties of its habitat, the climate (light, heat, humidity and electricity of the atmosphere), the inorganic foodstuffs, condition of the water, soil, etc. As organic living conditions, we consider all those relationships of the organism with all other organisms with which it comes into contact, most of which organisms have either a harmful or beneficial effect on it. Every animal has both friends and enemies amongst the others; those which favour its existence and those which harm it. The organisms which serve as organic food for others, or

which live as parasites on them, are also included in this category of organic conditions of existence". (Haeckel, 1866, Volume 2, p. 286-7).

Soon afterwards, his countryman Mobius (1877) introduced the concept of the *'biocenosis'*—"a community where the sum of species and individuals, being mutually limited and selected under the average external conditions of life, have, by means of transmission, continued in possession of a certain territory". No doubt Hensen (1887) had the concept of the biocenosis in mind when he coined the term *'plankton'* (predestined to drift), a term which Haeckel (1890) later developed, defined and popularized.

Since those pioneering days, the ecological approach has spread beyond the realms of marine biology—of Haeckel's plankton and Mobius' oysterbank —to include the entirety of nature; and in that time it has followed many paths, e. g., plant ecology, soil science, biogeography, animal ecology, urban ecology, and so on. The parallel evolution of ecology may have had its benefits, but it also had one unfortunate consequence: the terminology which evolved did little credit to the example set by the German school of pioneer ecologists the previous century. It has often been questioned whether ecology is really a scientific discipline, or rather a way of thinking. If terminology were the sole criterion, which luckly it is not,, one might conclude that ecology lacks discipline and its concepts lack clarity; much too frequently, useful information is hidden in terminological confusion, under the apologia of flexibility. The difficulties of wresting insight from the complexities of nature are too great to permit such luxury.

From time to time it has been argued (e.g., Friederichs, 1927, 1958; Sukachev, 1958) that ecology has advanced sufficiently to justify a sounder framework on which to hang the basic concepts common to all living systems. At just such a stage in the development of biology Linnaeus evolved his now universally accepted system of taxonomic nomenclature; today the diversity of living organisms in the biosphere are grouped, like with like, in a hierarchy of *'taxa'* whose basic unit is the *'species'*. So, in the best tradition of science, unordered information has been converted into ordered knowledge.

Today, people have become aware of the magnitude of human pressures upon the limited resources of the *'biosphere'* (Vernadsky, 1945) and the concepts of ecology have been appropriated and interpreted beyond the realm of science itself. Perhaps ecology should now put its ecological house in order so that the professional ecologist may communicate with both his colleagues and his fellow citizens.

There is no dearth of terms in the literature to express one ecological concept or another (e.g., Dansereau, 1957), but the logic of their relationships is either blurred or missing. As a result, perhaps, many terms are used by different authors in different ways. From the choice available, I have selected a basic few which permit one to weave a reasonably coherent conceptual fabric (see Table 1). I have drawn freely on Whittaker (1960, 1967: Whittaker and Woodwell, 1972) for material and inspiration, his gradient concept of ecological structure being the most generally useful that I can find and the most relevant to plankton ecosystems in particular. It may be no coincidence that, although his present field is the analysis of vegetation, he has also made a classic study of copepod communities (Whittaker and Fairbanks 1958).

TABLE 1. *Ecosystem Terminology*

Concept	Term	
	Species	Community
Ecology 12	Autecology 18	Synecology 18
Ecosystem 21	Monocenosis 9	Cenosis 8, 9
Ecosystem Components :		
Biotic	Species	Biocenosis 17
Physical	Habitat 18	Geocenosis 20
Functional	Niche 15, 18	Cenotype
Biotic Gradient :		
Space	Cline 16	Cenocline 23, 24
Time	Series 7	Sere 3, 18
Physical Gradient:		
Space	Habitat-gradient	Complex-gradient 23,24
Time	Period	Period
Biotic Discontinuity :		
Space	Gap 7	Ecotone 3, 18
Time	Quantum evolution 7	Relay 4

The *'ecosystem'* (Tansley, 1935) to ecology is what the *'taxon'* is to systematics. Taxonomic classification groups together those organisms which may be assumed to have closer genetic continuity with one another (in either space or time) than with those of other taxa. Ecosystem classification (*'cenology'*), on the other hand, groups together those biotic and physical entities which may be assumed to have closer functional relationship with one another than with those of other ecosystems. Whereas systematics uses the evidence of morphology to locate *'gaps'* (Ehrlich and Holm, 1963) along taxonomic gradients (*'clines'*—Huxley, 1939), ecology uses the evidence of species to locate discontinuities (*'ecotones'*—Clements and Shelford, 1939) along biocenotic gradients (*'cenoclines'*—Whittaker, 1960; Gauch and Whittaker, 1972). The plankton and the benthos, for example, are separated by an ecotone at the interface between the water and the substratum; the *'neuston'* is an ecotone at the interface between air and water; and adjacent plankton cenoclines are frequently separated by ecotones at oceanic convergences and divergences.

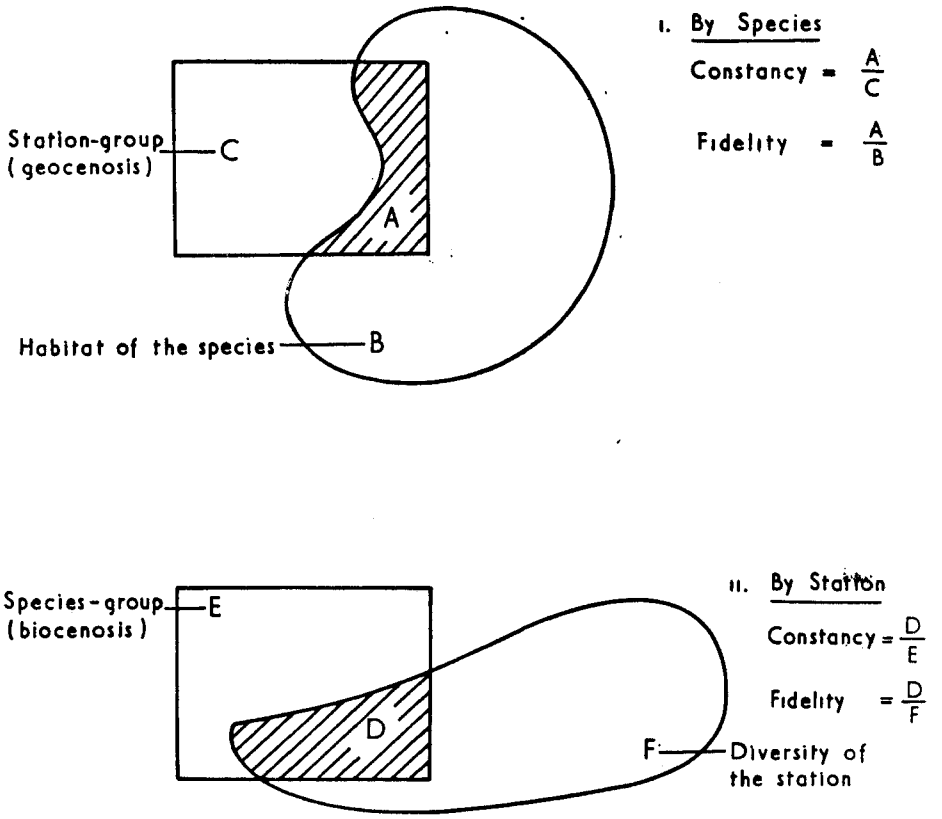


Fig. 1. Geometric representation of constancy and fidelity as applied to (i) Species, (ii) Stations. The area A is the intersection of B and C. The area D is the intersection of E and F.

Species evolve, not in isolation, but in association with other species of their biocenosis and with their physical environment (*'geocenosis'*—Sukachev, 1958). The total context of their evolution is the *'cenosis'* (= 'holocene' = 'cene') described by Friedrichs (1927, 1958), the study of ecosystems at this level being known as *'synecology'* (Odum, 1953). The biocenos s may be considered as "a system of tineracting siche-differentiated species" (Whittaker and Woodwell, 1972), whose separate habitats (Odum, 1953) form overlapping, but not necessarily coincident, sets whose common intersection is the *'geocenosis'* (Fig. 1). In other words, the geocenosis or 'habitat-complex' is the complement of the biocenosis or 'species-complex'. The geocenosis may be pictured as the functional arena of the unit ecosystem, or as the "ecological theatre" for the "evolutionary play" (Hutchinson, 1965).

The genotype of each species in the biocenosis carries information not only about the species itself but also about its unique way of life, or *'niche'* (Odum, 1953; Hutchinson, 1965), in relation to the interactive system of which it is a functional part. This information, stored within the decentralized gesotype-aggregate of the biocenosis is the means by which the biocenosis becomes adapted to its environment as an integral whole, a process which Sukachev (1958) has called 'cenogenesis'; the outcome is a mosaic of biocenoses adapted to the environmental mosaic of the biosphere. This composite, interactive, adaptive factor which determines the path of cenogenesis might be termed the 'cesotype'.

Sukachev (1958) distinguishes between cenogenesis and *'syngenesis'*, the latter being a more rapid type of biocenotic change due more to colonization than to evolution, and commonly known as *'succession'*. As the species of a given cenosis adjust progressively to one another, to the environment which they themselves create, and to their common geocenosis, the cenosis is said to be following a trend towards 'maturity', the biocenotic gradient spanning the period of that trend being termed as *'sere'* (Clements and Shelford, 1939). Progress towards maturity may occur in *'relays'* (Dansereau, 1954), each relay being dependent upon some prior event, for example colonization by some critical species.

Ecological insight is frequently achieved by considering ecosystems at a lower or higher level than the cenosis. *Autecology* for example, is concerned with the *'monocenosis'* (Friendriches, 1958), that is, the ecosystem at the species level. At a higher level, cenoses are grouped with others with which they have some element in common. Thus there is the *'biotic province'* (Dice, 1952) which emphasizes geographic and genetic continuity,—the raw material

of biogeography; and there is the *'community-type'* or *'biome-type'* (Clements and Shelford, 1939; Dice, 1952) which emphasizes biocenotic adaptation irrespective of genetic or geographic continuity (e.g., coral, mangrove, grassland, forest). Plankton is also a biome-type, as are the plankton sub-divisions which Haeckel (1890) also introduced, viz., phyto-and zoo-plankton; macro-and micro-plankton; epi-, meso-, and bathy-plankton.

The basis of cenology is the sampling survey, of which the plankton programme of the International Indian Ocean Expedition is a fairly typical example. Survey data constitute a Samples X Species matrix, the sampling point in oceanography being the *'station'*, a point in either space or time. Up till recently, analyses have typically been subjective, but it is now possible to introduce a measure of objectivity. Most classification methods are based on the 'R and Q techniques' of factor analysis (Cattell, 1952), known more commonly as 'normal and inverse analysis' (Williams and Lambert, 1961). The fundamental postulate in normal analysis is that the station is a sample of habitat to which the species present respond in varying degrees, providing 'tests' to locate discontinuities in the *'complex-gradient'* (Whittaker, 1960, 1967), i.e., to define geocenotic boundaries. The fundamental postulate in inverse analysis, on the other hand, is that species are defined by their individual niches which are satisfied to varying degrees by the stations sampled; consequently, samples may be used to locate discontinuities in the niche-complex, i. e., to define biocenotic boundaries.

'Diversity' is the number of species per unit sample, and *'ubiquity'* (frequency) is the number of samples per unit species. Neither should be confused with *'density'* which is the number of individuals of a given species per unit sample, or *'abundance'* which is the mean density for samples which contain the species (Greig-Smith, 1964). Diversity and ubiquity appear to be determined by the relative influence of biotic and physical factors, the extremes constituting what Sanders (1968) has called *'biologically accommodated communities'* e. g. rain-forests, coral reefs, abyssal seas) and *'physically controlled communities'* (e.g. sand-dunes, hypersaline bays, tundra, desert). Although diversity and ubiquity are interesting concepts in their own right, in cenology they frequently constitute a service of 'noise' or even error, the success of an analysis being limited by the uniformity of the 'tests' adopted. Nevertheless, the degree to which discrete cenoses will emerge in an analysis will depend basically on whether or not the survey area is highly structured; by oceanographic standards, for example, the Indian Ocean is highly structured because of the influence of the monsoon. Patterns emerge when 'station-groups' defined by normal analysis, and 'species-groups' defined by inverse analysis, are combined in a two-way matrix.

Some species find both niche and habitat only within a single station-group and are therefore said to be *'faithful'* to that station-group; this is the 'plankton-indicator' concept so familiar to marine ecologists. Some species are found at every station in the station-group; these are therefore said to be *'constant'* to that station-group. The constant species may or may not be faithful, that is to say it may or may not find a habitat in more than one station-group. The concepts of fidelity and constancy may be represented geometrically (Fig. 1). The terms are usually applied to species ('indicator-species') though, in principle, they may be applied to stations equally well ('indicator stations'). Fidelity and constancy have a common element: with relevance to species, this common factor is the intersection of the habitat of the species with the joint domain (geocenosis) of the species group (biocenosis). Fidelity is the ratio between this intersected area and the area of the habitat; constancy is the ratio between this intersected area and the area of the geocenosis.

The terminology that I have used in this discussion is summarized in Table 1. With the exception of *'cenotype'*, the terms are not original, though the choice may well be so. The sense in which some of the terms are used, e.g., 'niche' and 'habitat', agrees with that of some authors (e.g., Odum, 1953) and not with that of others (e.g., Dansereau, 1957), whilst other common terms (e.g., 'biotope') have found no place. However, if the holistic approach* to ecology has any merit, then I would suggest that the choice which I have made be judged in toto rather than by part.

I am indebted to Mr. K. R. Allen and Dr. D. J. Webb of this laboratory, and to Dr. D. J. Anderson, Botany Department, University of New South Wales, for reading the manuscript and for their critical comments.

*" The term ' wholeness ' has been much misused in past years. Within the organismic conception it means neither a mysterious entity nor a refuge for our ignorance, but a fact that can and must be dealt with by scientific methods." Bertalanffy 1952.

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CHAETOGNATHS IN THE UPWELLING AREAS OF THE ARABIAN SEA

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ABSTRACT

An attempt is made to study how the ecological theory that in a marine environment individual groups are distributed according to their place in the trophic level, applies in the distribution of chaetognaths in two well known upwelling areas in the Arabian Sea - the Somalian and southwest Arabian coasts. Population maxima of chaetognaths were found not adjacent to the centre of upwelling, but shifted to the fringe of the enriched area. Chaetognaths which occupy the tertiary level in the food chain need more time for their development and so the places of their maximum abundance appear at a greater distance from the centre of upwelling. Highest densities of juvenile chaetognaths were also restricted to the stations located away from the coast. This apparent increase in the abundance of chaetognaths towards the margin of the upwelling area was statistically tested and their rate of production was calculated.

INTRODUCTION

The distribution of different groups of planktonic organisms varies greatly depending on their place in the food chain; the higher the trophic level they occupy, the farther they are removed in space and time from the areas of enrichment (Vinogradov and Voronina, 1962. Due to upwelling the surface waters get fertilized and spread under the influence of local currents and the development of the primary and secondary producers are displaced in space and time. By the time the predators attain their population maxima in the sequence of biological events in the sea, they may be located quite some distance away from the centre of upwelling.

Chaetognaths are exclusively carnivores and they occupy the tertiary level in the food chain. Naturally areas of maximum chateognath population can be

expected to be located away from the upwelling areas. It is interesting to see how they are distributed in upwelling systems and how far this ecological theory holds truse for these organisms. The previous studies on the chaetognaths of the Indian Ocean (Vijayalakshmi, 1969) indicate that population maxima during the southwest monsoon period are not adjacent to the upwelling region but shifted towards the fringe of the enriched area.

The authors are grateful to Dr. N. K. Panikkar, Director, National Institute of Oceanography, Goa, for his keen interest in this work and providing facilities at the Indian Ocean Biological Centre.

Material and Methods

Four series of samples taken from the Somalia and Arabian coasts during July-August, the peak period of upwelling (Currie *et al.*, 1971), were selected

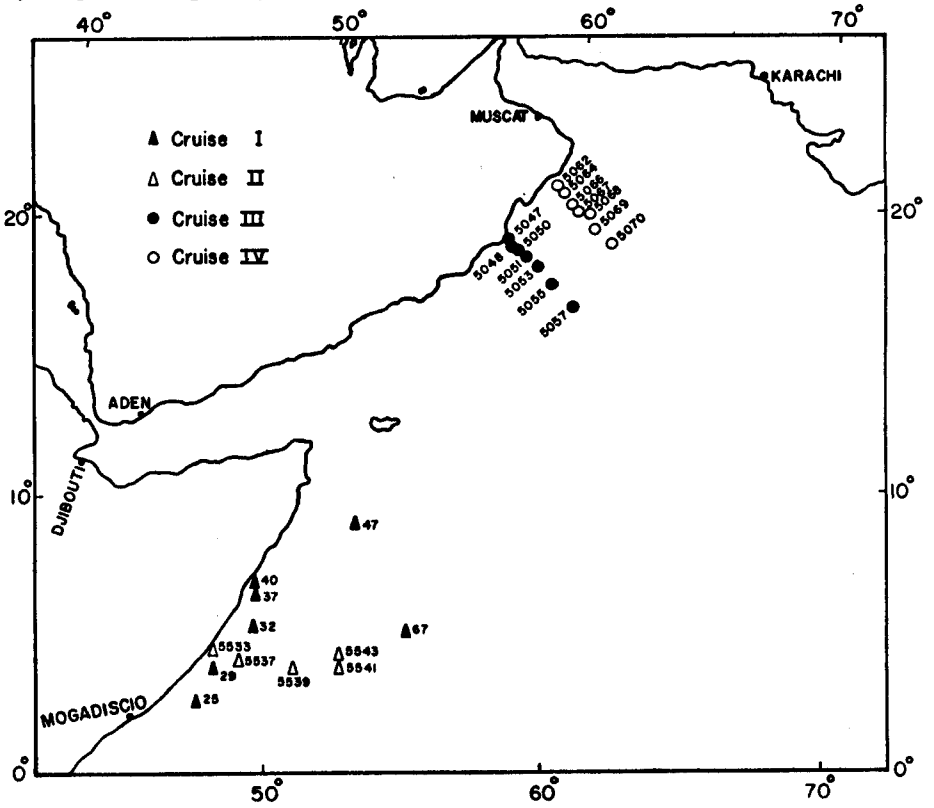


Fig. 1. Map showing the location of stations off Somalia and Southwest Arabia.
Cruise I — "Argo" collections during 12th - 29th August, 1964;
Cruise II — "Discovery" collections during 8th - 13th August, 1964;
Cruise III — "Discovery" collections during 10th - 13th July, 1963 and
Cruise IV — "Discovery" collections during 15th - 18th July, 1963.

from the International Indian Ocean Expedition (IIOE) collections for the present study. In all the four series the stations were worked from the coastal areas towards the sea, following the direction of the prevailing surface currents. The location of stations is indicated in Fig. 1. The details of the collections are given in the Handbook (IOBC, 1969). Chaetognaths from these stations were examined for species composition and stages of maturity. Based on the condition of the gonad the stages were isolated, those in which gonads are absent designated as juveniles, those with developing gonads as immature and those with fully developed gonads as mature individuals. The number of animals given always refers to number per standard haul (IOBC, 1969).

RESULTS

Fourteen species of chaetognaths—*Krohnitta pacifica, K. subtilis, Pterosagitta draco, Sagitta bedoti, S. bipunctata, S. enflata, S. ferox, S. hexaptera, S. minima, S. neglecta, S. pacifica, S. regularis, S. robusta, and S. pulchra*—were found in these collections. For the distribution curves only the common species were considered as the other species present constitute only an insignificant part of the total chaetognaths in these samples.

The abundance of the total chaetognaths and the common chaetognath species is represented in Fig. 2. In Fig. 2*a* the maximum density of chaetognaths (14288/std. haul) is seen at St. 47, located away from the Somali coast. Compared to the values at station 25, 29, 32, 37 and 40, the majority of the common species maintain high density at St. 47. The surface temperature in all these stations were low (22.44-24.22°C) indicating upwelling. However, at station 67 there is a sudden lowering of the chaetognath population. The hydrographical data for this station do not show any upwelling and the surface temperature was 27.20°C. Fig. 2*b* represents another section near Somalia and the results are almost identical with that in Fig. 2 *a*. These stations also indicate upwelling. There is no station beyond 5543 in Cruise II to compare chaetognath abundance with a non-upwelling station. Fig. 2 *c* shows steady increase in the abundance of chaetognaths towards the open ocean and the maximum value was found at station 5051. The density of chaetognaths was minimum at stations 5055 and 5057 and the hydrographical data for these two stations do not indicate upwelling. An almost similar pattern of distribution is observed in Fig. 2 *d*, another series of stations near south-west Arabian coast.

S. enflata was the dominant species and the proportion of the maturity stages of this species for the four cruises (Fig. 1) is shown in Fig. 3 *a*-3 *d*. The distribution curves show an increase in the population of different stages to-

wards the outer margin of the upwelling area. If juveniles are considered as an index to breeding the maximum population observed at stations 47 (Fig. 3 a), 5543 (Fig. 3 *b*), 5053 (Fig. 3 *c*) and 5070 (Fig. 3 *d*) would indicate these to be areas of intense breeding.

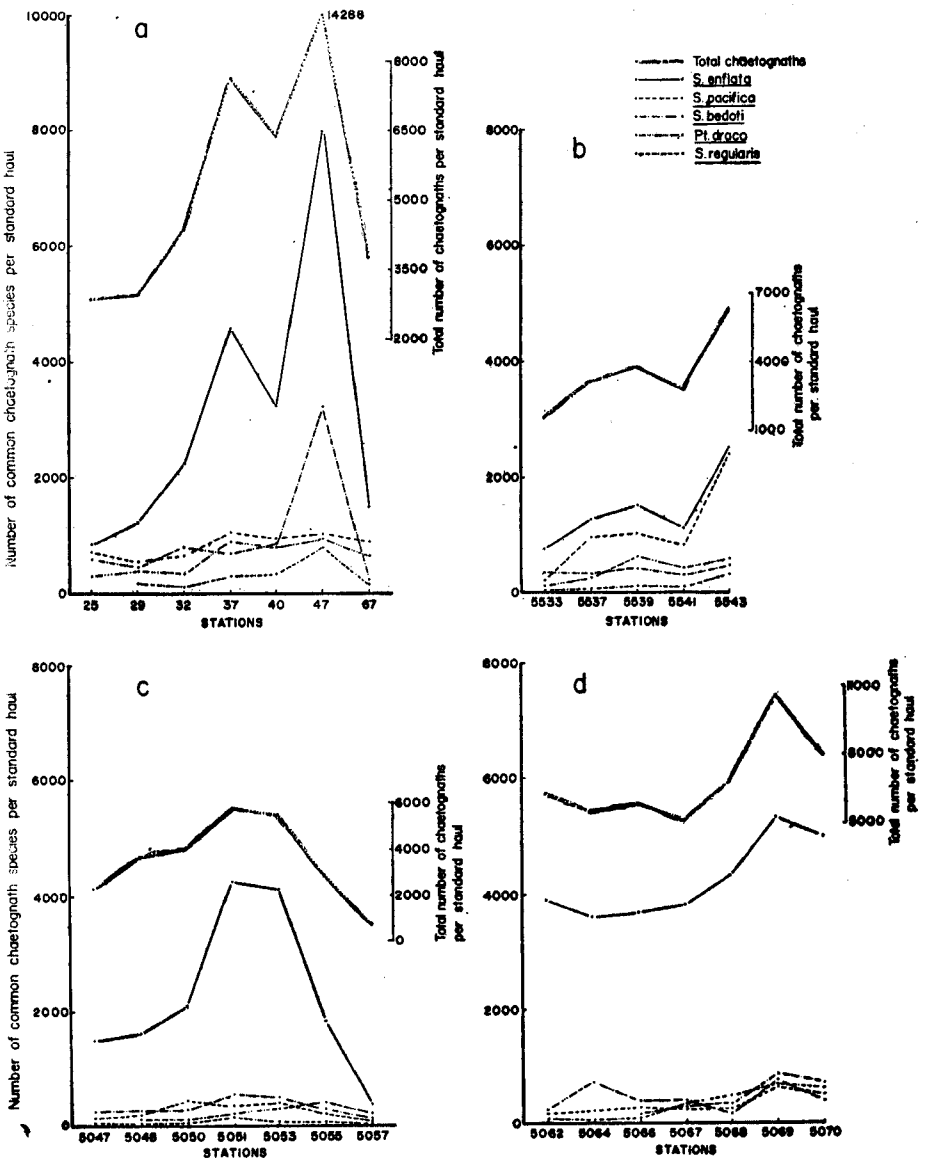


Fig. 2. Quantitative distribution of chaetognaths in the four cruises. a-Cruise I; b-Cruise II; c-Cruise III and d-Cruise IV.

All the stations having the maximum density of chaetognaths are on the outer limits of the upwelling areas. The upwelling area as indicated by the temperature distribution (25°C isotherm in July—Wyrtki, 1971) extends off the African coast to a distance of nearly 400 km and off the Arabian coast to nearly 100 km. The stations mentioned above are located farther out in the sea; St. 47 approximately at 268 km., 5543 at 447 km., 5053 at 121 km and 5070 at 363 km from the coast.

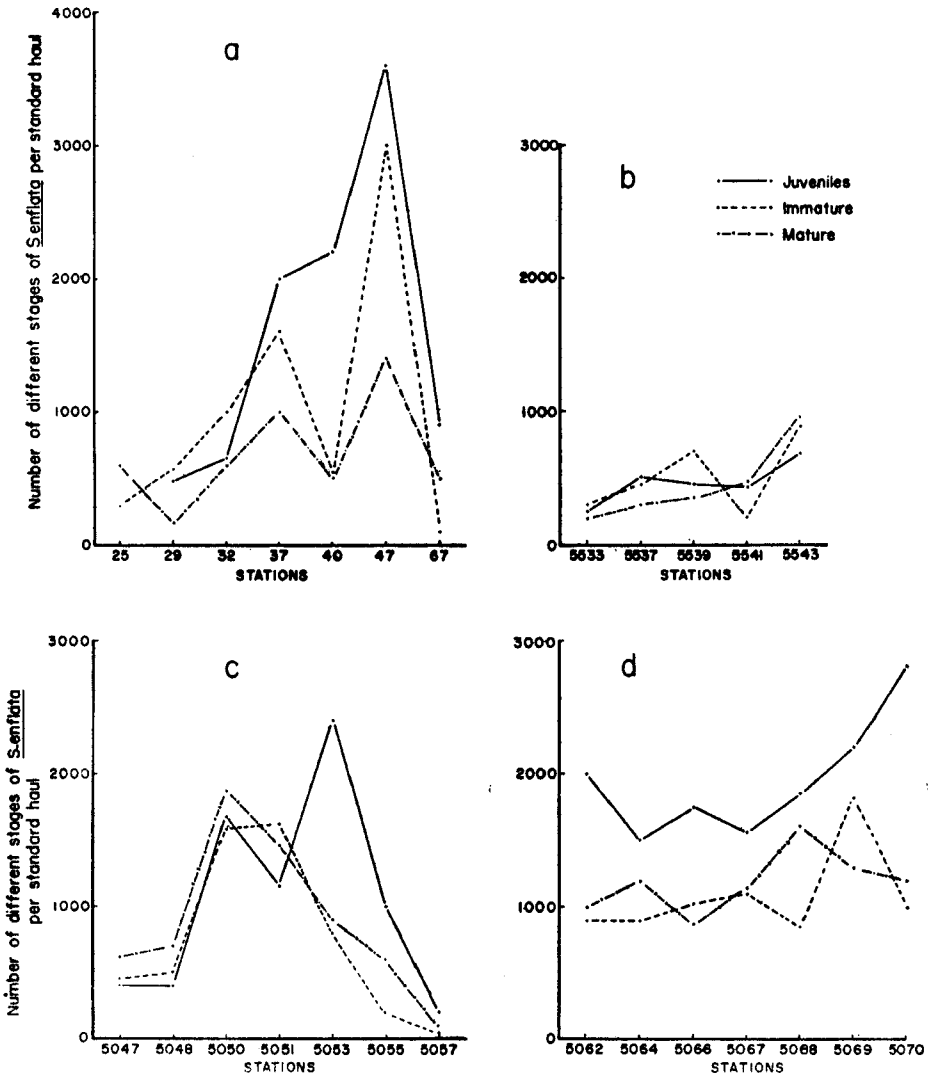


Fig. 3. Distribution of different maturity stages of *S. enflata* in the four cruises. a-Cruise I; b-Cruise II; c-Cruise III and d-Cruise IV.

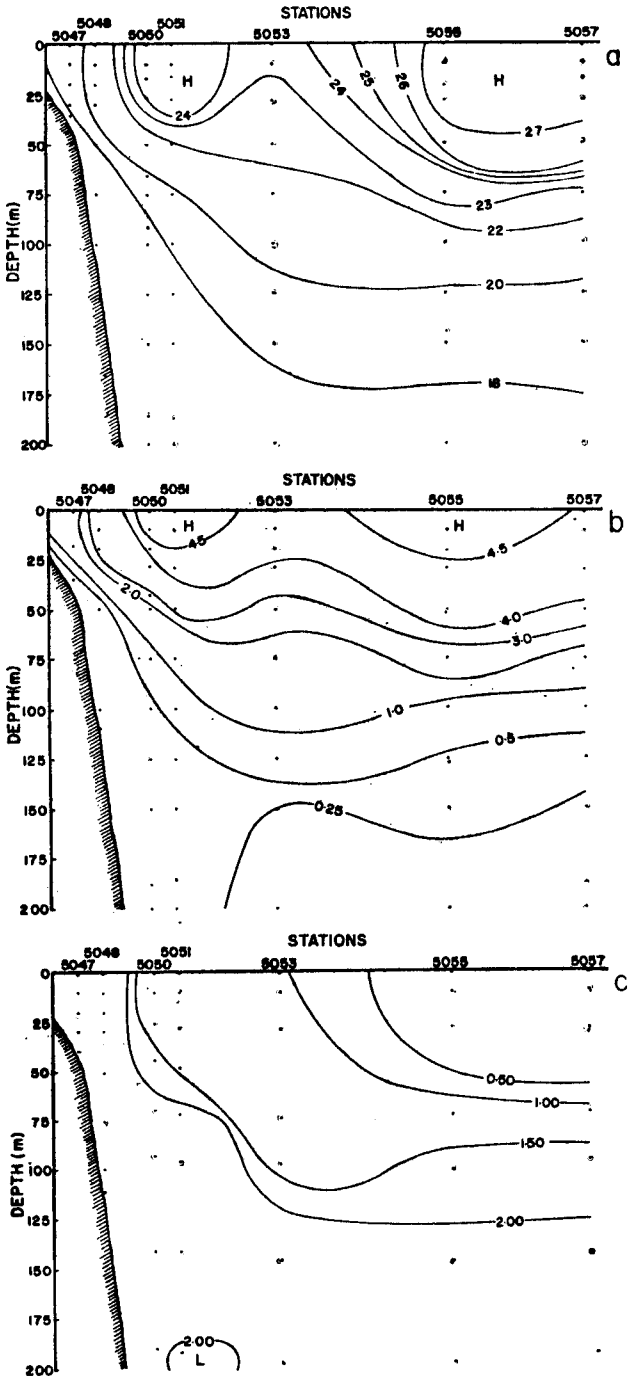


Fig. 4. Vertical distribution of temperature, oxygen and phosphate phosphorus in Cruise III. a-temperature °C; b-oxygen ml/l and c-phosphate phosphorus μg-at/l.

The hydrographical data for all the selected stations except station 67, 5055 and 5057 indicate upwelling. The vertical profiles of temperature, oxygen and phosphate values for the upper 200 m water column for Cruise III are depicted in Fig. 4 a-4 c. The first five stations indicate zones of upwelling as seen by the deepening of the thermocline, low temperature at the surface, low oxygen values and the high concentration of phosphate at the surface. Station 5055 and 5057 show the abrupt change in the hydrographical condition where there is no indication of upwelling.

This apparent increase in the population density of chaetognaths towards the periphery of the enriched area was analysed using the Chi-square test to infer whether the total chaetognaths were uniformly distributed over the different regions under study. The formula used for calculation of Chi-square is

$$x^2 = \Sigma \left[\frac{(fo - fe)^2}{fe} \right]$$

where

fo—observed number of individuals

fe—expected number of individuals

The significant difference in the relative abundance of *S. enflata* in the different regions was also tested by the same method. The calculated values of the Chi-square in both the cases are given in Table 1. From the Table 1 it could be seen that all the calculated values of Chi-square are highly significant ($p < .001$) indicating that different regions mentioned were having different rates of population density.

In order to examine which are the more productive regions under study, the data under different cruises were further analysed. The results are given in Table 2. It could be inferred that as far as total chaetognaths are concerned

TABLE 1. *Calculated values of x^2 under different regions*

Cruise	x^2 value for total Chaetognaths	Degrees of Freedom	Remarks	x^2 value for juveniles of *S. enflata*	Degrees of Freedom	Remarks
I	40071.54	5	$P<.001$	3640.5	4	$P<.001$
II	3485.21	4	$P<.001$	206.9	4	$P<.001$
III	1540.34	4	$P<.001$	1294.9	4	$P<.001$
IV	2929.14	6	$P<.001$	194.5	6	$P<.001$

the station 47 in Cruise No. I is 5 times more productive than station 25. In Cruise II the station 5543 is 4 times more productive than station 5533, in Cruise III, the station 5051 is 2.5 times more productive than station 5047 and in Cruise IV station 5069 is 1.68 times more productive than station 5062.

Regarding the juveniles of *S. enflata* station 25 in Cruise I is not at all productive and station 47 is 7.5 times more productive than station 29. In Cruise II the station 5543 is 2.7 times more productive than station 5533 and station 5053 is 6 times more productive than station 5047 in Cruise III. The station 5070 is more productive compared to all other stations in Cruise IV.

TABLE 2. *Production ratio under different regions*

Cruise	Stations	Production ratio of total Chaetognaths	Production ratio of juveniles of *S. enflata*
I	25:29:32:37:40:47	10:10:15:27:22:50 (Calculated $x^2_5 = 8.38$, not significant at 5% level)	0:10:14:42:46:75 Calculated $_4x^2 = 1.58$, not significant at 5% level)
II	5533:5537:5539:5541:5543	10:20:24:18:40 (Calculated $_4x^2 = 0.12$, not significant at 5% level)	10:20:18:17:27 (Calculated $_4x^2 =$ 0.02, not significant at 5% level)
III	5047:5048:5050:5051:5053	10:16:18:25:19 (Calculated $_4x^2 = 0.01$, not significant at 5% level)	10:10:42:29:60 (Calculated $_4x^2 = 0.87$, not significant at 5% level)
IV	5062:5064:5066:5067:5068: 5069:5070	100:88:93:82:108:168:127 (Calculated $_6x^2 = 0.18$, not significant at 5% level)	10:8:9:8:9:11:14 (Calculated $_6x^2 =$ 8.41, not significant at 5% level

DISCUSSION

Cushing (1971) in his comprehensive review on the upwelling areas in the world oceans has discussed at length the production cycle in upwelling systems. According to him the peak production reaches the surface not far from

the centre of upwelling and the plant and animal populations move away from the centre of upwelling. The dynamic boundary of the coastal upwelling is at about 100 km from shore. However, the effect of upwelling continues towards the open ocean and "the biological boundary must be at the imprecise edge of the wind system" (Cushing, 1971).

In a marine community—which may be defined as an aggregation of mixed taxa—the individuals in the unit are distributed according to the position they occupy in the trophic level. Animals like chaetognaths which feed on smaller zooplankton and whose position is higher than the herbivores, need more time for their development (Vinogradov and Voronina, 1962). Fig. 3 shows that the three maturity stages of *S. enflata* are represented in all the collections. However, maximum numbers of different stages are restricted to stations located away from the coast. Breeding of chaetognaths is continuous in tropical waters and periods of heavy spawning are superimposed on continual spawning (Owre, 1960; Vijayalakshmi, under publication). By the time the individuals reach maturity, currents might carry them away from the region of upwelling and the places of their population maxima appear at a greater distance from the area of divergence. As a result the zones of upwelling and the bulk of chaetognath population are divided in space and shifted to the margin of the enriched areas.

The surface current during July-August, the period under discussion, consists of a strong northerly Somali Current flowing nearer the coast off Somalia upto 8–10° North latitude. Around these latitudes the current turns eastwards. Similarly off the Arabian coast a coastal current flows in the northeast direction and offshore the general drift is eastwards. In both these areas the enriched waters reaching the surface as a result of upwelling are taken away towards the open sea in an easterly direction and this is reflected in the distribution of the plankton populations of different trophic levels. The tertiary population like that of the chaetognaths is removed farthest from the upwelling region.

The foregoing account on the chaetognaths in upwelling areas supports this ecological theory that in a marine environment individuals are distributed according to their place in the trophic level. Fig. 2 a and 2 c give a clear picture of this phenomenon where the lowering of the population density of chaetognaths beyond the h gh density observed in the zone of upwelling, and coincident absence of any hydrographical evidence of upwelling.

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OPTIMIZED TACTICS FOR OPEN-WATER MARINE PREDATORS

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ABSTRACT

Large carnivorous pelagic marine fishes are most often found to have been feeding on a heterogeneity of surprisingly small prey. Aside from the obvious abundance of small creatures in the sea, this behaviour may stem from optimization of predator-prey tactics based on a relatively sophisticated neurological response of the predator to potential prey.

INTRODUCTION

It has been frequently shown that large pelagic marine predators feed principally on very small prey. The occurrence in stomach content examinations of prey commensurate in size with the apparent capacity of the predator is very uncommon [see for example Allen and Aron (1957), salmon; Alverson (1963), tuna]. The same selectivity could be argued from the relative dimensions of successful artificial lures and baits in capturing fast-swimming open-water predators, where lures or baits are rarely as much as one-tenth of the length of the predators (i.e., simulating prey ca. one-thousandth of the predator's volume).

It is tempting to attribute this curious state of affairs merely to opportunism coupled with the abundance of the smaller prey. However, marine predators that depend on stealth or ambush for capture or which feed principally on injured or moribund prey do not find it necessary to feed on disproportionately small prey. Indeed, some fish (e.g., anglers, groupers, lingcod *Ophiodon elongatus*, sharks, etc.) are famous for their capaciousness. Thus the energetics of the open-water pre-predator chase may be involved in the pelagic predators' avoidance of healthy large potential prey in that environment.

One can visualize the energetics of an open-water predator to be as portrayed in Fig. 1, with a continuously declining level of energy represented by metabolic expenditure interrupted by a number of variable events involved in feeding. These latter events first take the form of a loss of total energy expended

in the chase, followed by an abrupt increase in total energy (for successful chases) represented by the ingestion of the prey. It is manifest that the sum of these series of events much ordinarily reverse the general trend of the metabolic slope and result in overall increase in total energy of the predator if it is to grow or reproduce. Assuming that the intake of active predators is of the order of five percent of their body weight per day, each day predators require fifty or more successful feeding events of prey of the order of one-thousandth of the predator's weight.

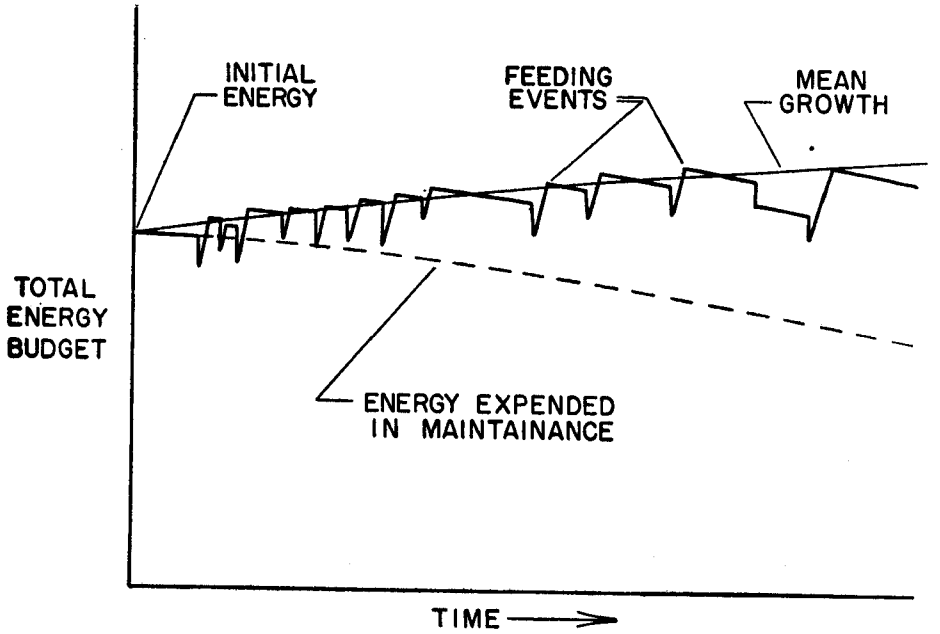


Fig. 1. Representation of feeding events involved in predator growth.

Analysis of the Energetics of Predator-prey Open-water Chase

In the following treatment we examine the tactics and neurological responses needed by a predator to optimize its energy budget in a simple single-prey/single-predator open-water chase in an ocean populated with a series of geometrically, phys ologically and hydrodynamically similar organisms. In such an ocean the predator's energy intake for a successful chase, Q_i, is proportional to the prey's mass, M_p, which is proportional to the prey's volume, V_p

$$Q_i \propto M_p \propto V_p = K_1' L^3_p = K_1 L_c{}^3 C^3$$

where L_p and L_c correspond to a linear dimension (e.g., length) of the prey and predator respectively, K_1 is a constant and $C=\frac{L_p}{L_c}$ (In this discussion the subscript p always refers to the prey's properties, the subscript c always refers to properties of the predator or carnivore and the K's are constants.).

It is important to note here that an efficient predator probably must be capable of judging the absolute volume of a potential prey. This is intuitively appealing because the predator's potential intake of energy is proportional to the volume of a potential prey.

The energy expended in the steady-state portion of the chase, Q_e, can be determined from the following relations :

$$Q_e = K_2 P_e t = K_2 F_c v_c t$$

where P_e is the power expended and t is the time duration of the chase. F_c is the force exerted by the predator and V_c is its velocity. We can simplify the treatment by assuming that both the predator and the prey travel at constant velocities during the entire chase. The more realistic case where both the predator and the prey start from rest and begin the chase with a sudden burst of speed can be treated in the same way. However, the velocity used in this case will be velocity appropriately averaged over the entire chase. We assume that the accelerative phases of the chase do not dominate the energetics. We estimate that the energy expended to achieve chase velocity is much less than the energy expended to overcome drag forces during the chase, and predators that depend principally on accelerative bursts appear to be subject to different feeding constraints, as noted above. In our case there will be no accelerations and the gross force exerted by the predator in locomotion will equal the drag force of the water:

$$F_c = K_s'' A_c V_c^2 = K_s' L_c^2 V_c^2$$

where A_c is the cross-sectional area of the predator and L_c is its linear dimension corresponding to L_p. The time of the chase, t, is given by

$$t = \frac{D}{(V_c - V_p)}$$

where D is the distance at which the predator elects to chase. As the reponse of open-water predator probably dominantly depends upon visual stimuli, the predator's decision to attack must depend in some way upon the physical size and distance of the prey, as well as, in nature, upon its type, behavior, etc.

As mentioned earlier, it is intuitively appealing that a predator could optimize his energy intake if it responds to the volume of the prey. Then the distance at which the predator initiates the chase may be proportional to the prey's volume, V_p or L_p^3. This is, however, not sufficient because the predator must also be able to determine volume relative to its own in order to avoid attacking prey of wholly disproportionate dimensions. Also it seems reasonable that larger predators will strike at larger distances. Considering these circumstances and putting the relation in the most general form, we assume that D behaves as

$$D = K_4 L_c \left(\frac{L_p}{L_c}\right)^3 = K_4 L_c C^3$$

where K_4 is a dimensionless constant.

Studies have shown that both the cruising velocity and maximum velocity of a marine animal is proportional to its length raised to some power,

$$V \propto L^m$$

The most commonly quoted values of m are between 1/3 and 1, but for the present discussion we shall leave m unspecified as its value within the quoted range will not greatly affect the results. For the more complicated example where the fish accelerate from rest, the final result should not be much different, and in either case the exact value of this coefficient will not change the general conclusions of this analysis.

Combining all of the factors specifying the predator's expended energy, we obtain

$$Q_e = K_5 L_c^2 L_c^{3m} \frac{L_c C^3}{(L_{ic}^m - L_p^m)} = K_5 L_c^{3+2m} \frac{C^3}{(1-C^m)}$$

In order to evaluate the predator's energy budget we take the ratio

$$R = \frac{Qi}{Q_e} = K L_c^{-2m} (1 - C^m)$$

To examine absolute gain [i.e., $\Delta Q = (Qi - Qe)$] all constants would need to be closely evaluated. Some of the constants are poorly known and we have thus chosen to explore the problem through relative ratios, $\frac{R}{K}$.

Optimization Of Energetics

In Fig. 2 we plot the optimization ratio as a function of C (for m=1/2; see below). It is the curve labelled **n**=3. The ordinate scale is relative. Two features are obvious from this curve : first, the energy ratio is optimized for small prey (that is, the value of $\frac{R}{K}$ is greatest for small values of C) and second, the optimization curve is roughly parallel to the curve of common abundance of marine animals in the open ocean. The product of the curves of energy optimization and of abundance will greatly favour the predator that responds in the way described by our model. Furthermore, this model satisfies the empirical observation that pelagic mar ne predators predominantly feed on small prey. The conclusion here is that predators must optimize the energetics of the chase using quite sophisticated means to judge their prey before attacking.

Now, we consider what happens if the predators have a simpler response to the prey. In particular we can generalize the expression for D and assume that

$$D = K_4 L_c \left(\frac{L_p}{L_c}\right)^{\mathbf{n}} = K_4 L_c C^n$$

where for simplicity n is a positive integer.

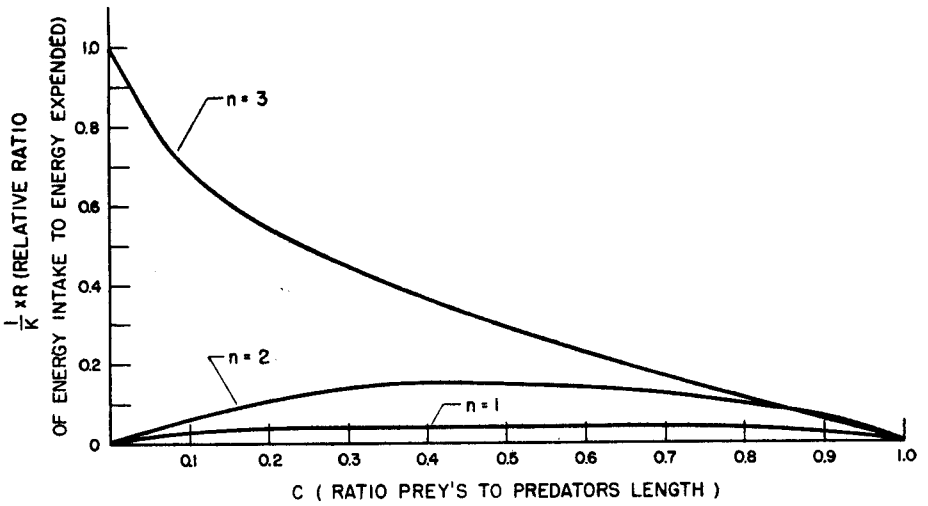


Fig. 2. Relationship of relative energy ratios to relative prey size for three levels of sophistication of response.

The case n=0 corresponds to a predator living in turbid water. It might strike at any prey that came within visible range and its responses is thus independent of such a sophisticated decision-making process. The cases thus n = 1, 2, 3 mean that the neurological system of the predator is, in order of increasing sophistication, capable of judgement based on a one–, two– and three-dimensional representation of the prey. The case n = 1 requires the predator to identify and respond to the size of the prey through only the plane angle subtended by the prey's extremities; the case n = 2 requires the predator to respond to the solid angle subtended by the prey and to its distance. These are, of course, simpler observations and neural processing than the case we previously considered, n = 3, which requires the predator not only to identify the solid angle and to detect the absolute range of the prey through some range-finding clues (such as clarity of the prey's image, parallax or perhaps stereoscopic vision) but also to judge absolute volume.

Whether the predator observes the absolute length or area of the prey, the predator needs almost the same sensory apparatus but only linear neural processing. The need to incorporate these and the range into a judgement of absolute volume requires non-linear neural processing [e. g., $V_p \propto (A_p)^{3/2}$.]

Combining all of the factors specifying the predator's expended energy in this more general case, we obtain

$$Q_e = K_s L^2_c L_c^{3m} \frac{L_c C^n}{(L_c^m - L_p^m)} = K_s L_c^{3+2m} \frac{C^n}{(1 - C^m)}$$

Now the exercise is to find the ratio, C_{max}, that maximizes the predator's

energy intake relative to its energy expenditure. We take the ratio

$$R = \frac{Q_i}{Q_e} = K L_c^{-2m} C^{3-n} (1 - C^m)$$

and set

$$\frac{\partial R}{\partial C} = K L_c^{-2m} \{ (3-n) C^{2-n} (1-C^m) + C^{3-n} (-m) (C^{m-1} \} = 0$$

giving

$$C_{max} = \left(\frac{3 - n}{3 + m - n}\right)^{1/m} .$$

For the purposes of illustration let $m = 1/2$. The conclusions, based on the expressions for R and C_{max} above, are independent of the value of m we choose, except for the special case of $m \leq 0$ (velocity is independent of or inversely related to size) which is unrealistic except perhaps in special environmental conditions. Then we have

n	C_{max}
0	$(6/7)^2$
1	$(4/5)^2$
2	$(2/3)^2$
3	0

The only realistic alternative here is $n = 3$ (although this analysis shows that the predator should chose prey of size zero, according to the discussion in the next paragraph they will also do very well, to attack prey of merely small size); even for $n = 2$, $L_p \simeq 1/2\ L_c$, a situation that is not observed in nature for predators of this sort.

In this analysis we can assume that each of the primary constants are the same in each case. The only possible exception is K_4, which is the result of a decision. However, the definition of D may remove any dependence of K_4 on n. Thus the absolute comparisons between the results of the several levels of sophistication in the predator's decision can be carried out without any special normalization. In Fig. 2 we plot the relative optimization ratio, $\frac{R}{K}$, as a function of C. (It should be noted that since constants are not evaluated, the values of $\frac{R}{K}$ are relative, and a value less than unity is not to be interpreted as a net energy loss.)

Conclusions

It is seen that the tactic involving $n = 3$ will result in the predator attaining a higher ratio of intake to loss for all prey that can realistically be consumed

—say, $C < 0.25$. The other two tactics result in decreasing ratio for the smaller organism and this result follows independently of normalization. Furthermore, as mentioned above, the trend for the $n = 3$ curve is roughly parallel to the curve of abundance. This exercise tells us that the predator capable of judging volume and range should chase very small prey in order to optimize its energy balance. As this case predominates in nature, we can conclude that predators do indeed rely upon sophisticated perceptual mechanisms and decision making.

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THE PRESENT U. S. CONTRIBUTION TO THE INTERNATIONAL DECADE OF OCEAN EXPLORATION

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ABSTRACT

The International Decade of Ocean Exploration for the 1970's was proposed in the U. N. General Assembly in 1968. The General Assembly then invited member states to formulate proposals for national and international scientific programs and decided to transmit these proposals to UNESCO for the Intergovernmental Oceanographic Commission (IOC). The IOC in September 1969 recognised the purpose of increasing knowledge of the ocean and its resources for the benefit of mankind. The role played by the United States in its implementation is briefly discussed. The U. S. Academy of Sciences and the National Academy of Engineering prepared detailed recommendations and called upon eminent scientists from academic, governmental, technical, industrial and international communities as advisers. The National Science Foundation supports the U. S./IDOE research projects in four programme areas: environmental quality, living resources, environmental forecasting and seabed assessment. In the U. S. contribution to the IDOE the National Science Foundation has stressed the importance of scientific excellence in projects which require the concerted efforts of many participating institutions and investigators. The role played by US/IDOE Office in providing a way of ensuring the evolution of scientifically sound projects are also dealt with in this paper.

INTRODUCTION

In 1968 "an historical and unprecedented adventure—an International Decade of Ocean Exploration for the 1970's" was proposed in the United Nations General Assembly. In December of that year, the U. N. endorsed the idea of a coordinated long-term program of oceanographic research, and formally welcomed the proposed International Decade of Ocean Exploration as an important element thereof. The General Assembly endorsed "the concept of an International Decade of Ocean Exploration to be undertaken within the framework of a long-term program of research and exploration..." It further invited member states to formulate proposals for national and international scientific programs and agreed activities to be undertaken, and to transmit these proposals

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to UNESCO for the Intergovernmental Oceanographic Commission (IOC) in time to begin the Decade in 1970.

At its Sixth Session in September 1969, the IOC recognized the purpose of the expanded program to be: "to increase knowledge of the ocean, its contents, and the contents of its subsoil and its interfaces with the land, the atmosphere, and the ocean floor to improve understanding of the processes operating in or affecting the marine environment, with the goal of enhanced utlization of the ocean and its resources for the benefit of mankind..." A Group of Experts on Long-Term Scientific Policy and Planning was established, and its terms of reference were, in part, to develop the scope and content of the Long-Term and Expanded Program of Ocean Explration and Research of which the International Decade of Ocean Exploration is an important element (Anon, 1970).

At the Seventh Session of the Intergovernmental Oceanographic Commission in October, 1971, additional impetus was given to the International Decade of Ocean Exploration when specific projects were described as a part of the Decade. Particular emphasis was placed on a Global Investigation of Pollution in the Marine Environment (Anon, 1971 *a*). The first major planning meeting for the working group will take place in early 1973.

Having been the nation to originally propose the International Decade of Ocean Exploration, the United States was prepared to take an early role in its mplementation. The U. S. National Academy of Sciences and the National Academy of Engineering prepared detailed recommendations for the scientific and engineering aspects of the United States' contributions to the International Decade of Ocean Exploration. The Academies called upon distinguished scientists and others from the academic, governmental, technical, industrial, and international communities as advisors. The group examined the scientific and engineering goals, priorities among them, capabilities required to achieve them, and the products and benefits to mankind to be anticipated. Results of the study were set forth in a report entitled, "An Oceanic Quest—The International Decade of Ocean Exploration" (Anon, 1969 *a*). Although a comprehensive treatment of the program, the report was based on a much higher budget level than that which exists.

In late 1969, the Vice-President of the United States formally announced the country's intention to contribute to the International Decade of Ocean Exploration and assigned responsibility for the U.S. contribution to the National Science Foundation (NSF). NSF is an independent agency of the U. S. Government established in 1950 "to promote the progress of Science..." and authorized "to foster the interchange of scientific information among scientists in the United States and foreign countries... (and) to initiate and support specific scientific activities in connection with matters relating to international co-operation..." In giving the Foundation responsibility for the planning, management, and funding of the United States' portion of IDOE, the Vice President proposed goals to:

1) Preserve the ocean environment by accelerating scientific observations of the natural state of the ocean and its interactions with the coastal margin—to provide a basis for (a) assessing and predicting man-induced and natural modifications of the character of the oceans; (b) identifying damaging or irreversible effects of waste disposal at sea; and (c) comprehending the interaction of various levels of marine life to permit steps to prevent depletion or extinction of valuable species as a result of man's activities;

2) Improve environmental forecasting to help reduce hazards to life and property and permit more efficient use of marine resources—by improving physical and mathematical models of the ocean and atmosphere which will provide the basis for increased accuracy, timeliness, and geographic precision of environmental forecasts;

3) Expand seabed assessment activities to permit better management—domesticcally and internationally—of marine mineral exploration and exploitation by acquiring needed knowledge of seabed topography, structure, physical and dynamic properties, and resource potential, and to assist industry in planning more detailed investigations;

4) Develop an ocean monitoring system to facilitate prediction of oceanographic and atmospheric conditions—through design and deployment of oceanographic data buoys and other remote-sensing platforms;

5) Improve worldwide data exchange through modernizing and standardizing national and international marine data collection, processing, and distribution; and

6) Accelerate Decade planning to increase opportunities for international sharing of responsibilities and costs for ocean exploration, and to assure better use of limited exploration capabilities.

In developing the program, the National Science Foundation has drawn on: the Intergovernmental Oceanographic Commission's "Comprehensive Outline of the Scope of the Long-Term and Expanded Program of Oceanic Exploration and Research" (Anon, 1970); the report entitled "Global Ocean Research" (Anon, 1969 *b*) prepared by a Joint Working Party nominated by the International Council of Scientific Union's Scientific Committee on Oceanic Research, the Food and Agriculture Organization's Advisory Committee on Marine Resources Research, and the World Meteorological Organization (Advisory Group on Ocean Research); the "First Report of the Group of Experts on Long-Term Scientific Policy and Planning"; *An Oceanic Quest* (Anon, 1969 *a*); the various Resolutions and Recommendations of the U. N. General Assembly and the Intergovernmental Oceanographic Commission; the U. S. Vice-President's stated IDOE goals; and other relevant documents. The Foundation has since pro-

vided the management and financial support for the United States' contribution to the International Decade of Ocean Exploration (Anon, 1971 *b*).

The International Decade of Ocean Exploration has been launched with programs that are, in keeping with IOC requirements, significant.

Research Projects

The National Science Foundation supports the U. S. IDOE research projects in four program areas: environmental quality, living resources, environmental forecasting, and seabed assessment (Anon, 1971 b). Certain of these projects are briefly discussed below, and countries which have scientists participating in them and others are listed in the Appendix.

Environmental Quality Program

The purpose of the Environmental Quality Program is to assess, understand, and predict the impact of man on the marine environment. Studies are supported to determine present day concentrations of pollutants and trace compounds in the environment, and to provide knowledge of: sources and rates of input, dispersal and transfer mechanisms, effects on organisms, and fates of pollutants in the marine environment as suggested in "Marine Environmental Quality" (Anon, 1972 *a*).

A Baseline Measurement Project for determining the present levels and regional distribution of selected pollutants (chlorinated and petroleum hydrocarbons, and heavy metals) in inshore and open ocean organisms has been completed and the results assessed and published as "Baseline Studies of Pollutants in the Marine Environment and Research Recommendations" (Anon, 1972 *b*). The purpose of this one-year project was to provide data on which to base recommendations for research on the effects of pollutants on marine communities and ecosystems.

The Pollutant Transfer Process Project is concerned with research on the fluxes of chlorinated hydrocarbons, petroleum hydrocarbons and heavy metals into the ocean and the means whereby these pollutants are taken up by marine organisms and transferred in the food chain. The project's purposes are to determine which mechanisms are important in pollutant transfer and the environmental factors affecting the transfer processes. Such a project was considered necessary for determining whether the oceans are becoming measurably polluted and as a pre-cursor to large-scale laboratory and field experiments on the effects of pollutants on marine organisms.

The Geochemical Ocean Sections Study (GEOSECS) involves the measurement of trace elements, stable and radioactive isotopes, major ions, dissolved gases, nutrients and hydrographic parameters (temperature, salinity) in water samples collected at 20 to 50 depths at approximately 140 stations on cruise tracks extending from the Arctic to the Antarctic in the Atlantic and Pacific oceans. The cruises will last about 18 months and the tracks follow the appro-

x'mate trajectory of bottom water. The measurements cited above, all of which wi!l be made on the same water samples, will provide quantitative data which will be used to calculate oceanic mixing and diffusion, and at the same time provide a baseline for the levels of fission products which have been added to the ocean as a result of man's activities.

Living Resources Program

The objective of the Living Resources Program is to provide a sc'entific foundation for better management and use of the ocean's biolog cal resources. Research efforts will rely on the application of advanced methods in the biologi-cal, chemical, and physical marine sciences. The projects will focus the necessary scientific and technical resources needed to complete comprehensive ecosystem studies.

The upwelling regions of the world oceans, where about 50% of the total fish catch occurs, are the areas where the Coastal Upwelling Ecosystem Analysis (CUEA) project is be'ng conducted. Spatial and temporal scales of circulation and nutrient and organism distributions are being described in terms of their role in processes causing and affecting upwelling and in the context of developing a total upwelling systems model so that environmental perturbations can be predicted. The upwelling areas being investigated are off Peru, Oregon, California and North-west Africa.

Environmental Forecasting Program

The Environmental Forecasting Program seeks to develop improved physical and mathematical models of the ocean and atmosphere to provide the basis for increased accuracy of environmental forecasts. Comprehensive studies in large-scale ocean-atmosphere coupling, mid-ocean dynamics, paleo-oceanography, and deep ocean circulation form the core of th:s program.

The Climate: Long-range Investigation, Mapping, and Prediction (CLIMAP) Project will improve our understanding of changes in climate and ocean circulation from the mid-Pleistocene to the present. The project includes extensive paleontological, sedimentological and geochemical analysis of existing ocean sediment cores. The analyses are used to reduce previous ocean circulation systems which are intimately linked to climate. Ocean surface temperature and sa!inity charts will be constructed for four periods: 700,000 years ago (mid-Pleistocene base); 120,000 years ago (last interglacial period); 17,000 years ago (last glacial stage); and 6,000 years ago (post-glacial thermal maximum). The research program is closely integrated with studies on climate as determined from analyses of ice cores from Greenland and the Antarctic.

The North Pacific Experiment (NORPAX) is an experiment jointly supported by the U.S. Navy's Office of Naval Research and the National Science Foundation. The research is designed to improve our understanding of ocean-atmosphere couping in the North Pacific Ocean and the effects of this coupling

on the North American continental climate. Oceanographic (temperature, salinity, currents) and meteorological (wind directions, speed, rainfall, humidity) parameters will be measured from specially instrumented buoys, islands, ships, and aircraft. The data will be collected simultaneously throughout the North Pacific, and telemetered to a single, shore-based computer for analyses and interpretation. Previously identified regions of anomalously "hot" or "cold" sea surface temperatures and their interactions with, and effects on, marine atmospheres and continental climate are of immediate interest.

The Mid-Ocean Dynamics Experiment (MODE) is designed to identify mesoscale eddy-like motions in the ocean. Specifically, MODE seeks to understand the dynamics, energy sources, and role of mesoscale eddies in the ocean so that the eddies can be properly incorporated into numerical (predictive) models of the mean ocean circulation. Field experiments are designed in the context of theoretical ideas so that they relate to previously proposed dynamical hypotheses. Preliminary studies south of Bermuda have determined instrument spacings for a more thorough experiment to take place from March through July, 1973 at the same location. The latter experiment will utilize a variety of moored and drifting sensors for measuring currents, salinity, temperature and bottom pressure.

Seabed Assessment Program

The Seabed Assessment Program supports exploration of the continental margins, deep-sea floor, and mid-oceanic ridges to identify new areas of natural resources and increase our understanding of the natural processes which produce these resources.

The Eastern Atlantic Continental Margin Study (Anon, 1971 *c*) of the structure of sediments of the continental margin from Cape town, South Africa, to Portugal is being done with seismic reflection, seismic refraction, magnetic, gravity and bathymetric surveys along geophysical traverses extending normal to the coast. The traverses are made at approximately 200 km intervals, and several extend out to the Mid-Atlantic Ridge to permit correlation with data to be collected on subsequent traverses to be made on the Western Atlantic Margin of South America. Continental margin projects are expected to provide fundamental information on the origin of the South Atlantic Ocean Basin, the movement, through sea floor spreading, of South America away from Africa, and the buried features on the continental margins which may be indicative of oil or gas deposits.

The Nazca Lithospheric Plate Program is a study of the processes which take place during crustal formation and destruction at the diverging and converging edges respectively of the Nazca Plate, a major tectonic plate in the East Pacific. The processes occuring in the area where the plate material is subducted under the continental margin (in the Peru-Chile trench) and the

associated processes which produce metallic ore deposits in the Andes are of particular interest.

The Mid-Atlantic Ridge Study (Anon, 1972 *c*) also involves tectonic plates, but the emphasis is directed at the area where crustal material is first formed along the Mid-Atlantic Ridge. The research program, still in its formative stage, will make substantial use of submersibles for observing and collecting material *in situ,* deep-towed sensing instruments such as side-scanning SONAR, and high precision temperature detection units in the regions of the ridge itself.

Philosophy for Program Development

In developing the U. S. contribution to the IDOE program, the National Science Foundation has stressed the importance of scientific excellence in projects. Furthermore, the projects must be of such a scale that they are not amenable to attack by single investigators or institutions, but require the concerted efforts of many participating institutions and investigators. Another important aspect in program development to which the Foundation adheres is that the Decade is based on an international sharing of responsibilities for the costs of project support.

As far as specific project development is concerned, the U.S./IDOE office has relied upon working scientists to develop program plans. Direct scientist-to-scientist communication and discussions at international meetings of working scientists, such as those supported by the Scientific Committee on Oceanic Research, appear to provide a way of insuring the evolution of scientifically-sound prjoects. Following the development of a program, scientists are encouraged to approach the National Science Foundation with an outline of the research plan. If the concept appears sound and funds are available to support the effort, the investigators are asked to submit a formal proposal while, at the same time, advising their foreign colleagues that support of the U.S. port on of the program is a possibility. The final process, prior to funding a project, is review by other scientists in the appropriate discipline, the IDOE Proposal Review Panel, and the National Science Foundation staff.

Appendix. *List of countries with scientists and/or research institutions co-operating in International Decade of Ocean Exploration Projects*

Angola	F. R. of Germany	New Zealand
Argentina	France	Nigeria
Belgium	Gabon	Peru
Bolivia	Ghana	Portugal
Brazil	Iceland	R. of South Africa
Cameroon	India	Sierra Leone
Canada	Italy	Spain
Chile	Japan	Sweden
Colombia	Liberia	Togo
Congo	Mauritania	United Kingdom
Denmark	Mexico	U. S. S. R.
Ecuador	Netherlands	Venezuela

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SOME ASPECTS OF THE BIOCHEMISTRY OF MONOGENEAN PARASITES OF MARINE FISHES

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ABSTRACT

The extent of water content, dry matter, protein-N and non-protein-N has been determined in the monogenetic trematode *Capsala laevis* and compared with other trematodes. The absolute values of these showed increase in relation to fresh weight, but at different rates, suggesting the possible presence of the phenomenon of chemical heterauxesis. Percentage of dry matter showed a decline while absolute of dry matter showed an increase with increase in fresh weight in *Capsala laevis*. Percentage water showed an increase whereas percentage protein-N and non-protein-N decrease in relation to fresh weight in the monogenean studied. Amino acid composition of *Capsala laevis* is presented and compared with data available on trematodes. Nature of the proteins in clamps, body spines and egg shell, characterized histochemically, is presented.

INTRODUCTION

It is well know that monogeneans, after a brief period of free-swimming larval phase, attach to hosts and grow to adult during which the body form remains essentially unchanged. But their growth is a continuous process, being considerably great after first attaining sexual maturity (Sproston, 1945). Moreover, it is known that various parts of these grow at different rates. Such a feature is revealed in these and other helminths from the works of Gallien (1935), Sproston (1945), Ramalingam (1960, 1961, 1968) and Dawes (1962). Sproston, from her studies on *Kuhnia scombri,* has shown that the haptor, body width, oral sucker, anchor and clamp increase in size allometrically in relation to body length. Later Ramalingam (1961), in *Lithidiocotyle secunda,* has shown that the increase in the length of the haptor and the addition of clamps against body length follow allometry in the vegetative and reproductive phases. In *Cemocotylelloides,* which has asymmetrical haptor with clamps differing in number on the two sides, Ramalingam (1968) has shown that the rate of growth of the haptor as well as the addition of clamps in it proceed isometrically upto a particular stage after which the rate of increase proceed unimpeded on one side whereas on the other side the rate is greatly retarded and ceases more or less after a particular stage. This feature has been attributed to the functional change taken over by the side of the haptor associated with the mode of attachment to the gills. Besides, it has been shown that the rate of addition of

clamps and growth of the haptor beyond the isometrical level proceeded allomerically in the immature and mature male-female phases of activity. A support to the possible occurrence of heterauxesis in helminths is further illustrated in the growth studies made on *Fasciola hepatica* by Dawes (1962). He has shown that the growth pattern of suckers, pre-and post-acetabular regions and other organ systems follows allometry. However, Frankland (1965) from her studies on *Diclidophora dentitulata,* has suggested that the growth of organs like haptor, pharynx and clamps proceeds, isometrically.

Though the phenomenon of heterauxesis is known to be exhibited by a number of animal organisms in their growth and has been extensively applied to different morphological characters in various groups, its application to the chemistry of the tissues has not been extended. Such an approach affords considerable scope, in view of the metazoan organisms in its passage from fertilization to maturity passes through a long succession of stages which are characterized just as much by changing chemical composition as by changing morphological characters (Needham, 1942). Just as organs or structures are as parts of morphological totality, so also the substances or groups of substances are as parts of chemical totality. A natural follow-up would therefore be to enquire into the regularities which the constituents oil this chemical totality exhibit during its continuous increase in mass. Teissier (1931) was the first to apply heterauxesis to chemical development of organisms. He studied a number of chemical entities such as water, fat, ash, phosphorus in the larvae of meal worm and wax moth and found them to obey the Huxley's relation as the totality grew. Though in subsequent years such a phenomenon has been reported in a number of animal groups, similar information is meagre in parasites.

Changes in the chemical entities like water, fat, carbohydrate, protein, etc. have been reported in a number of parasites in relation to factors like starvation of hosts (Reid, 1942; Goodchild, 1961), bileless and normal hosts (Goodchild, 1961), location of parasites in alimentary canal and tissues (Campbell, 1960), larval and adult as well as same larvae but in different hosts (von Brand and Bowman, 1961). However, information on chemical composition and their changes in helminths developing normally through various phases of growth is insufficient to suggest the presence of any specific pattern (Hopkins and Hutchinson, 1958). These authors, from their studies on the changes in the total nitrogen composition during larval and adult phases of the large cat tapeworm *Hydatigera (Taenia) taeniaeformis,* have shown it to follow a specific pattern during development with characteristic "breaks" associated with physiological change. The larvae showed a decrease upto the stage of infection of the adult after which there was a rapid increase, remaining thereafter more or less about the same level. These authors in 1960 have also shown in this parasite the dry weight/fresh weight ratio to vary between the immature and mature stages.

Information on changes in the chemical composition with the growth of monogeneans is not available (Brand, 1952, 1966) and it would be of considerable interest in view of the fundamental difference in the life history of this group, in being direct and is a continuous process of growth subsequent to attachment after the brief larval phase unlike other parasites which involve metamorphosis into different larval phases with one or more intermediate hosts before reaching the final hosts to complete the growth to adult form.

In the present investigation changes in the water, protein, non-protein N contents of the monogenetic trematodes *Capsala laevis* parasitizing the marine fish *Histiophorus gladius* were studied in relation to growth.

Material and Methods

Live specimens of the monogenetic trematode *Capsala laevis* obtained from the marine fish *Histiophorus gladius* formed the material for the investigation. These parasites were found on the ventro-lateral body surface of the host, matching well with their background and making them imperceptible on a cursory glance but are revealed of their presence on keen look. Specimens, thus collected, were brought to the laboratory within half an hour after collection, washed in distilled water. The adhering water was removed between filter paper and their fresh weights were determined. Subsequent to weighing, they were dried in a vacuum desiccator over concentrated sulphuric acid to constant weight and their dry weights were determined.

Individual specimens thus dried were analysed for its protein and non-protein N. Each specimen was ground in a mortar with 5% trichloroacetic acid and the homogenate was transferred to a centrifuge tube. Its volume was made upto 10 ml and centrifuged to separate the precipitate. The supernatant and the precipitate were analysed separately for their nitrogen content by the micro-Kjeldahl method of Steyermark (1951).

Water, protein N and non-protein N are expressed as absolute values (mg/animal) as well as in percentages. In addition, the non-nitrogenous matter for each of the specimens is calculated from its dry weight on the one hand and the protein N and non-protein N on the other and these values are expressed as above.

The procedure of Smith (1960) was followed for the chromatographic analysis. Fresh specimens of *Capsala laevis* were homogenized and the homogenate was hydrolysed with 6N HCl, 10 times its volume and refluxed at 110°C for 18 hours. The hydrolysate was evaporated over a boiling water bath to dryness and the dried residue was dissolved in 10% isopropanol. It was spotted and the components were separated by ascending two dimensional chromatography. The paper was dried and sprayed with 0.2% ninhydrin in butanol.

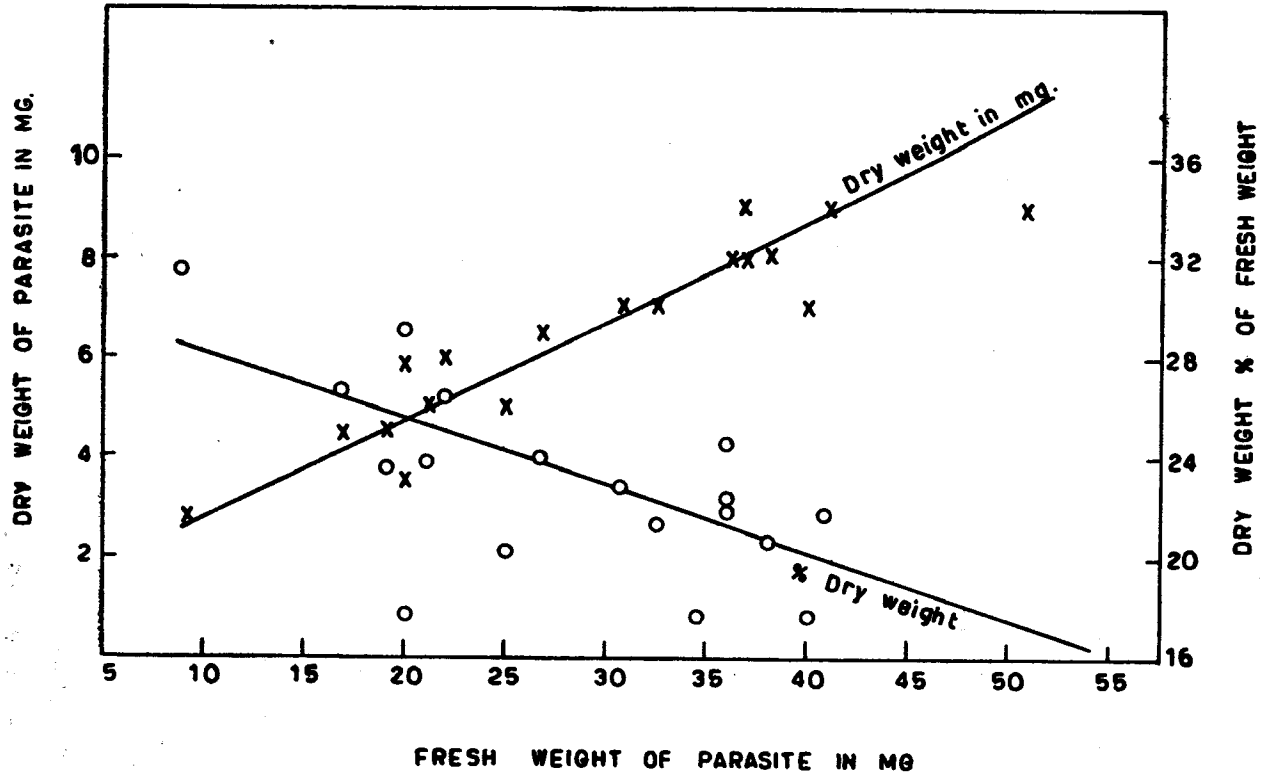


Fig. 1. Absolute and percentage values of dry weight as functions of freshweight during the growth of the monogenetic tremode *Capasala laevis*.

TABLE 1 *Percentage and absolute values of some chemical components of the monogenetic trematode Capsala laevis during growth*

Fresh wt. in mg.	Dry wt. in mg.	Dry wt. percentage of fresh wt.	Water content in mg.	Percentage of water of fresh wt.	Non-protein nitrogen percentage mg/animal	Non-protein nitrogen percentage of fresh wt.	Non-protein nitrogen percentage of dry wt.	Protein nitrogen mg/animal	Protein percentage of fresh wt.	Protein percentage of dry wt.	Non-nitrogenous matter in mg/animal	Non-nitrogenous matter in percentage of fresh wt.	Non-nitrogenous matter in percentage of dry wt.
9.0	2.8	31.12	6.2	68.88	0.081	0.9	2.9	0.339	25.000	75.625	0.600	6.7	21.4
17.0	4.5	26.47	12.5	73.53	0.202	1.2	4.5	0.426	15.625	59.375	1.635	9.6	36.3
19.0	4.5	23.68	14.5	76.32	0.157	0.8	3.5	0.387	13.000	52.125	1.924	10.1	42.8
20.0	5.8	29.00	14.2	71.00	0.364	1.8	6.3	0.546	16.875	58.750	2.023	10.1	34.9
20.0	3.5	17.50	16.5	82.50	0.085	0.4	2.4	0.300	9.375	53.750	1.540	7.7	44.0
21.0	5.0	23.81	16.0	76.19	0.219	1.1	4.4	0.473	14.375	59.375	1.825	8.7	36.5
22.0	6.0	27.27	16.0	72.73	0.148	0.7	2.5	0.520	15.000	54.375	2.602	11.8	43.4
25.0	5.0	20.00	20.0	80.00	0.126	0.5	2.5	0.412	10.000	51.250	2.299	9.2	46.0
27.0	6.5	24.07	20.5	75.93	0.196	0.7	3.0	0.614	14.375	58.750	2.466	9.1	37.9
30.5	7.0	22.95	23.5	77.05	0.206	0.7	2.9	0.574	11.875	51.250	3.206	10.5	45.8
32.5	7.0	21.23	25.5	78.77	0.364	1.1	5.2	—	—	—	—	—	—
34.5	5.2	17.68	29.3	82.32	0.259	0.8	5.0	0.740	14.375	88.750	0.316	0.91	6.1
36.0	8.0	22.23	28.0	77.77	0.249	0.7	3.1	0.700	13.500	55.000	0.376	9.4	42.2
36.5	8.0	21.91	28.5	78.09	0.273	0.7	3.4	0.661	11.250	57.500	3.596	9.9	45.0
36.5	9.0	24.66	27.5	75.34	0.140	0.4	1.6	0.668	15.000	60.000	4.685	12.8	52.1
38.5	8.0	20.78	30.5	79.22	0.340	0.9	4.3	0.657	10.625	51.250	3.554	9.2	44.4
40.0	7.0	17.50	33.0	82.50	0.210	0.5	3.0	0.572	8.750	51.250	3.215	8.0	45.9
41.0	9.0	21.95	32.0	78.05	0.249	0.1	2.8	—	—	—	—	—	—
51.0	9.0	17.65	42.0	82.35	0.287	0.6	3.2	0.782	10.625	54.375	3.825	7.5	42.5

The histochemical procedures for characterizing the proteins were adopted from Pearse (1968), details of which have been dealt with elsewhere (Ramalingam, 1971, 1972, a, b, c, and d).

Results and Discussions

The results on the water content, non-protein, protein and non-nitrogenous matter obtained in the different sized specimens are presented in Table 1.

The data reveal that the percentage of dry matter of *Capsala laevis* calculated against fresh weight ranges between 17.5% to 31%, the average being 22.82%. It is presented along with the results on percent of dry matter reported for digeneans for comparsion in Table 2.

TABLE 2. *Dry weight of trematode parasites in percent fresh weight compared with that of Capsala laevis*

Name	% dry matter	References
Digenea		
Paramphistomum cervi	28 - 30	Lazarus, 1950*
Fasciola hepatica	17.8, 17.3	Flury and Leob, 1926* Weinland and Von Brand, 1926.
Monogenea		
Capsala laevis	17.5 to 31 (22.82)	

*Cited in Brand (1952, 1966).

The protein content of parasites often has been calculated, as is customary for free-living organisms, by multiplying the experimentally determined N content by 6.25 or one of the other conventional factors. Thus earlier studies on the "protein" content of helminth parasites have been based on total N. of the species. Though this procedure undoubtedly gives a fairly accurate value in many instances, its validity is open to question, as has been expressed by Reid (1942) and Campbell (1960) who have pointed out that such a procedure, based on total N, of protein due to the large percentage of N being contributed NPN. In cestodes Salisbury and Andersen (1939), Eisenbrandt (1938) and Campbell (1960), found 10 to 16% of the total N to consist of non-protein N. In view of these the protein N values of the parasite *Capsala laevis* were determined separately.

The results obtained, on protein in *Capsala laevis,* is expressed of dry substances and it showed percent a range from 88.75 to 51.25, the average being 59.53. These are presented in Table 3 along with the results reported for digenetic trematodes for purposes of comparison.

The absolute values of non-protein nitrogen varied from 0.081 to 0.364 mg whereas the protein N varied from 0.339 to 0.782 mg per animal in the weight

range analysed. The non-protein N that is calculated as % of total N showed a range of 13.89 to 40%, the average being 27.77%.

The difference obtained after subtracting the total N from dry weight is considered as non-nitrogenous material which wuold include other organic substannces and inorganic materials. The absolute values of the non-nitrogenous material showed a range of 0.6 to 4.685 mg per animal in the weight range analysed, the average being 2.51 mg.

TABLE 3. *Protein content of trematode parasites compared with that obtained on Capsala laevis*

Name	Protein in % of dry substances	References
Digenea		
Fasciola hepatica	58	Weinland and Brand, 1926
Fasciola gigantea	67	Goil, 1958
Gastrothylax crumenifer	49	Goil, 1958
Paramphistomum explanatum	53	Goil, 1958
Monogenea		
Capsala laevis	88.75-51.25 (59.53)	

A perusal of the data on the changes in the chemical entitles in relation to increase in weight of the parasite, presented in Table 1, provides an insight into the pattern of changes in these which becomes very much clearer on being plotted. In Fig. 1 the absolute value of dry weight and % age of dry weight are plotted against fresh weight. It reveals that while dry weight increases the percentage of dry weight decreases whereas with the increase in fresh weight, there is also increase in dry weight as percentage of fresh weight.

However the absolute values of water, non-protein nitrogen, protein nitrogen and non-nitrogenous matter showed a progressive increase with increase in fresh weight, at different rates (Fig. 2). Evidences for similar differences in the rates of increase in the various chemical entities with increase in weight can be had from the patterns of increase in the protein, phosphatides cerebrosides sulphatides in rat brain during growth (cited in Needham, 1942).

Next to water, protein is known to be the major constituent of living organisms. In the normal environment characteristic of the species, organisms tend to maintain the water content at a constant level referable to some basic relationship such as the water/protein ratio (Nicol, 1960). A knowledge of the extent of water content as well as protein/ water ratio and their relation with increasing size would be of considerable interest.

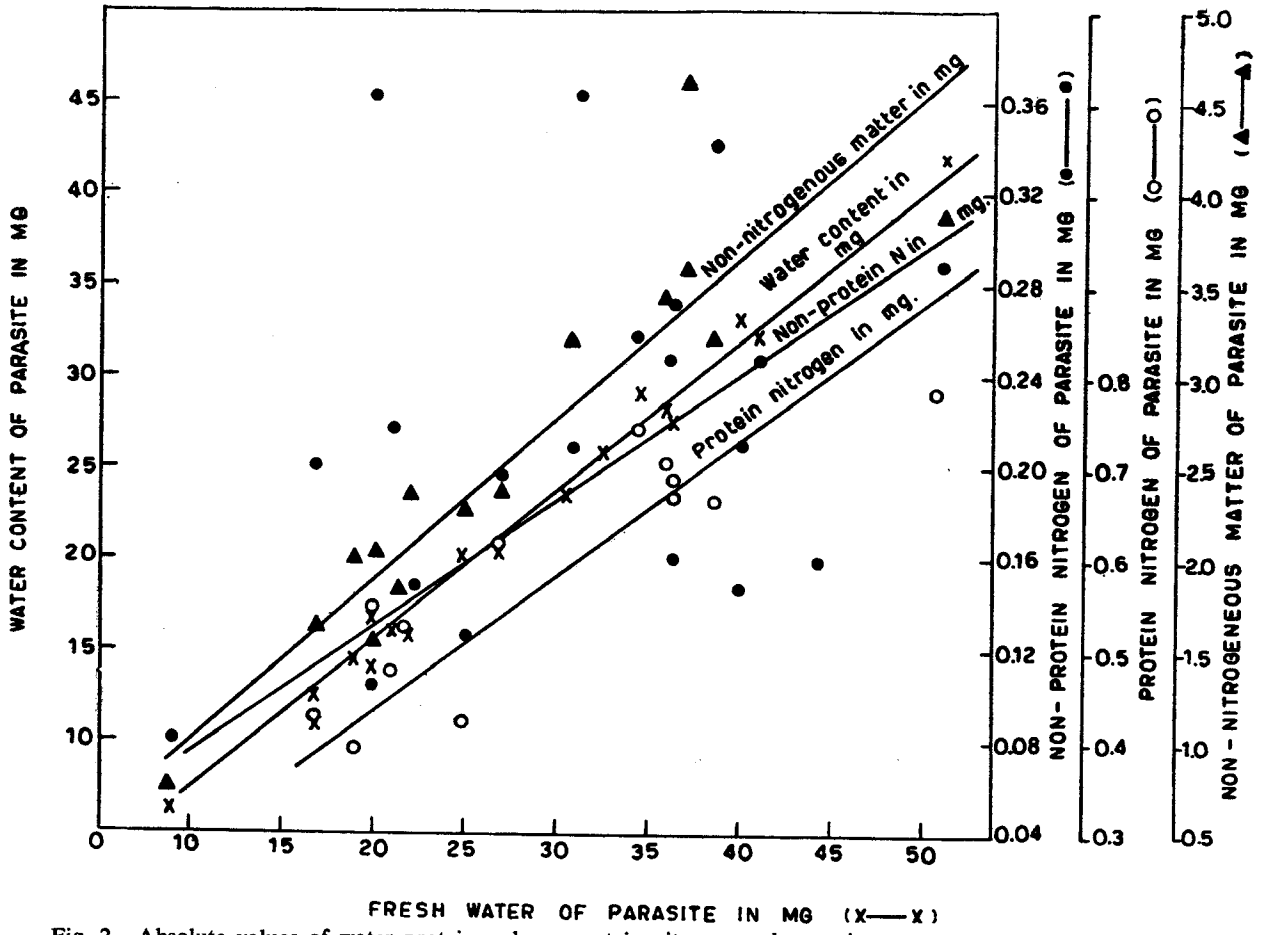


Fig. 2. Absolute values of water protein and non-protein nitrogen and non-nitrogenous componants (expressed as mg/animal) as functions of freshweight during the growth of the monogenetic trematode *Capsala laevis*.

It is seen from Fig. 3 the percentage values of non-protein nitrogen decrease in relation to growth when the percentage of water content shows an increasing trend. Such an inverse relationship has been noticed with reference to blood protein and percentage water content of blood of millipedes (Ravindranath, 1972).

The foregoing study reveals the trends in the variation of the major chemical constituents in relation to growth. The total amount of all these components increase with age. But there are differences in their increasing trend. It may be noted that protein is continuously synthesized and added to tissues, whereas non-protein nitrogen falls in aging adults. It may not be unreasonable to infer that free amino compounds such as amino acids, phenolic amines and amino sugars may fall in their total amounts after the attainment of maturity of these parasites. Their fall may reflect their utilization in the synthesis of glycoproteins involved in the egg shell (Clegg, 1963). The declining trend in non-protein nitrogen at later stages of growth with correlated increase in protein nitrogen would indicate that tissue non-protein nitrogen may be precursor for the tissue protein in aging adults. But in juveniles the sources may be from food or medium.

In the light of the above findings it would be of interest to know the qualitative nature of the protein. Preliminary electrophoretic observations made in the total homogenate *Capsala laevis* and *Pricea multae* reveal the heterogenity of proteins as has been reported in other helminths. Electrophoretic observations on the liver fluke *Fasciola hepatica* reveal the presence of at least six fractions (Thorsell, *et al.*, 1964). A similar heterogenity of proteins has been shown in the cestodes (Kent, 1948, 1957 a, and b).

Proteins have also been characterized by their amino acid composition (Bailey, 1950—cited by Young, 1963). Such characterization of the protein of helminths has not been attempted. Although amino acid composition of the different protein fractions have not been attempted in the present study, amino acid composition of whole *Capsala laevis* has been carried out by hydrolysing the homogenete of fresh mature specimens which revealed the presence of at least 17 amino acids, which are presented in Table 4 along with the data available on some helminth parasites to enable a comparison.

Yet another method of characterizing the proteins is by histochemical methods (Pearse, 1968). The reactive groups of both C and N terminal amino acids as well as the predominant amino acids can be identified by this method. Histochemical tests carried out on entire, fresh unfixed monogeneans reveal the presence of different kinds of proteins. Thus when *Pricea multae* parasitizing the gills of *Scomberomorus gottatus* was subjected to DMAB-nitrite test of tryptophane, the cuticle, clamps and tests showed intense positive reaction where-

TABLE 4. *Amino acids of some parasites compared with that obtained of Capsala laevis*

	Moneizia expansa Kent, 1947*	*Moneizia expansa Campbell, 1960*		*Thysanosoma actinoides* Campbell, 1960		*Cittotaenia perplexa* Campbell, 1960		Anuran iung fluke Vilar Alvanez 1955*	*Capsala laevis* fresh material hydrolysed
		PAA	NPAA	PAA	NPAA	PAA	NPAA		
Analine	+	+	+	+	+	+	+	+	+(1)**
Glycine	+	+	+	+	+	+	+	+	+(2)
Valine		+	+	+	+	+	+	+	+(4)
Leucine	+	+	+	+	+	+	+	+	+(4)
Iso leucine	+	+	+	+	+	+	+		+(4)
Proline		+	+	+	+	+	+		+(2)
Phenylalanine		+	+	+	—	+	—		
Tyrosine		+	+	+	+	+	—		+(4)
Serine		+	+	+	+	+	+		+(1)
Cystine		+	+	+	+	+	+	+	+(3)
Threonine		+	+	+	+	+	+		+(1)
Cysteine		+	+	+	+	+	+	+	
Methionine		+	+	+	+	+	+		
Arginine	+	+	+	+	—	+	—		+(2)
Lysine		+	+	+	+	+	+		+(4)
Histidine	+	+	+	+	+	+	+		
Aspartic acid	+	+	+	+	+	+	+		+(2)
Glutanic acid	+	+	+	+	+	+	+		+(3)
Hydroproline									+(4)
Tryptophane		+	—	+	+	+	—		
Ornithine		+	+	+	—	+	—		+(2)
Unidentified		1	0	1	0	1	0		+

PAA = Protein amino acids. NPAA = Non-protein amino acids. (*cited by Brand, 1966);
**No. given in bracket indicates the intensity of the spots.

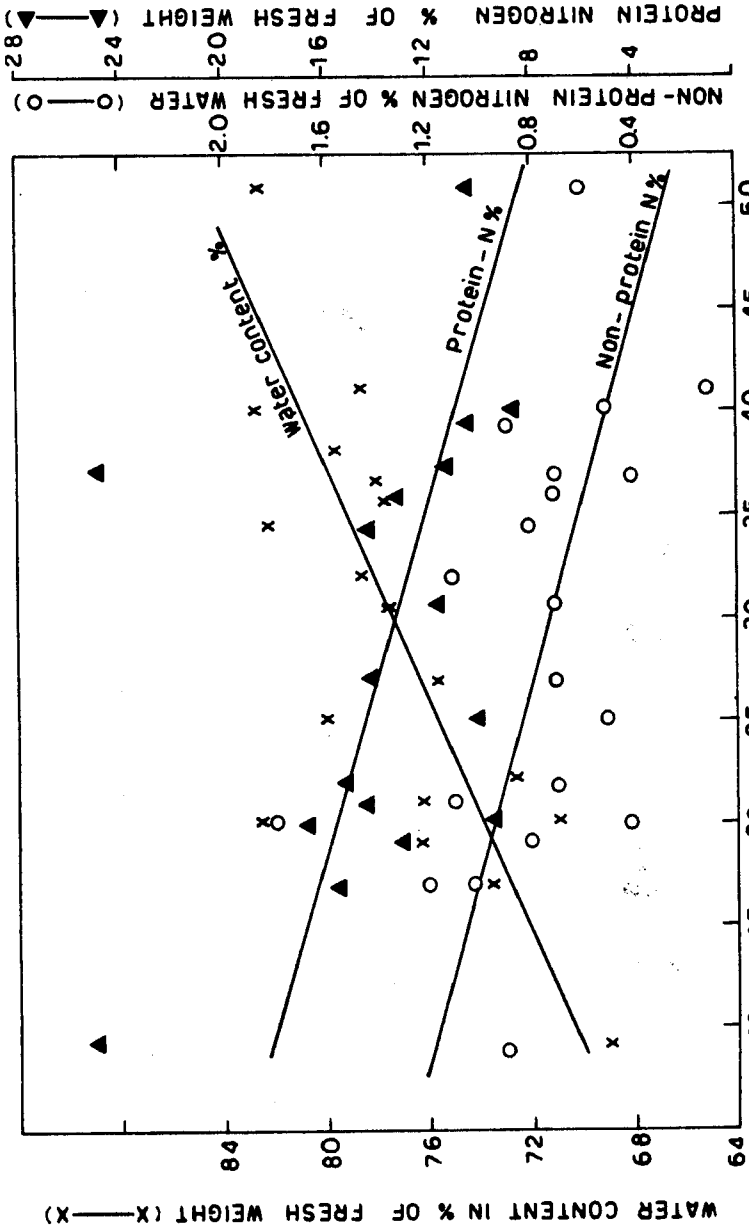


Fig. 3. Percentage of water, protein and non-protein nitrogen as functions of freshweight during the growth of the monogenetic trematode *Capsala leavis*

as vitelline cells, egg shells and hamuli were negative to it. Further characterization of clamp protein showed its similarity to the tegumental spine protein of *Fasciola hepatica* (Ramalingam, 1972c) (Table 5). The characters may be summarized as follows :

1. They have an affinity to acid fuchsin of Mallory's stain.
2. Their staining was not affected by detanning agents such as sodium hypochlorite, diaphanol.
3. They are positive to Millon's, Morner's and Xanthoproteic tests.
4. They stained with basic dyes such as Toluidine blue-light green pH 7.2 and methylene blue.
5. They showed bluish fluorescence in U.V. light, which was not affected by lipid solvents indicating the presence of dityrosine.

Clamps of these monogeneans were negative to sulphydryl and disulphide groups, as well as in the absence of chitin and tanning. The clamp protein of these monogeneans is thus in agreement with the report of Lyons (1966) on the monogeneans of the fishes of temperate waters. The problem posed by the above author regard ng the hardening of clamp protein is solved by histochemical methods (Ramalingam, 1972*a*). Regarding other skeletal elements of monogeneans preliminary studies reveal some similarities as well as differences which will be published elsewhere.

A compar son of the skeletal proteins of these monogeneans with the egg shell protein synthesized and secreted by the parasites may reveal remarkable differences.

The egg shell is devoid of tryptophane and contains sulphur and dityrosine (Ramalingam, 1972 d) very similar to egg shells of *Fasciola hepatica* (Ramalingam, 1972 b). It is of interest to note that in these the egg shells are devoid of phenolic tanning (Table 6) (Ramalingam, 1972 b, d). It has been suggested in the above studies that the peloxidase present in them may bring about linking of the tyrosine monomers lead ng to hardening of the egg shell.

The origin and source of the egg shell protein and the enzymes are not clear at present. It is likely that the peroxidase responsible for dimerization of tyrosine is synthesized by "serosen" cells of Mehlis' gland. A support to this suggestion is derived from the salivary glands of human being wherein serson cells have been attributed to formation and secretion of enzyme whereas mucosen cells are responsible for the secretion of mucoproteins (Bevelander, 1970). Presence of similar dimorphic cells is not uncommon in Mehlis' gland of helminth parasites (Ujiie, 1936; Williams, 1960; Gonnert, 1955, 1962; Kohlman, 1961; Loser, 1965; Ebrahimzadeh, 1966 and Threadgold and Irwin, 1970). Preliminary observations support the above possibility. Yet another

TABLE 5. *Results of tests for proteins on clamp sclerites of monogeneans Pricea multae, Pseudomicrocotyle sp. from the gills of Scomberomorus guttatus*

Tests	Results
Mallory's triple stain (Lillie, 1954)	Red
Mallory's after sodium hypochlorite treatment	Red
Millons	+
Xanthoproteic	+
Morners	+ (dark green)
DMAB – Nitrite	+
P–diphenyldiamine	—
Ninhydrin	+
Bromophenol blue (aqueous)	+
Sakaguchi's reaction for arginin	—
Nitroprusside	—
Lead acetate	—
Performic acid – Alcian blue	—
Toluidine blue – light green in buffer of pH 7.2 (Andersen and Weis-Fogh, 1964)	Sapphire blue
Methylene blue in glycerol-water (1:1) (Andersen and Weis –Fogh, 1964)	Blue
Fluorescence in U. V. light at 366 nm (Andersen and Weis –Fogh, 1964)	Bluish white
Fluorescence in U. V. light at 366 nm after ammonia vapour (Andersen and Weis–Fogh, 1964)	Intense blue
Fluorescence in U. V. light at 366 nm after hot pyridine	Bluish white
Fluorescence in U. V. light at 366 nm after treatment in iodine (Udenfriend, 1962)	—

+ = positive ; — = negative.

source of the protein and enzyme of egg shells could be vitelline cells. In the vitelline cells number of authors reported the occurrence of phenol oxidase (Smyth, 1954, 1956; Smyth and Clegg, 1959; Burton, 1963; Ma, 1963; Wilson, 1967; Clegg and Smyth, 1968; Coil, 1969 and Threadgold and Irwin, 1970) but it was not characterized. In the monogenean *Pricea multae* it has been character zed in detail. The enzyme is substrate specific. It acts only on catechol, hydroquinone and pyrogallol and not on L-tyrosine, DL-3, 4-dihydroxy phenylalanine (dopa), and protacatechuic acid.

TABLE 6. *Staining and histochemical reactions obtained on the mature brown egg shells of a monogenean Pricea multae and a digenean Fasciola hepatica*

Tests	Egg shells of	
	P.multae	*F. hepatica*
Mallory's triple stain (Lillie, 1954)	Refractile	Refracticle
Mallory's after sodium thioglycollate	Red	Red
Millon's	+	+++
Xanthoproteic	+	+++
Morner's	+	+++
Lead acetate	dark green	dark green
Sodium nitroprusside	+	+
Performic acid Alcian blue	+	+
Ferric ferricyanide	+	+
DMAB – nitrite	—	—
Aqueous bromophenol blue	Red	Red
Ninhydrin	Violet	Violet
	+++	++
Argentaffin	+	+
Ferric chloride	—	—
Toluidine blue (Ramalingam and Ravindranath, 1970)	—*	—*
Dimethyl para diphenylene diamine (after heating) Feigl, 1960.	—	—
Catechol method of Smyth, 1954	++	++
Catechol method after heat treatment at 80°C for 10	—	—
Toluidine blue-light green in phosphate buffer pH 7.2	purple	saphire
Methylene blue in glycerol-water (1:1)	+ blue	+ blue
Fluorescence in U. V. light at 366 m u wavelength	Yellow	Yellow
Fluorescence in U. V. after treatment in iodine	—	—
Fluorescence in U. V. after treatment in sodium thioglycollate	bluish	bluish
Fluorescence in U. V. after treatment in sodium thioglycollate followed by iodine	—	—
Fluorescence in U. V. after catechol	—	—

*Showed no green metachromasia

+ = positive ; — = negative ; +++ = intensely positive.

In the absence of monophenolase activity, the phenolase of *Pricea multae* agrees with the enzyme commission nomenclature (EC 1.10.3.1), (o-diphenol: oxygen oxidoreductase) in showing an affinity to di-and polyphenols. However, it differs in being specific only to deaminated and decarboxylated di-and polyphenols as well as in its affinity for para diphenol.

The substrate-specificity of the phenolase of *Pricea multae* strongly recalls the phenolase found in the unhardened cuticles of insect *Periplaneta americana* and the larval cuticles of *Calliphora vomitoria.*

The enzyme exists as a proenzyme (Ramalingam, 1970) and is activated by detergents, lipid solvents and protein denaturing agents. The enzyme exhibits maximum activity between 45° and 55°C and at a pH range between 7.0 to 7.4.

Fixatives such as formalin and ethanol activate the proenzyme whereas activated enzyme is inhibited by formalin.

Inhibitors such as potassium cyanide, sodium azide and phenyl thiourea activate the latent enzyme but inhibit the activated enzyme. The double action resembles that of sodium azide on latent mitochondrial ATPase (Ramalingam, 1971). Attempt to characterize the protein of vitelline cells is in progress. An interesting feature that has been observed in monogenean vitelline cells is that they contain glycoprotein in the early stages whereas in later stages it showed no sign of it. Further work is in progress regarding the significance of such chemical metamorphosis of protein.

I thank Dr. M. H. Ravindranath for the keen interest he evinced in this invest gation.

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SOME ASPECTS OF THE MARINE LIVING RESOURCES OF THE INDIAN CONTINENTAL SHELF

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ABSTRACT

The continental shelf around India has played a significant role in the traditional exploitation and utilisation of living resources. Its physical characters, expanse and formation are discussed. These factors, apart from governing and modifying benthic production, are also responsible for supporting primary and secondary production in bathy-pelagic and pelagic zones.

At the present time the exploitation of fish in India, out of the total area of 447.6 thousand sq. kilometers of shelf, is limited only to a small part of the continental shelf within a few kilometers from the coast line. The present fish catch can be doubled with the existing technology but require greater inputs.

The production rates in selected areas have been discussed. The coastal productivity characteristics and the differences in magnitude of production in the shelf along the east and west coast of India have been brought out. It is suggested to start regional and national programmes along the shelf for each ecosystem and utilisation of backwater and estuarine areas of about 74,000 lac acres for aquaculture and intensive food production.

INTRODUCTION

The oceanic food resources have been attracting greater attention during the last few decades. Man has been planning to obtain increased quantity of food from sea. Apart from augmenting exploitation of the traditional food items newer items are being looked for. Valuable food items which are available but not fully exploited are receiving greater attention. It is in this aspect that the resources of the continental shelf have a very important role for development in immediate future. In view of this, exploitation and research of continental shelf is stressed for gathering increased knowledge of bottom and its resources. The shelf, apart from being a direct substratum for benthic animals, is also a store house for dead and non-living matter which, in turn, influence all production chains starting from breaking down of dead materials and enrichment process through primary and secondary level to the fishery resources.

The continental shelf around India (upto 200 m depth) has an area of 447.6 thousand sq. kilometers; out of this the east and west coasts have an area of 90.8 and 310 thousand sq. kilometers respectively and the islands—Andaman, Nicobar and Laccadives together—have an area of 46.8 thousand sq. kilometers (Chatterjee *et al.*, 1968). The continental shelf on the west coast is more than three times as large as that of the east coast and a similar trend is reflected in fish landings also (Panikkar and Jayaraman, 1966). It is very well known that three-fourth of the total fish catch is landed on the west coast and very good trawling grounds exist off Bombay, Saurashtra and Kerala coasts (Panikkar, 1969). Apart from the expanse of the shelf the west coast has the environmental conditions which are specially favourable for high production. The well-known causes of high productivity of shelf region and coastal areas (including hydrography and nutrients) are not discussed here but it is proposed to define broad perspectives for research goals for obtaining higher yields from the Indian continental shelf.

From the later half of the last century till now considerable faunistic work of high scientific quality has been done, particularly during the last two decades. The coastal laboratories of the University departments, State and Central Fisheries Organisations have contributed a great deal although most of these studies were limited to a small geographic area on a particular subject. The work done so far broadly relates to the following two categories :

1. Faunistic and taxonomic studies.
2. Ecology, biology and distribution of commercially important species of various groups.

Highly specialised work has been done in these fields but all these studies now need to be co-ordinated for a comprehensive study of the bionomics and ecology of the shelf and a study of the ecology of trawling grounds along the shelf.

I express my sincere gratitude to Dr. Panikkar for initiating and developing an environment for oceanographic research in the country. I also thank Dr. S. Z. Qasim for organising through the good office of the Marine Biological Association of India the publication of this commomoration volume which is a fitting tribute to Dr. N. K. Panikkar.

The Biological Production and The Continental Shelf

a) *Chlorophyll :* Studies on biological production in the Indian Ocean covering extensive areas were undertaken during International Indian Ocean Expedition but the information on the shallow coastal areas of the continental shelf is lacking. Important contributions in the field have been made through various national programmes including those of America, Australia, Japan, Russia

and India. Based on such data chlorophyll values (mg/m²) around Indian coast are shown in the Figs. 1 and 2 (Humphrey, 1966; Zernova and Ivanov, 1964).

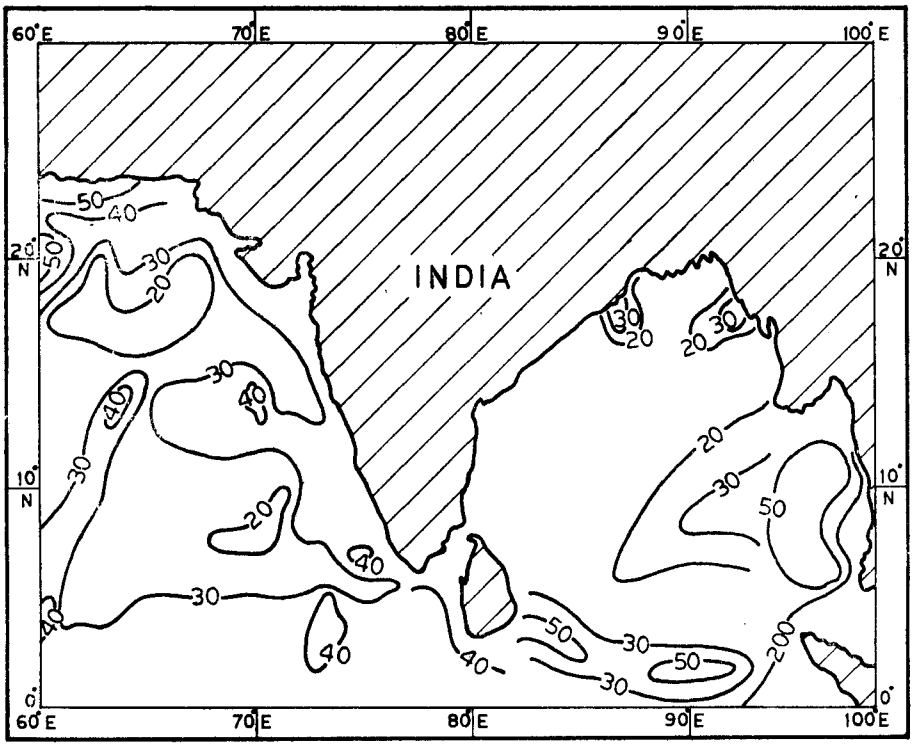


Fig. 1. Distribution of chlorophylls around Indian coast during north east monsoon (mg/m²).

Patterns of the values of biological production extrapolated from the above mentioned works present a general idea but it needs to be studied in detail regarding its geographical localisation, seasonal variation etc. In this direction beginning has already been made and at National Institute of Oceanography similar work is in progress at few locations along the central west coast of India.

Evidently large parts in the Indian Ocean and the continental self support a sizeable plankton crop throughout the year although a phenomenon comparable to spring bloom of phytoplankton of the temperate oceans does not appear to exist. However, the quantity of this crop is considerably influenced by monsoons and seasonal high production does occur. Studies by Saijo (1964) and Saijo and Takesu (1965) for the top 50 meter layer in the Indian Ocean show

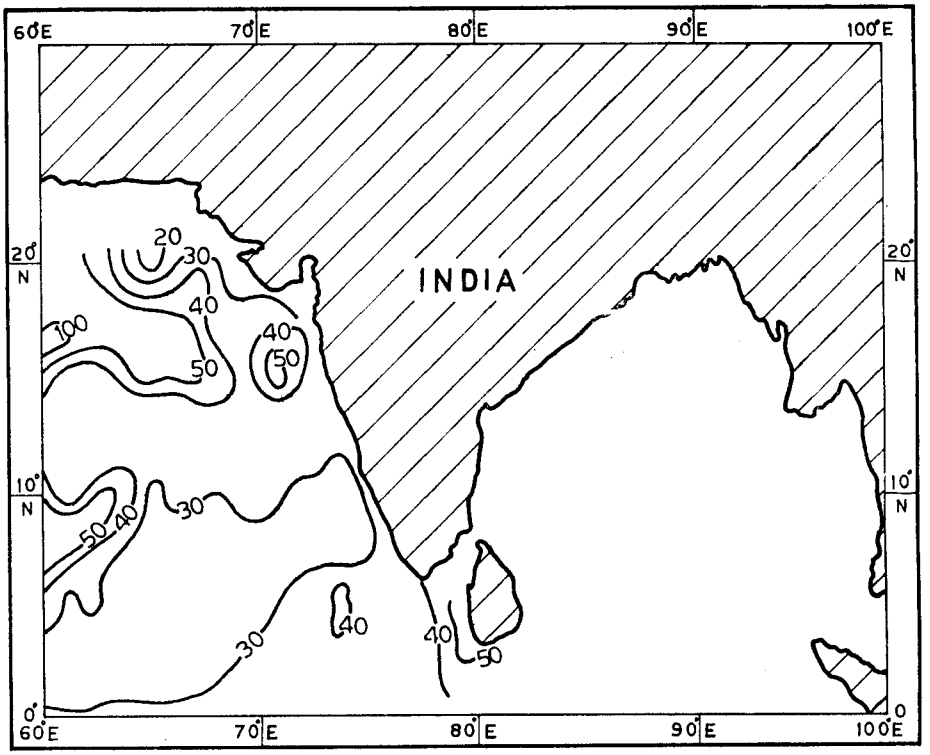


Fig. 2. Distribution of chlorophylls around Indian coast during south west monsoon (mg/m^2).

that the significance of netplankton in photosynthetic activities is generally very small. On the other hand phytoplankton with the size between 0.8 and 90 μ plays the major share in the production activity. He further stated that the studies on the size distribution of phytoplankton will give an important basis for the explanation of the geographical and seasonal variation of primary production. Similar studies on the Indian continental shelf are also necessary to enable us to understand the seasonal and geographical variation in pelagic fish yields.

b) *Primary Productivity:* Primary productivity has been extensively studied during International Indian Ocean Expedition in the open parts of the Indian Ocean and we have a genenral picture from Ryther *et al.* (1966). For coastal areas some data is available based on the work carried out by Central Marine Fisheries Research Institute and National Institute of Oceanography. The production values are higher on the shelf and decrease towards the open sea. The mean value on the western continental shelf is 1.19 g C/m^2/day upto

50 m, from 50-200 m it reduces to 0.43 g C/m²/day. On the east coast the production on the shelf is 0.63 g C/m²/day. Beyond the continental shelf the difference in the rate of production in Arabian Sea and Bay of Bengal are comparatively less, the mean values being 0.18 and 0.19 g C/m²/day respectively. However, there are pockets of high production such as Wadge Bank where the production reached to 4.55 g C/m²/day. This shows that these areas are comparable with most productive areas of other oceans. Based on these values it has been estimated that the potential resources over the entire shelf region of both the coasts would be 2½ to 3 times the present yield (Nair *et al.*, 1968). The work in this field is of very recent date and it needs extension particularly along the shelf.

c) *Zooplankton studies:* The zooplankton studies have a special role in production-oriented research in that they help in suggesting productive areas. Chidambaram and Menon (1945) have shown that along Malabar and South Kanara coasts the fish landings are directly proportional to the quantity of plankton. Keeping in view of the extensive interest of many organisations in this field, it is necessary to re-orient their research for a common national objective to achieve maximum output.

Considerable work has been done by different research laboratories on the various aspects of plankton research and a comprehensive bibliography has been published (Prasad, 1964). Subsequently during International Indian Ocean Expedition, plankton studies were given priority. Based on this work, plankton atlases have been published on total zooplankton biomass in the Arabian Sea and Bay of Bengal and the Indian Ocean; distribution of copepoda and decapod larvae and the distribution of fish eggs and larvae in the Indian Ocean (Panikkar, 1968, 1970).

The studies on zooplankton biomass for the period April - October off Cochin indicate that the production is high along the coast and decreases towards offshore areas, the total biomass values along the coast are of the order of 30 g/m² and gradually decrease to 10 g/m². The region west of 60°E is as area of very low production.

Further, the Gujarat coast, from the Gulf of Kutch to the Gulf of Cambay, has low plankton biomass, of the order of 5 to 10 g/m². However, during night in the same region, a progressive increase in biomass was noted towards the rim of the continental shelf. The summarised picture of the zooplankton biomass is given in Fig. 3. Seasonal and geographical variations exist in zooplanktonic biomass along the continental shelf on the west coast but this entire shelf is more productive than the central and the central western parts of the Arabian Sea. Similarly in Bay of Bengal localised areas of high biomass exist off West Bengal, off Andhra coast and in the Gulf of Mannar and Palk Bay. On

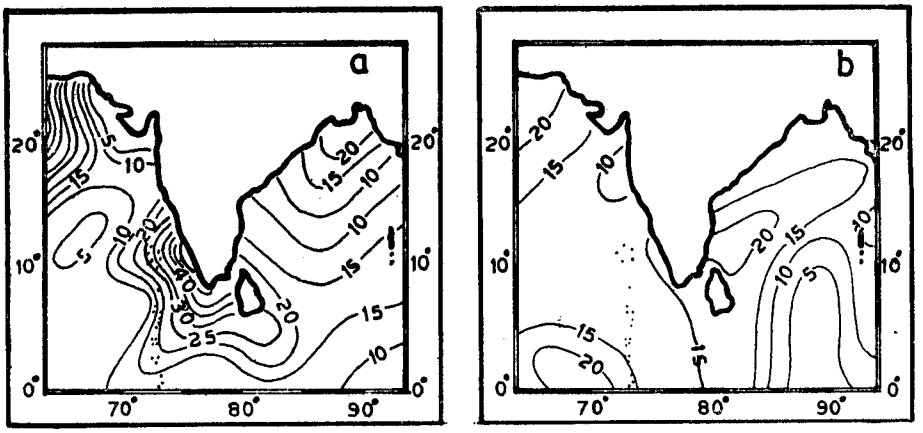


Fig. 3. Distribution of zooplankton biomass (mg/m^2)
a) South west monsoon b) North east monsoon.

the basis of organic production and zooplankton studies Prasad *et al.* (1970) estimated that fish production in the Arabian Sea should be at least three times higher than that in the Bay of Bengal.

Similar detailed picture of production estimates for coastal areas is not available at present; therefore, immediate requirement is to take up productivity studies along the Indian continental shelf both in the Arabian Sea and the Bay of Bengal and around the Islands. At least in selected regions work should be started immediately.

Fish Production on the East and the West Coasts

The continental shelf contributes a large portion of the fish catch. In India marine fish landings during 1970 was 1.07 million tons and most of this was fished from a narrow coastal belt. The world catch during the same year was 69.3 million tons and a major part of this came from the continental shelf (FAO, 1971). In India, fishing is mostly restricted to the 50 m depth line. In some cases localised fishing is carried out beyond 50 m depth but this effort at national level is almost negligible. Evidently the entire marine fish catch including pelagic and demersal fisheries comes from a small fraction of the shelf area and a larger shelf area between 50 and 200 m depth zone remains practically unexploited.

Sardines, mackerels and tunas are the major component of the commercially important fishes. These on an average (1967-68) constitute around 51% of the marine fish catch. On the west coast they constitute 56% of the catch as against 23% on the east coast. On the west coast where fishing effort and fish landings are higher, demersal fish landings are comparatively less and the major

share is represented by sardines and mackerels. On the east coast, position is modified and demersal fisheries constitute a major part of the catch. The comparative importance of the pelagic and the demersal fisheries on the two coasts and the percentage composition of various groups of fish are shown in Fig. 4.

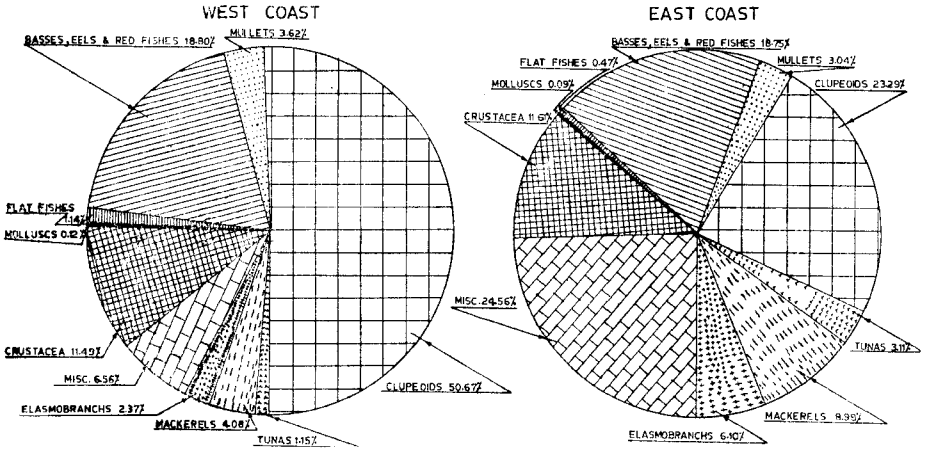


Fig. 4. Composition of fish landing on the Indian coast. (Average 1967–1968)

Though well-known differences exist in the quantity of fish landings on the east and the west coast the important groups constituting the demersal fishery on the two coasts are the same. However, regional differences are exhibited in abundance of elasmobranchs and the crustacean catch on the west coast is significantly higher. Minor differences exist in the other groups also. This group composition and their abundance also influence the rate of trawl catches. The trawl catches in kg per hour of trawling along different parts of the two coasts are shown in Fig. 5.

The average catch per hour is about 50 to 60 per cent lower on the east coast. If catch per hour is an index of the abundance of fish, the magnitude of difference in fish landings along the two coasts should be less. Other biological differences between the Bay of Bengal and the Arabian Sea discussed earlier also cannot completely account for the differences in the quantity of landings. There are other contributory factors as well, which result in low fish landings on the east coast. Comprehensive picture on number of fishing villages, active fishermen, fishing crafts, mechanised vessels, total fishing efforts and the trawl catches on the two coasts is given in Fig. 6. It is seen that the major differences exist in the area of the continental shelf and the number of mechanised vessels. The area of the continental shelf for trawling is not a limiting factor but it is the small number of mechanised fishing boats on the east coast that are responsible for the low catch. Thus a greater input in the form of mechanised vessels and ancillary facilities are required to increase catches from the Bay of Bengal. In this case the example of Tamil Nadu is very illustrative, where with the introduction of mechanised vessels the fish landings increased

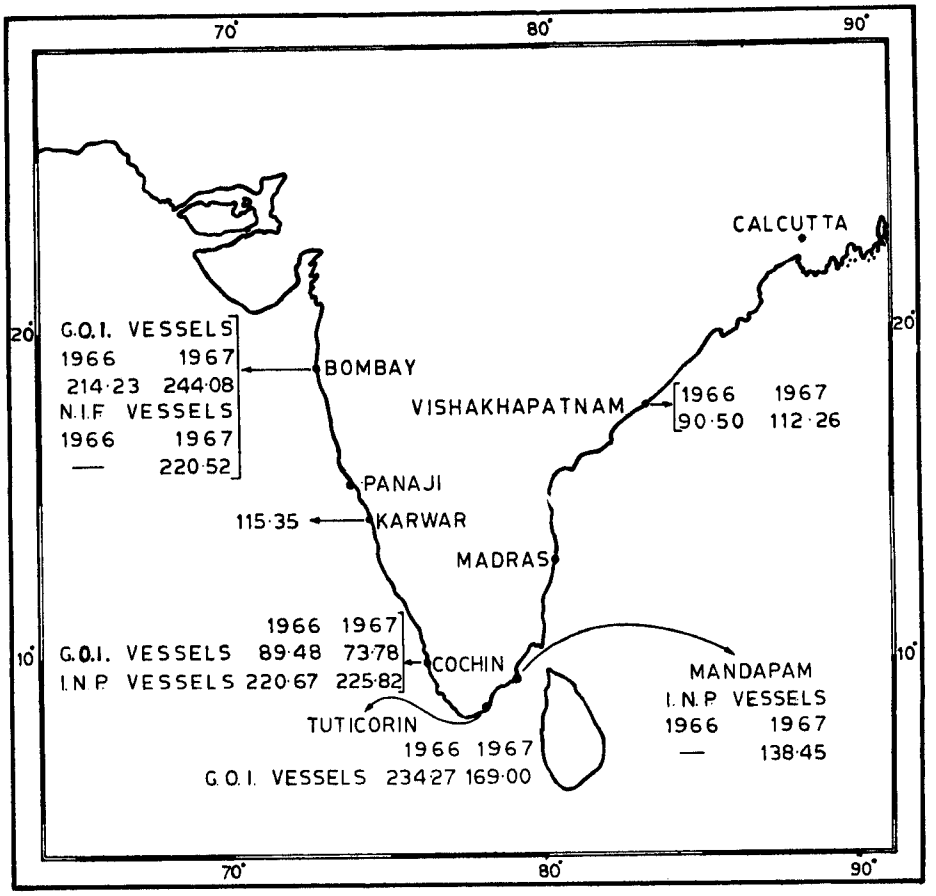


Fig. 5. The trawl catches in kg./hour (1966; 1967) along continental shelf.

four times between the years 1950-51 and 1965-66, and more offshore grounds are reported which are estimated to have a stock of 84,000 tons (Chacko, 1968). Good resources for elasmobranchs have been reported on the east coast and in areas around Andaman and Nicobar islands (James, 1968). Off Vishakhapatnam three times increase in the catches of the cat fish, *Tachysurus* sp. is estimated by the use of powered vessels (Sekharan, 1968). Exploratory fishing by medium sized trawlers off Tuticorin have shown existence of rich fishing grounds between Lat. 8°00' - 9°10'N and Long. 77°30' - 79°00E (Pai and Pillai, 1968). The presence of such productive grounds and increase in fish catch with increase in the number of powered vessels indicate that the fish resources in the Bay of Bengal are under-exploited. It is estimated that with the greater number of modern fishing boats the production from the same area can be increased two folds. Similarly the catches from the shelf area on the

west coast can be doubled. To achieve this, the essential requirements are greater inputs of fully equipped mechanised vessels, exploitation of the demersal fisheries of the upper continental slope and shelf edge (Silas *et al.*, 1968) between 100 and 426 m depth zone and greater diversification of catches.

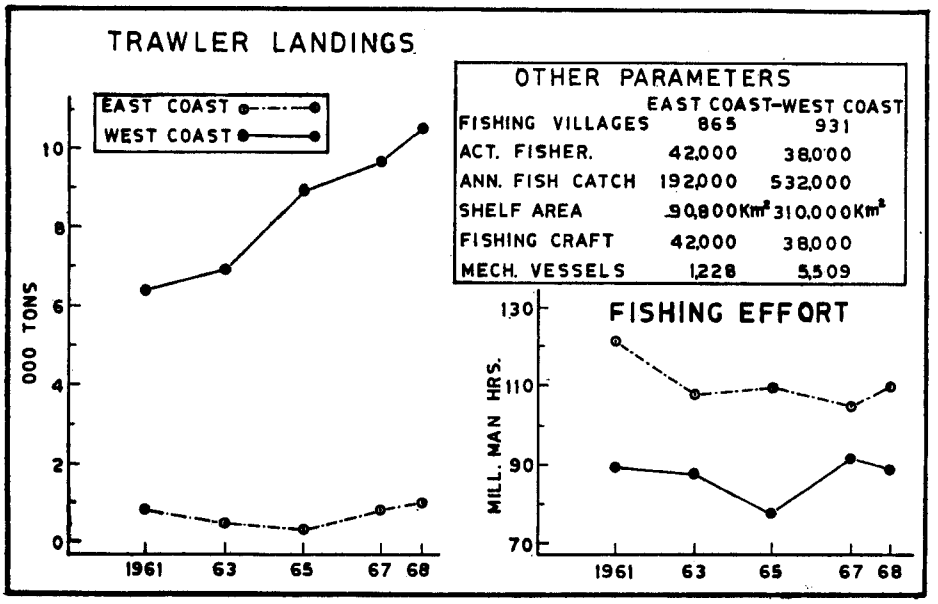


Fig. 6. Fishing parameters and trawler landings on the east and the west coast of India.

Fishery Potential

Various estimates of the fishery potential of the Indian Ocean put the resources potential between 4 and 40 million tons. However at the present level of exploitation yield has been estimated around 11 million tons (Prasad *et al.*, 1970) as against present production of 2.7 million tons. Detailed estimates for production of the commercially important fish groups on the Indian continental shelf are not available. However, based on a study conducted by Food and Agriculture Organisation of the United Nations (1970) the estimates of potential for demersal fish and crustaceans are given below in the table.

Table 1.

Catches and estimated potential of demersal fish and crustaceans (in 1,000 tons).

Region	Demersal Fish		Crustaceans		Total	
	Catch	Potential	Catch	Potential	Catch	Potential
Eastern Indian Ocean	575	1000	68	110	643	1110
Western Indian Ocean	504	1700	22	140	526	1840
Total Indian Ocean	1079	2700	90	250	1169	2950
Possible increase in catch as % of the potential		60%		64%		60.3 or 1781

Based on the present rates of exploitation and various estimates for future potential, broad estimate for increase in India's share as percentage of the total potential are also indicated in the table 1. It is expected that by 1985 about 1.8 million metric tons of demersal fish and crustaceans can be harvested.

Other independant estimates for additional potential of fish production in million metric tons are 0.21 for inshore region upto 20 m depth, 0.60 for offshore region from 20 to 80 m depth and 1.80 for deeper part of the shelf 80 - 200 m. Thus the total additional potential for the continental shelf upto 200 m depth is 2.17 million metric tons. Data suggest that the fisheries of the continental shelf are under-exploited and bold initiative and finance are necessary for technological expansion and better utilisation of the potential.

Proposed National plan for Multidisciplinary Ecological Concept

The development and pre-investment survey of the living resources of the shelf is a gigantic task. In order to precisely determine potentialities, maximum sustained yield and the pattern of seasonal production, it is absolutely essential to develop a multidisciplinary ecological concept at national level. This should be worked throughout the year in a geographical grid to cover all the coastal ecosystems. The investigations should be undertaken along transects suitably worked out to give a comprehensive coverage from the coast line to 200 m depth. A series of stations should be worked along each transect and at each station observations should be taken at different depths from surface to botton.

The ecological studies in geographical expanse and time series at each point of observation should generally include bacteria, epibenthos, demersal and pelagic populations and should be supported by primary and secondary productivity and environmental studies including nutrients and hydrology. This will enable us to demarcate different ecosystems, the knowledge of which is absolutely essential for further expansion and management of marine living resources including fisheries. These investigations will also help in solving outstanding problems, like the extent and intensity of upwelling and the ecology of some of the important coastal complexes which support pelagic fisheries of mackerel and oil sardines.

Backwaters and Estuaries

Backwaters and estuaries represent a transitional zone between fresh water and sea and form an important integral part of the marine environment. Apart from being productive they are the breeding grounds for some species, nursery for larval forms and also contribute to the productivity of the adjoining areas. Certain lagoons have been reported to have primary productivity ten times higher than the adjoining sea (Blanc *et al.*, 1967). High rates of production have been reported from Cochin backwaters (Qasim *et al.*,

1969) and from Mandovi and Zuari Estuaries in Goa (Dehadrai, 1970 a and b). Backwaters unlike the open sea can be managed for mariculture to give high yields.

Extensive areas of backwaters and estuaries of about 74.4 lac acres exist all along the Indian coast (Mitra, 1970) and their statewise breakup is given in the Table 2 below:

TABLE 2. *Estuaries and Backwaters (Arae in lac acres)*

State	Backwaters	Estuaries
Andhra Pradesh	5.0	8.0
Gujarat	9.2	10.0
Kerala	5.0	1.0
Madras	2.0	1.0
Maharashtra	2.0	1.0
Mysore	2.0	0.5
Orissa	0.2	7.5
West Bengal	10.0	10.0
Total	35.4	39.0

These areas represent a very significant potential. On the east coast the fish production from Chilka Lake, a brackish water lagoon, yields on an average an annual fish catch of 3700 tons (Jhingran and Natarajan, 1968).

It is through the mariculture and intensive management of these backwaters and lagoons that manifold increase in production can be achieved.

IMPORTANCE OF ISLANDS

In recent years the islands in the Arabian Sea and the Bay of Bengal have received attention and their importance on food resources are being realised. The shallow submerged platforms and slopes of Andaman-Nicobar islands in the Bay of Bengal and the Laccadives in the Arabian Sea together have an area of 46,800 sq. km, which constitutes about 9.5% of the area of the Indian continental shelf but the fish landings from these areas constitute less than 1% of the marine fish catch of India. Evidently these are very much under-utilised.

Around Andaman and Nicobar islannds the fishing methods, crafts and gears used are indigenous and fishing is confined to narrow coastal belt on east coast of Andaman and neighbouring islands (Kumaran, 1968). During the International Indian Ocean Expedition R/V *Anton Bruun* had undertaken trawl survey in the Bay of Bengal around Andaman Islands. Between 8 and 49

fathoms depth they obtained a catch of 58 lb of fish per hour but between 50 and 99 fathoms the average was only 4 lb of fish per hour of trawling (Pruter, 1964). Around Laccadives and Minicoy during 1951-65 the average landings were 440 metric tons. The areas around these islands are productive (see Qasim and Sankaranarayanan, 1970; Qasim and Bhattathiri, 1971 and Qasim *et al.*, 1972) and these islands also have an organised pole and line tuna fishery. These islands are excellent centres for development of the oceanic fisheries in this region.

The preliminary results of the recent work of the Indian National Science Academy on the Arabian Sea Islands also indicate that the areas around most of the islands in the Konkan group are also productive and can support sizeable fishery (personal communication, Parulekar and Goswami). Thus the yield around Arabian Sea can be increased many folds and these islands can play a role in the development and management of fisheries.

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THE TIDES OF THE OCEANS—A NEW PRESENTATION OF THE PRINCIPLE LUNAR TIDE M_2

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ABSTRACT

A realistic picture of the tides of world oceans requires considerable amount of data both from the coastal waters and from the open ocean. The data from the open ocean is seriously lacking at present. Three methods have been suggested to provide an image of the oceanic tides. The limitations of each of these methods have also been pointed out. Using the available informations, a picture of principle lunar tides – M_2 of the oceans has been given. This is an improvement over the picture presented by the author earlier.

INTRODUCTION

The question of the distribution of the oceanic tides in time and space can easily be answered, if the cotidal and cophase lines of the most important semi-diurnal and diurnal tides could be presented properly. At present this is possible only partially. The reasons for this are well known. The tide-generating forces of the moon and the sun can be specified in all their details for the coastal areas, but not for the oceanic regions. Frictional effects, the reflexion of the tidal waves due to the complicated bottom topography and the density stratification in the open oceans, influence the propagation of the tidal waves too strongly.

Three methods are available at present to attack the problem of the oceanic tides and all these three have been applied here; the first is a theoretical one, the second is an empirical method and the third is a semi-empirical method. The theoretical method includes a straightforward integration of the system of the hydrodynamic equations. Besides the tide generating force as an external force, friction is also taken into account. Complete analyti-

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We are very happy to receive this article of late Prof. Dietrich from Dr. F. Schott. Those who have known Prof. Dietrich would appreciate how earnest he was in his promises and having promised to write for this special number he fulfilled it in his life time.

cal solutions of these equations, including the real bottom topography of the oceans have not been obtained up till now. Thus the approximation models of excessively generalized oceans have been developed by numerical integration. The empirical method, on the other hand, is based on the observations of the tides in the open ocean. This method can be applied if the harmonic constants of the most important tides are known from a grid of several hundred observation-points in the open ocean. However, the first measurement of the tides in the deep sea was carried out in 1965. Since then, only a few more records have been added. We should, however, hope that at least within the next decade many more records of the oceanic tides at about one month's interval will be available from many deep sea positions.

The large number of stations, from where harmonic constants have been published are restricted almost entirely to the coastal areas of the world ocean. Since a tidal wave changes its shape as it travels from the deep ocean towards the shelf and particularly towards the shallower part of the shelf near the coast, the known harmonic constants at these coastal positions are not valid for the open ocean, even closeby.

In these situations a semi-empirical method, such as the one applied by the author (Dietrich, 1944*a*) provides some solution. It cannot be the final answer as it is based on empirical data and theoretical results. There is no doubt that both these methods will be improved with time. The method, however, makes use of the harmonic constants from coastal stations, especially from the oceanic islands and from these the effect of the tidal waves on the shallow coastal regions can be estimated. Moreover, from the hydrodynamic expressions, the positions of the nodes and the amphidromies can also be derived. In this way, the world maps for the M_2, S_2, K_1 and O_1 tides have been developed. These maps are being used in many textbooks and manuals. Several other authors have arrived at similar results on tides (see Vallain, 1952; Bogdanov and Magarik, 1967). The purpose of this paper, therefore, is to reexamine the results available by applying the semi-empirical method which is limited to the M_2 tide. This seems necessary because although some progress has been made in recent years, neither the theoretical nor the empirical methods have given a satisfactory representation of the oceanic tides up till now.

Theoretical Methods

Analytical solutions of the equations of motion have been provided by using grossly simplified models of the oceans (spheric biangle, constant water depth). These have given an insight into the number of amphidromies (Doodson, 1936 and 1938). More recent investigations have advanced our knowledge by integrating numerically the hydrodynamic equations—the so-called initial boundary-value problem from the work of Hansen (1948). It is thought to be a boundary-value problem because the solutions have to satisfy the kinematic boundary conditions along the coasts, i.e. the velocity component normal

to the coast must disappear. The system of differential equations is changed into a system of difference equations and the ocean is covered by a grid of points, at which the unknown current velocities and sea level variations are calculated. If one starts with arbitrary initial values of this function, the current velocities and sea level variations can be calculated from the difference equations. As a result of friction, the influence of the arbitrary initial values is soon damped and the solutions are merely determined from the tidal forces.

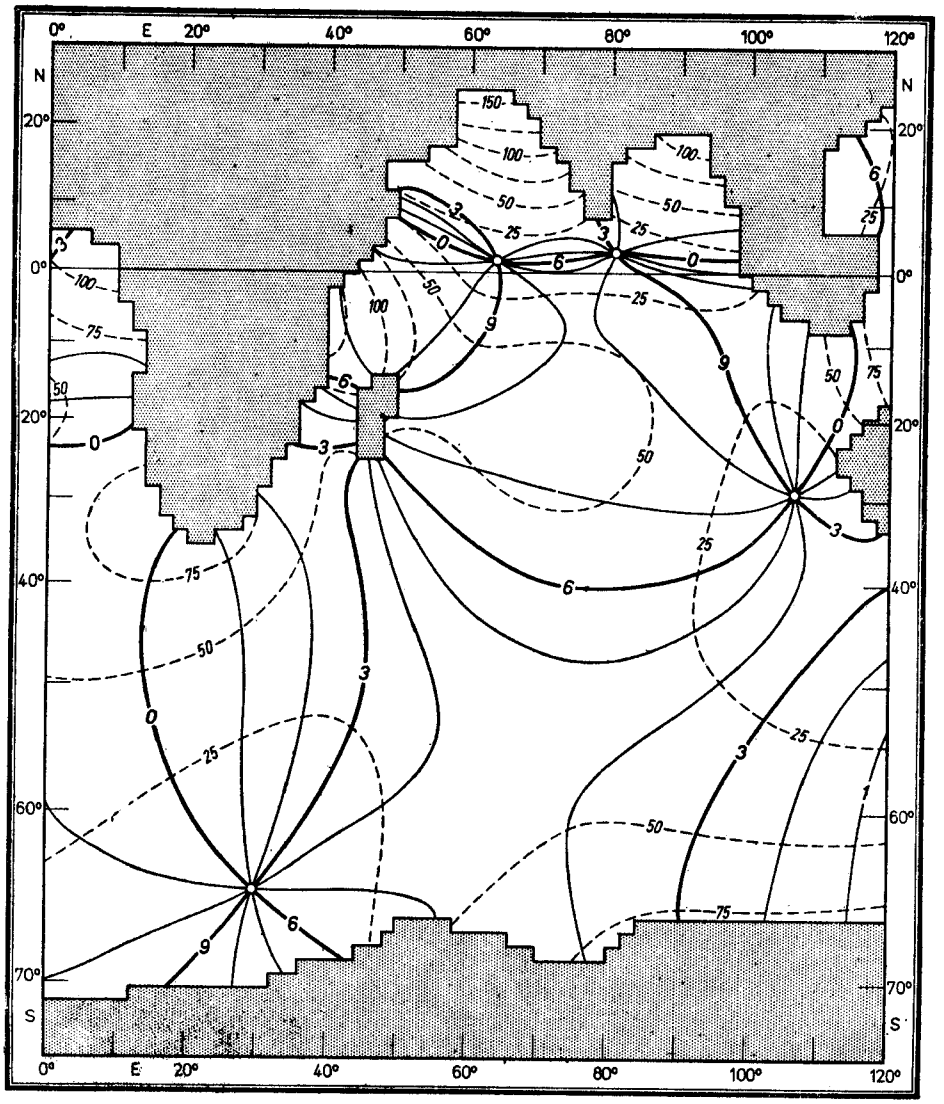


Fig. 1. Theoretically calculated distribution of corange lines (in centimetres) shown as broken lines, and cotidal lines, (in Greenwich lunar hours) shown as solid lines of the M2-tide. Part of the map taken from Pekeris and Accad, 1969.

Representations of the M_2 tide in the world ocean have been derived independently by Pekeris and Accad (1969) and by Zahel (1970) using the mathematical boundary-value method and without the knowledge of any tidal measurements. The model by Pekeris and Accad is based on a one-degree net (60 nm side-length at the equator), which means that a considerable amount of data for a large computer to analyse; Zahel uses a four-degree net (240 nm side length). Even the one-degree grid net is too wide for the calculation of the tides on the shelf-areas. Because the dispersion of tidal energy largely takes place on the shelf areas, it cannot be expected that this method can

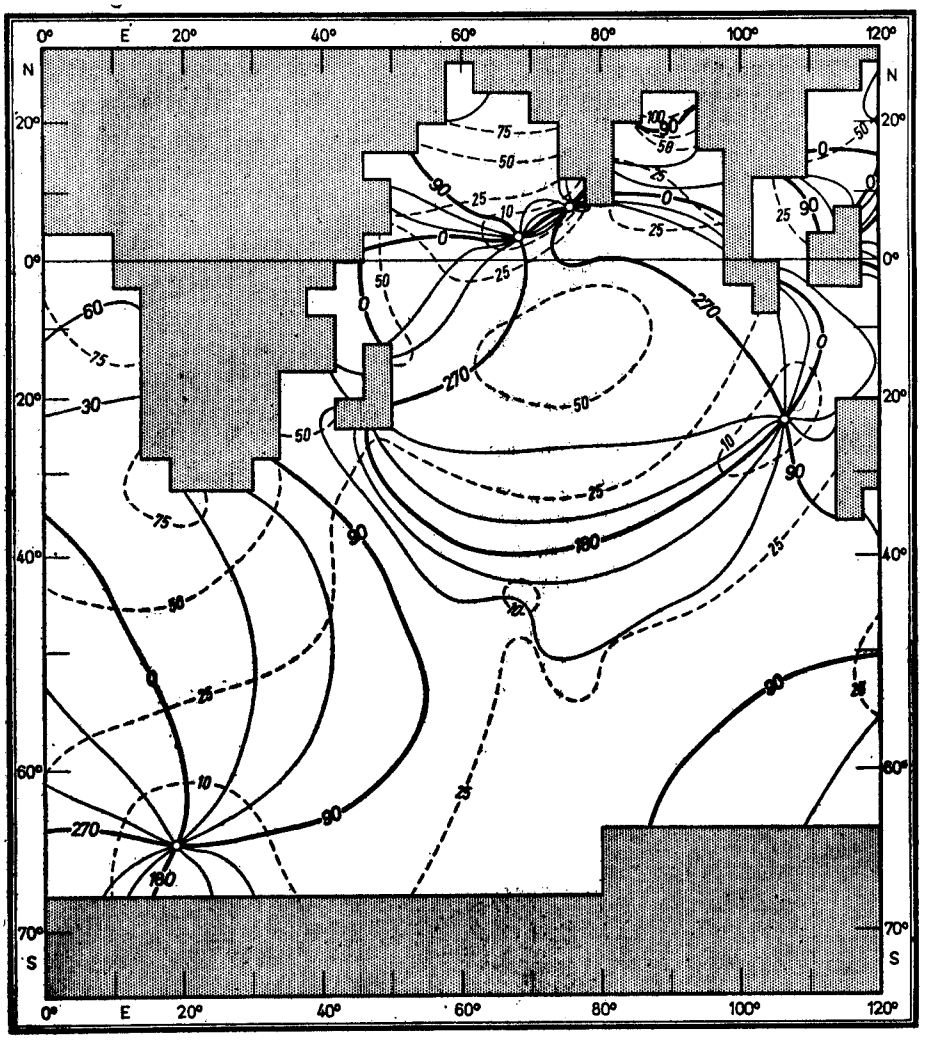


Fig. 2. Theoretically calculated distribution of corange lines (in centimeters) shown as broken lines and cotidal lines (in Greenwich lunar hours) shown as solid lines of the M2-tide. Part of the world map taken from Zahel, 1970.

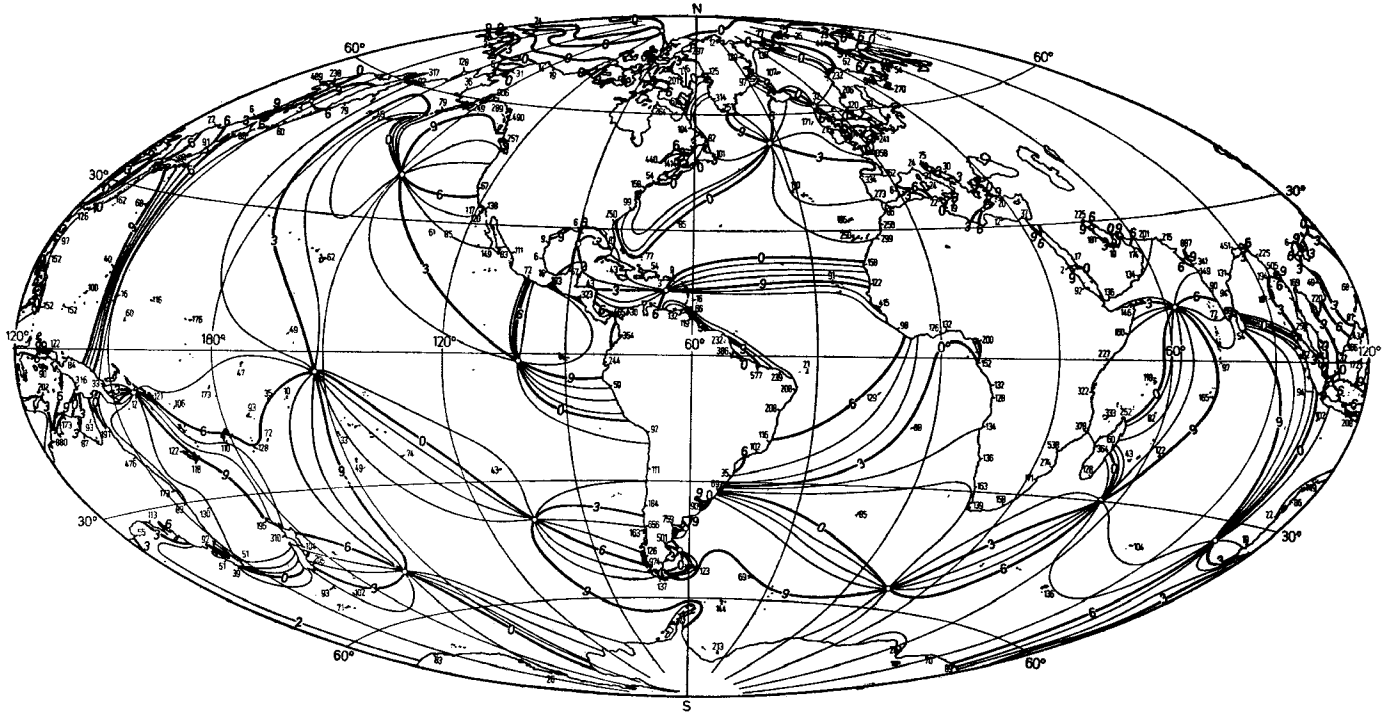


Fig. 3. Semi-empirically deduced distribution of cotidal lines (in Greenwich solar hours) of the M_2 - tides in the world Ocean. Numbers along the coast indicate observed mean spring tidal range of the semi-diurnal tides, 2 ($M_2 + S_2$) (in centimeters). The former map published by Dietrich (1944) has been revised.

describe the tidal observations at the coasts. To do this, a better knowledge of the frictional conditions and of the transformation of energy of surface tides into internal tides as well as a smaller grid size for the calculations are necessary. For these, at present, the capacity of even the largest computers is insufficient. Hence, the results obtained by Pekeris and Accad and by Zahel have their own importance but these are mainly confined to describing the oscillation system of the semi-diurnal M_2 tide in the deep sea.

From the world maps based on these works, the various regions of the Indian Ocean can be studied (Figs. 1 and 2). The drawings of the cotidal and corange lines are such that the two figures can be compared, among each other things, with the semi-empirical representations of the phases shown in Fig. 3. The cotidal lines related to Greenwich have been shown in Figs. 1 and 2 in lunar hours, and in Fig. 3 in solar hours. These give a difference of 25 minutes per half a day. The corange lines in Figs. 1 and 2 give the double amplitude of M_2 in centimeters, but in Fig. 3 they include $2(M_2 + S_2)$, i.e., spring tidal range in centimeters. The two theoretically calculated representations of the M_2 tide in Figs. 1 and 2 are remarkably similar in phases as well as in ranges.

Empirical Methods

These methods attempt to make tidal measurements in terms of sea level (pressure) registrations at many points of the ocean bottom at thousands of metres depth as well as in terms of current and density registrations in the water column above. The unusually high precision in the instruments used for measuring external pressures up to 600 atm, with an accuracy of sea level $\pm$ 1 cm, of current speed with $\pm$ 1 cm/sec, accuracy of water temperature with $\pm$ 0.02°C and of salinity with $\pm$ 0.02°/oo accuracy became possible only within the last few years, especially for the pressure registrations at great depths for at least 4 weeks continuously. The first deep-sea tide gauge for oceanic depths has been developed by Sutton *et al.* (1965), and subsequently by Eyries (1968), Snodgross (1968) and Filloux (1969). The instruments are very complicated and expensive; their launching depends on the weather conditions. The danger, however, for losing them is great. Therefore, it is not surprising to find that only a few analysed time-series are available. Among these, are 4 records from the gear 1968 and pertain to a profile perpendicular to the Californian coast extending about 1000 km into the open ocean. These records were made by Munk *et al.* (1970). The instruments during these observations had worked for several weeks at 4400 m depth. From the success of these recordings it is evident that empirical data collection of the oceanic tides on a global scale is possible and it is only a question of time before it materialises. It is also necessary to develop cheaper instruments so that many more countries and institutes are able to participate in a world wide programme. Such a programme has been

arrived at by an international Working Group which was established by Scor in 1967 largely as a result of the initiative taken by Munk.

Semi-empirical Methods

From the facts noted above it is clear that neither the theoretical nor the empirical methods provide a full description of the ocean tides. It is therefore necessary to make some derivations and these have been done by Dietrich (1944). The solution of the problem seems to be based on the harmonic constants of coastal areas obtained from the data collected from oceanic islands and on the system of amphidromies, which were derived from theoretical considerations (number, position, sense of rotation of the amphidromies). In the present report, the results of 1944 have been considerably improved because in all 6000 coastal stations with harmonic constants which were available at that time could now be increased by almost 1000 more, with highly valuable new records from the oceanic islands of the Pacific Ocean and from the Antarctica However, along the shelf regions the tides have been modified to such an extent, that the increase in the number of coastal observations has not provided a better insight into the tides of the open ocean than before. A striking example is of the Patagonian shelf, where the existencies of a special oscillation system with two amphidromies of semi-diurnal tides is similar to what has been found in 1944.

The results of the revised representations of the M_2-tide have been summarized in Fig. 3. The cotidal lines have been plotted and the system of the amphidromies includes all reliable harmonic constants. The range expressed as the spring tidal range $2(M_2 + S_2)$ has been given only for the selected coastal points. The tremendous influence of the shelf on the tidal range dose not permit to extend the isolines into the open sea from the coastal observations alone.

Since both theoretical and empirical methods do not allow for a realistic representation of the oceanic tides, it is very desirable that tidal observations from oceanic islands are carried out more intensively than before. These should last for at least one month.

Comparison Between The Result Of The Three Methods

A comparison between the theoretical and the semi-empirical method is possible from the presentation of the cotidal lines which have been shown in Figs. 1-3 for the region of the Indian Ocean. Some differences in the three figures are evident, but as far as the main features are concerned (number of amphidromies, their sense of rotation and their geographical position) the deviations between the three representations are not large. Instead of the theoretically calculated two amphidromies, only one has been confirmed by the empirical method from the North Indian Ocean. Probably the complicated

bottom topography has been insufficiently taken into consideration in the theoretical method because of the coarse grid. Moreover, the semi-empirically derived amphidromy, south east of Madagascar, is very doubtful. Further observations in this region are necessary from oceanic islands such as Crozel and Prince Edward Islands.

A comparison of results using both the methods on M_2 tide is possible only for the profile off southern California. This has been shown in Table 1.

TABLE 1. *Comparison of phases G (hours) and amplitudes H (cm) of the M_2-tide in the eastern Pacific Ocean based on the observations of Munk et al.* (1970) *and from the theoretical calculations of Pekeris and Accad* (1969), *Zahel* (1970) *and from the semi-empirical results of the present author*

Position		Depth	Munk *et. al.*		Pekeris and Accad (1°grid)		Zahel		Dietrich	
ρ(N)	ϒ(W)	in m	G	H	G	H	G	H	G	H
31°02'	119°98'	3640	4.9	42.6	00.1	75	1.6	9.3	4.9	—
32°14'	120°51'	3700	5.2	42.5	00.0	63	4.8	9.0	5.1	—
27°45'	124°26'	4200	4.4	28.6	11.5	70	10.7	19.4	3.8	—
24°47'	129°01'	4400	3.3	18.8	11.7	65	10.9	29.8	2.8	—

The differences between the phases of the M_2-tides as observed by Munk *et al.* (1970) and those semi-empirically deduced by the present author are very small. However, the results obtained from the theoretical methods (Pekeris and Accad, 1969; Zahel, 1970) differ widely from the observed amplitudes and phases. This is because of the existence of an amphidromy in that area. It is of interest to note that the theoretical mehods provide only the basic knowledge on the oscillation system of the ocean tides but not on the local tides themselves.

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SOME FEATURES IN THE BIOGEOGRAPHY OF THE ICHTHYOFAUNA OF THE INDIAN OCEAN

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ABSTRACT

The paper summarises the investigations on some important features of the zoogeography of the Ichthyofauna in the Indian Ocean with special reference to the widely distributed families Clupeidae, Engraulidae and Carangidae.

Investigations on the ichthyofauna of the Indian Ocean are of vital importance both from theoretical and practical standpoints. The Indian Ocean can and must yield more fish for the high density of population which lives in the surrounding countries. The potentialities of such an increase, as pointed out by Panikkar (1966 and 1968) have been increasingly realised during the last few years. The total catch taken from the Indian Ocean which, according to my estimate has reached 2,000,000 tons in 1960 (Rass, 1965), increased to 2,780,000 tons in 1970 (FAO, 1971).

The ichthyofauna of the Indian Ocean is most closely related to that of the western Pacific, being in fact a part of a unique Indo-West Pacific fauna (Ekman, 1953).

At the same time some connections can be traced with the ichthyofauna of other regions and these, require further zoogeographical analysis. The fact can be exemplified by the widely distributed families of Clupeidae, Engraulidae and Carangidae which are rich in species.

The large family of Clupeidae, is comprised of 6-7 subfamilies about 50 genera and 190 species (Svetovidov, 1952; Rass, 1971). The family, dates back to Lower Cretaceous (Berg, 1955). More than 50 species of this family live in the Indian Ocean off the coasts of India, Ceylon and Burma (Day, 1889). The interrelations of some Indian Ocean groups of this family is of great interest. The tropical-boreal subfamily Alosinae (Clupeidae) consists of three genera: *Hilsa, Gudusia* and *Alosa*. *Hilsa* species are anadromous, entering the rivers

of the Indian and West Pacific Oceans along the coasts of southwestern Africa upto Indonesia and Korea. The genus has five species: three of them are Indo-West Pacific: *H.kelee* (Cuv). *H.toli* (Val.) and *H.ilisha* (Ham.Buch.) and two are West Pacific: *H.reevesii* (Rich.) and *H.macrura* (Blkr.). The genus *Gudusia* (related to *Hilsa* but differing from it and from *Alosa* by its smaller scales is represented in the rivers of India and Burma by two species: *G.chapra* (Ham. Buch) and *G.variegata* (Day). The genus *Alosa* occurs on both the coasts of the Atlantic: six species—along the coasts of North America, six species along the coasts of western Europe, three species in the Black Sea Caspian basin and three species in the Caspian sea (Svetovidov, 1964).

Most of these species are anadromous, but freshwater forms too are known. In the waters of America, the genus falls into two subgenera (*Alosa* s.s., *Pomolobus*). In the European waters it forms up to 30 subspecies. The findings of fossil remains of related genera and species (*Pseudochilsa* Menner and others, from the Miocene of the southeastern Caucasus) point to some connections between the ranges of the genera of this group. The history of these connections may be presumed to be the following: the primary ancestral forms, related to the species of the genus *Gudusia,* inhabited the rivers of southeastern Asia. A part of their descendants migrated downstream into the seas of eastern and southern Asia, became anadromous and gave rise to the generic group *Hilsa.* Another part of their descendants migrated westwards, crossed the Atlantic Ocean and began inhabiting the waters of America as *Alosa* species.

The explanation to the great diversity of forms in this genus as observed from the Caspian Sea lies in the history of the genus during the Meotis-Akchagyl period. During the last junction of the Caspian Sea with the Ponto Azov basin, its ancestors invaded its still unoccupied pelagic zone and have flourished there ever since (Svetovidov, 1952).

The purely tropical subfamily Pristigasterinae, comprising of 8 genera and nearly 50 species (Fowler, 1941; Hildebrand, 1964; Norman, 1966; Whitehead, 1970), is more richly represented in the waters of America than in the Indo-West-Pacific zoogeographical region. Three out of the four Indo-West-Pacific genera : *Ilisha, Pellona, Opisthopterus* and *Raconda* also occur at the coasts of America along with the four purely American genera *Odontognathus, Pristigaster, Pliosteostoma* and *Neoopisthopterus;* and only *Raconda* is lacking. The genera *Ilisha, Pellona, Opisthopterus* are represented in the Indo-West-Pacific waters by marine or estuarine species (*I. elongata, I. filigera, I. indica, I .megaloptera, I. macrogaster, I. pristigastroides, P. ditchela, O. tardoore, O. valenciennesi*), and in the American waters by freshwater species, mainly of the Atlantic basin (*I. amazonica, P. castelnaeana, P. flavipinnis*) and marine species at the Atlantic (*P. harroweri, P. narragansetal*) and the Pacific (*O. dovii, O. macrops, O. aequatorialis*) coasts.

A species of the genus *Ilisha, I. africana,* occurs along the Western coast of Africa, thus connecting in a remarkable way the western and eastern ranges of the genus which is separated by the African continent and the Atlantic Ocean.

Unlike *Ilisha* and *Pellona,* the genus *Opisthopterus* does not occur along east of America. It is represented in the waters of the Indian Ocean, and Indo-Australian archipelago by *O. tardoore* and *O. valenciennesi,* and at the western shores of tropical America by *O. dovii, O. macrops* and *O. aequatorialis.*

The spreading of the subfamily Pristigasterinae seems to have another course and apparently reflects another epoch so different from that of Alosinae.

Interesting and somewhat enigmatic is the history of *Etrumeus teres* (De Kay) belonging to the subfamily Dussumierrinae (Dussumieridae), whose distribution has recently been described by Whitehead (1963 and 1965). The species occurs mainly in warm-temperate waters off southeastern Africa, southern Australia, Japan, the Hawaiian and Galapagos Islands, at the western and eastern coasts of North America; it has been encountered also in the Red Sea and in the eastern part of the Mediterranean.

Since the species does not occur in the eastern part of the Atlantic Ocean it is thought "most likely that the Mediterranean specimen is an immigrant from the Red Sea" (Whitehead, 1965, p. 236). However, fossil remains of *Etrumeus* have been encountered in the Miocene deposits of Sicily and Algier in the Eocene-Oligocene periods of Germany and Irak (Danilchenko, 1964). Thus the species appears to be a relict in the Mediterranean.

The family Engraulidae with 16 genera and 120-130 species probably appeared during the Eocene. Fifteen genera at present inhabit the coastal tropical and subtropical waters of America, Africa, Asia and Australia but one genus, *Engraulis,* lives in the warm-temperate waters of both northern and southern hemispheres. In contrast to the Clupeidae, the American tropical and subtropical genera of Engraulidae do not occur along the coasts of Asia, while the Asiatic genera are absent on the coasts of America. Only the warm-temperate *Engraulis* occurs in the southern and northern waters of America (with the exception of the Atlantic coasts of North America), Europe. Africa, Asia and Australia. The aloofness between the American and Asiatic Engraulidae can be accounted for by their coastal modes of life as compared to the Clupeidae, as well as by relatively later appearance historically. Recent findings of Whitehead (1964) on the representatives of the genus *Engraulis* indicate their distribution in tropical waters of Central America (off the coasts of Venezuela and Tobago), in the waters of western Africa, off the Comoro and Seychelles Islands in the Indian Ocean, to the west of Japan on Long. 175°E, and along the shores of Indonesia.

According to Soviet and Japanese data for the western waters of the Pacific and from the American data for the Hawaiian Islands, larvae, fry and adult specimens of Engraulidae may be carried by the currents away from the coast for several hundred miles, without losing their vitality. The presence of *Engraulis capensis* in the western waters of the Arabian Sea, may be explained from the drift coming from the southern coast of Africa, particularly because the presence of a patch of relatively colder water has been reported off the eastern coast of Africa between northern Madagascar and Southern Arabia. The appearance of the warm-temperate species *E. capensis* off northern Madagascar and the Seychelles can also be explained from the above assumption. It will be shown below that an analogous picture is presented by the family carangidae.

The family Carangidae includes some 30 genera with more than 200 species. Like Engraulidae, nearly all the representatives of Carangidae are found in tropical and subtropical waters, and only the species of the genus *Trachurus* (like the genus *Engraulis*) are characteristic of temperate waters along the coasts of America, Europe, Africa, Asia and Australia. Similar to the findings of the warm-temperate genus *Engraulis* in the northwestern waters of the Indian Ocean described above, some specimens of the genus *Trachurus* have been discovered by Soviet scientists in the north-western part of the Arabian Sea, in the Gulf of Aden, the Gulf of Suez and the Red Sea. These were compared with the specimens from the Mediterranean *Trachurus mediterraneus* and the species has been described as an Indian subspecies *T. mediterraneus indicus* Necrassov (Necrassov, 1966 and 1970). However, a comparison with the South African species *T. capensis* shows that the above subspecies is very close to the latter as regards the number of scales on the lateral line (65-75 in the former and 66-76 in the latter), differing substantially in this character from the Mediterranean forms with 72-95 scales. (Necrassov, 1970). The distribution of this species in the north-western part of the Arabian Sea is confined to the areas of cooler waters than that of the genus *Engraulis*.

All these findings indicate that while the ichthyofauna of the Indian Ocean as a whole belongs to the fauna of the Indo-West Pacific region, ancient connections can be traced between it and the Atlantic-Mediterranean ichthyofauna (as regards the Clupeidae-Alosinae, Pristigasterinae and Dussumierinae). Apparently more recent connections seems to result from the penetration of warm-temperate species of *Engraulis* (Engraulidae) and *Trachurus* (Carangidae) into the western waters of the Arabian Sea. The recent immigrants are evidently able to exist in the tropical waters of the Arabian Sea. The presence of a patch of relatively cool water between northern Madagascar and Southern Arabia is the only area which seems incompatible to them. If this assumption is correct we may expect to find in the warmer region many more representatives of warm-temperate ichthyofauna, not typical of the Indo-West-Pacific zoogeographical region.

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HISTORY OF ARAB NAVIGATION IN THE INDIAN OCEAN

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ABSTRACT

The paper describes a brief history of the Arab navigation based on the original Arabic sources from the 9th century onwards. The old literature indicates that the Arabs had a good knowledge of the wind-directions, currents and tides. They also knew the most favourable seasons for sailing from the different ports. The Arabs described the reversing currents in the North Indian Ocean and made several interesting observations on bioluminescence, discoloration of sea water, etc. They also made references on the light houses at the entrance of Persian Gulf and on the eddies, ascending currents and cyclonic winds.

Arab navigation in the Indian Ocean had deep connections with the Indian and Persian nautical traditions. These probably dates back to the first century when the Sanskrit "Jataka Mala" (maritime code) was written. The highly cultivated knowledge of the Arabs on nautical matters could be attributed to their knowledge of the stars, their eagerness to undertake extensive voyages and their desire to translate the relevant works in other languages into Arabic. The impact of nautical traditions of the Arabs on the Portuguese and Turkish navigations has been of considerable value.

INTRODUCTION

In ancient history, the Indian Ocean was known to the Egyptians, Greeks and Romans. Thus in 1478 B.C. Queen Hatchepsut (18th Dynasty) of Egypt sent an expedition to explore the East Coast of Africa. Chronicles of this expedition are recorded on the walls of her temple in Deir el Bahari, upper Egypt. The vivid relief scenes depict Egyptian ships being loaded with myrrh-resin, ebony, ivory, gold, incense woods, apes, dogs, panther skins and the like, from the coast of Somalia; while exotic Indian Ocean fishes feature in nets under-water. This marks the first known maritime expedition in history.

The "Indian Ocean" also features in the geography books such as "Almagest" of Ptolemy and the "Seven Climates" written by Ancient Greek and Hellenistic scholars of Alexandria in the 3rd and 4th centuries A.D.

Roman ships also circumnavigated this Ocean, but written accounts available on such expeditions, apart from being scarce, are devoid of useful navigational information.

Connections between the Arabs of Yaman, Hadramut and Oman with Persia and India on the one hand, and with the East Africa on the other, via maritime routes, preceeded the spread of Islam by several centuries. However, the first written account on the seasonally reversing currents in the North Indian Ocean appeared only in the 9th century A.D. (Aleem, 1967*a*).

Preislamic Arabs had a good knowledge of the stars, the moon and winds, which they utilized for agriculture and for travel by land and sea. Such a knowledge is found scattered in preislamic Arabic poetry and in books of *Noa* (winds) and are summarized in the 9th and 10th centuries by Al Jahiz, Al Dinawari, and Al Sufi. The latter enumerates in his book "Images of Planets" about 250 stars in their chaste Arabic names. Al Biruni (c. 1000) also comments on preislamic astronomy in his "Chronology of Ancient Nations".

Islam spread quickly from Arabia into the surrounding countries in the 7th century A.D. and in less than two centuries the Moslem Empire extended from the Atlantic Coast of Iberia and North Africa to Transoxania (middle Asia). Thus it became necessary to describe land and sea routes, customs and economy of the various countries and adjust the positions of the towns more accurately. Hence knowledge on regional, mathematical and astronomical geography flourished during the 9th and 10th centuries. It is in such books written by the Arabs during this period that a history of navigation in the Indian Ocean can be traced. Already the legacy of Ancient Greece, India and Persia had been translated into Arabic in a special *Diwan,* under the direct supervision of the *Khalifs* of Baghdad like Al Mansur (762) and Al Mamun (813). Soon afterwards, the Arab contributions in arithmetic, algebra and astronomy, among others, flourished and the Greek instruments such as the *Astorlabe* and "Quadrant", used also in navigation, were modified or perfected.

Arab scholars were more pragmatic than their Greek predecessors; they relied in their description of seas and oceans on direct observation and experience. Their challenge to the Greek philosophers and theoreticians with regard to the description of the Indian Ocean, in particular, appears in accounts written by Al Mukaddasi (985) and others as we shall see later.

Although references to nautical books and "maps" of routiers as used by the Arab pilots in the Indian Ocean have been made by, the Ibn al Fakih (902), Al Massoudi (947) and Al Mukaddasi (985), original works from this period remained inaccessible to us. This gave the impression that such works were either lost or were never written at all. It was not until Ferrand (1921-23) discovered the nautical instructions of the Arab pilot Ahmad Ibn Magid and of

his contemporary Sulayman Al Mahri that our knowledge of the Arab navigation in the Indian Ocean in Medieval times began to flourish once again (see Aleem, 1968*a*).

Ibn Magid witnessed the arrival of the Portuguese in the Indian Ocean towards the end of the 15th and in the beginning of the 16th century, and both Ferrand (1922*a*) and Soviet orientalists such as schomovsky (1957) admit that he was the pilot of Vasco de Gama to India. However, we have arrived at a different conclusion as we shall see in the following page. The impact of Arab navigation on the Portuguese also deserves a comment.

Immediately after the Portuguese expeditions, the Indian Ocean became an area of great enterprise by the Turks, British and Dutch. Thus the age-long sea-faring tradition in the Indian Ocean is difficult to understand without reference to the Arabs. However, a history of the Arab navigation in the Indian Ocean could not be adequately covered earlier. Certain important omissions are obviously on the record. These are : the history of the mariners compass "*bousssole*", details of astro-navigation and instruments employed, kinds of ships employed and classes of the different sailors on the ships. Finally the origin of technical nautical terms employed by the Arabs, which certainly had Greek, Persian, Indian, Turkish and Byzantine influences, apart from the Arabic impression left on such languages, have not been properly investigated. The indentification of names of ports, islands and coasts with contemporary names also deserves more investigation.

Sea Routes to China and Africa

Descriptions of these routes are mentioned in the books on sea tales and these should be considered while describing the early sources of Arab navigation in the Indian Ocean. This type of literature arose in Moslem Siraf and Basra—the two important ports in the Persian Gulf, where Arab and foreign pilots and traders met, narrated their adventures of high seas and described the new exotic lands, islands and peoples. Such stories have been given a romantic touch, and these have perserved in the well known tales of Sindbad the Sailor in the Arabian Nights. These, according to de Goeje (1890-93), formed the origin of legends such as that of San Brandan in the Medieval Europe. Nevertheless, these books reflect some authentic material on navigation, besides the vivid description of such remote places as Java, Sumatra and China.

The oldest written sea voyage in Arabic is known as the "Voyage of Sulayman the Merchant" which dates back to 851 and is ascribed to Ibn Wahab, who apparently took refuge in China during the "Revolution of Zing" in Baghdad. Some more additions in the book were made later on by Al Sirafi (916) and this book is considered an important source on the ethnology of India and China (Ferrand, 1922b). It also contains a description of the maritime route from

Siraf to Canton which the ships used to cover in "cycles" during a period of 4 months. These were summarized as follows : from Siraf to Mascat, then to Kalam (on the Malabar Coast) and to the ports of Ceylon (Sarandib), then across the Bay of Bengal (Sea of Harkand) to the Isle of Lingbalus (Nicobar), from there to Kalabar (Malacca) and from Malacca round Siam and then to the Isle of Haynan and from there to mainland China to the Port of Khanfu (Canton); some ships used to sail farther north to Korea and probably also to Japan. This route was commonly taken by the Arab and Persian pilots between the 7th and 9th centuries and already in the 8th century there was a strong Moslem community in Canton which controlled most of the external trade to China (Kammerer, 1935). Arab pilots felt at home in India and Ceylon and Ibn al Fahih (902) adds that the Indians on the Malabar Coast charged the Arab ships only between 10-20 *Dinars* for fresh water, while a Chinese ship would pay 1000 *Dinars* for the same. Arab ships also travelled from Nicobar to Java and Sumatra, where several Arab families settled and from there sailed to the Philippine Islands later on; these were mostly of *Hadramuti* origin.

Moreover, the *Yamani* tribes of *Azds* sailed more often to the east and settled along the coast of Africa in Zanzibar, Madagascar and further south to Sofala and Mozambique. The Sultans of Zanzibar ruled over this island until recently.

Another interesting book of sea tales is "Wonders of India". It is a collection of sea tales written by a pilot known as Buzruk Ibn Shahryar between 900-905. Apart from the breath-taking sea adventures, the book also includes some very interesting observations on winds and currents in the southern seas.

Ibn al Fakih (902) describes the difficulties of navigation in the Sea of Barbar (Abyssinian Sea) and notes that the Arab pilots travelled in this sea "with the cord and not with the arc". The same author while describing the "lighthouses" erected on a small island at the entrance of the Persian Gulf, comments on eddy currents. Similarly, Al Biruni (c. 1000) gives an intelligent observation that the currents were ascending from the sea bottom as judged from the "displacement of nets".

Treatises on Astronomical and Regional Geography

Apart from the knowledge taken from the Greaks which has been translated into Arabic, the early Moslems also readily assimilated the Persian and the Hindu knowledge, before they made their great contributions in science. Thus in 770 Al Fazari presented at the court of Al Mansur a learned Hindu named Manka who introduced "*Siddhanta*" a treatise on astronomy according to Hindu methods, which was immediately translated. Al Fazari is also noted as the first Moslem to have constructed an *Astorlabe*. This instrument was perfected by

the Arabs, and Al Zarkali (1050) who is the author of "Toledo Tables", is credited for the integral *Astorlabe.**

Arithmetic and algebra also flourished along with astronomy and the celebrated works of Al Khwarizmi (835-844) on astronomy, and on the Indian methods of calculation (*De Numero Indico*) and on algebra were translated into Latin by Adelard of Bath and Gerard of Cremona.

The most celebrated work in the astronomy of the period is due to Al Battani (852-929) who wrote a large treatise and compiled astronomical tables which show an advance on the work of Al Khwarizmi. It shows a divergence from the Indian methods. These tables left an impression on the great maritime discoveries of the 15th and 16th centuries by the Spanish and Portuguese. Al Battani is also credited for laying the foundation of modern trigonometry. The divisions of a scale known as Al "Khwarizmi's Stick", which is used for measuring the altitude of stars is based on trigonometric functions. The stick was later replaced by a string knotted at intervals and adjusted to the centre of wooden tablets for measuring the altitude of stars above the horizon from the ships at night. The "sined quadrant" is also attributed to Al Khwarizmi.

Advances on regional geography were the outcome of the expansion of the Moslem Empire as stated previously and these flourished also in the 9th and 10th centuries. These books entail informations on lands, mountains, rivers, dimensions of seas and oceans, islands, economic resources and customs of people. Such informations were found useful for administrative purposes. These books also contain interesting informations on nautical matters, such as winds, currents, tides and cycles of maritime routes. They are known in their Arabic names as "Takween Al Buldan" (geography) and "Al Masalik wal Mamalik" (Books of Routes and Kingdoms).

Chief among these are : Ibn Khurdazbah written in 846, which contains the first account on the seasonally reversing currents in the North Indian Ocean, of Ibn Al Fakih (902) referred to earlier and that of Al Massoudi (947) known to Europeans in its Arabic name "Prairies of Gold". This book is considered as an encyclopedia of geography and history.

Other classical Arab geographers of the 10th century, such as Al Balkhi, Istakhari and Ibn Hawnal, illustrated their geographical books by maps which are known collectively as the "Atlas of Islam". These maps show an advance over the ancient Greek maps to such a degree that they include a round earth, devoid of pictures of animals and show more accurately the location of different regions. As already mentioned, Arab geographers of the 10th century already

*Arabs excelled in the determination of directions and positions of places relative to Mecca, the Qibla of Islam, used for determining the direction of prayer.

dissociated themselves from the ancient Greek theories on geography and relied upon their own experience. This is most evident from the work of Al Mukaddasi (985) and in particular from his account on the Indian Ocean which can be translated as follows :

> "As for me I have sailed in this Sea for about 2000 *farsakh* ($\sim$ 6000 miles) and circumnavigated Arabia from Kulzum (Suez) to Abadan, apart from drifting on islands and in high seas. I befriended Sheikhs (pilots) born and raised in this Sea, shipowners, mathematicians, deputies and merchants. I found out that all these were among the most knowledgable on this Sea, of its ports, winds and islands. I asked them about it, its routes and boundaries and *have seen with them books on these matters ;* these they study, rely upon and act according to what they contain. This relieved me enormously after much thought and contemplation (of these problems) ....."

Al Mukaddasi goes on to compare his practical knowledge with what had been written or drawn earlier in maps of this Ocean and mentions the discussions he had on the Coast of Aden with a shipowner whose vessels circumnavigated the Ocean to its extreme boundaries, and on matters of winds, bays, dangerous approaches, lighthouses, etc.

Al Massoudi (947) also acknowledged the experiences of *Omani* and *Sirafi* pilots in the Indian Sea, the Sea of China (South China Sea), the Sea of Zing, the Sea of Kolzum (Red Sea), etc., and he also concludes that the knowledge of these pilots was different from what had been stated previously by the Greek philosophers with regards to areas and dimensions of the oceans.

At a later date, Al Idrisi completed his geography book entitled "Nuzhat al Mushtak" in Palermo (Sicily) in 1154 and this book enjoyed a special reputation for centuries not only in the East, but also in Europe. This book combines descriptive and mathematical geography with a large number of maps and charts.

Reference should also be made to two other important geography books by Al Hamaoui (1250) and Abul Feda (1321). Apart from new additions on northern latitudes, including the Baltic Sea, the latter author refers to navigational instruments used by the Arabs.

COSMOGRAPHIA

Books on the wonders of sea and land, known also as *Mirabilia* enjoyed a wide popularity until recently. These books provide a mixture of legends with facts and are not altogether devoid of descriptions of oceanic phenomena such as the discoloration of sea water, mass mortality of fish, cyclones, poisonous

fish, bioluminescense, etc. (Aleem, 1968 *b*). Famous among these are the treatises of Al Garnati (1162), Al Kazwini (1280) and Al Dimishki (1325). Cyclonic winds known to these authors by *Al Tannin* (Dragon) have been explained by Al Kazwini as resulting from the impact of two winds blowing from opposite directions. Finally, travel books such as the "Voyage of Ibn Battuta" (1356) to India contains an interesting description of the islands in the Indian Ocean and the customs of people.

Arab Nautical Instructions

Technical works on Arab navigation written in the 9th and 10th centuries are not available as such, although references to them have been made successively by Ibn al Fahik (902), Al Massoudi (947) and Mukaddasi (958).

That such books were known only to professional pilots may be inferred from the account of Al Massoudi that the Arab seafaring tradition was gained by long experience and passed from one generation to the other.

It is also possible that such a difficult subject might not have attracted as much popularity as the books on *Mirabilia.* Poetry was the form in which such a material could have been written in order to facilitate memorising it, i. e. "Mnemotechnique".

A few extracts of these on the difficulty of navigation in Barbara and Hafuni are mentioned by Ibn Al Fakih (*loc. cit.*) as stated previously.

However, the discovery of the nautical instruction of Ibn Magid (1433—1510 ?), the famous Arab pilot of the Indian Ocean, by Ferrand (1921-23) has thrown much light on the nautical matters given by his predecessors. Ibn Magid refers to Arab nautical instructions written 300 years before his time in the same form of poetry known as *Kasida* or *Urjuza* in which he wrote most of his works.

The works of Ibn Magid and his contemporary Sulayman Al Mahri are considered as the most complete document on Arab navigation in the Indian Ocean during the Medieval ages.

Commentary on this work and on the Arab astronavigation has been made by Ferrand (1928), De Saussure (1928) Schomovsky (1957) and Aleem (1967 *b, c.* and 1968 *a.*) Ibn Magid's contributions entail :

1. Sailing instructions based on astro-navigation and descriptions of routes from South Arabia to East Africa until Sofala, to Madagascar, to Sind, Malabar and the East Coast of India. Details of favourable times for sailing with regards to winds and currents are given for all ports and seasons of the year.

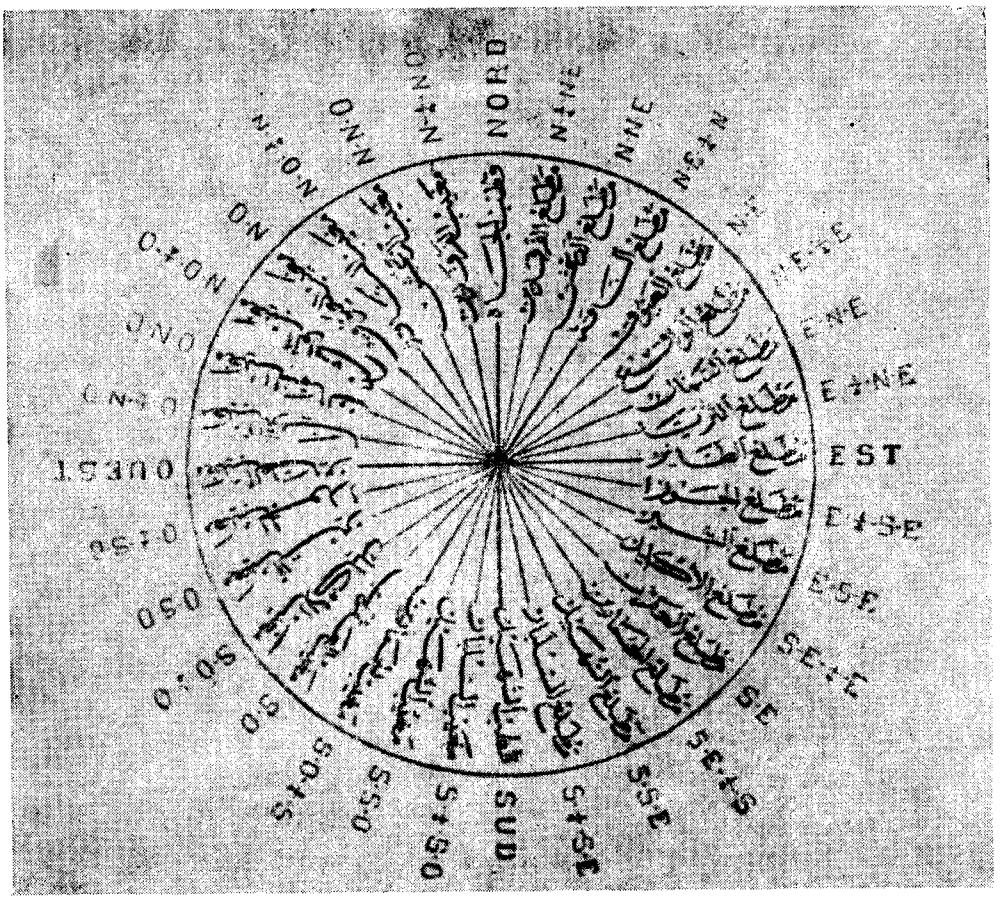


Fig. 1. Azimuthal wind rose of Ibn Magid.

2. Complete knowledge of stars and constellation, their altitudes and relative angles for determining the latitudes and adjusting the ships course. The relative movements of γ and β of the small bear (Alfarkads) in their 6 cases around *Polaris* were described by Ibn Magid and Al Mahri. This together with the mansions of the moon were utilized to determine the time at night. These phases of "Alfarkads" were not known to the Portuguese.

3. Ibn Magid was the first to adjust the magnetic needle of the compass on a pivot to enable it to move freely (Aleem, 1968*a*). His azimuthal wind-rose (Fig. 1) comprises 32 rhumbs or *"Khuns"* divided into 224 *isba,* so that 1 *isba* is equivalent to 1° 37' or to 97 nautical miles. The unit of distance is the *Zam* (probably an Indian word), which is equivalent to 12 nautical miles.

4. Ibn Magid is credited also for a treatise on useful signs used as navigational aids; these such as soundings, nature of the bottom, dangerous reefs, description of approaches, observations on birds, fish and seaweeds, on the colour of the water, as well as on winds and currents.

5. The same author is also credited for a "maritime code" incorporating a set of rules and regulations to be observed by pilots and crew for the "safety of the ship, passengers and cargo". This code seems more advanced and up-to-date than the Sanskrit code "Jataka Mala" (Sylvain Levy, 1918) or the code of the Kingdom of Malacca written by the Moslem pilot Mahmoud Sah in the Malayan language (Ferrand, 1928).

It is to be noted that although the Arabs perfected the *Astorlabe* and "Quadrant" at an early age, they scarcely used these instruments in navigation at sea, for the error resulting from the movement of the ship interferes with the correct readings. Instead, they used wooden tablets which depended on measuring the angle between the celestial body, the observer's eye and the horizon. The distance between the observer's eye and the adjusted tablet is graduated according to trigonometric functions as stated earlier. It is upon this principle that the instruments known as *Kamal, Balisti* and *Arablete* are graduated.

The *Astorlabe* was first known in Europe in 1054, after the Arabic sources (contractus de Vehringen: *De Mansura Astorlabii*) while the first mention of the "Quadrant" in Europe dates back to 1276. This is also known after the Arabic sources were translated by Robert d'Angles in Montpellier.

Hentry, the Navigator was among the first to use an *Astorlabe* at sea in his voyage to West Africa in 1455, while Diego Gomez was among the first to use the quadrant in navigation carried out in 1462.

Arab cartographers also left an impression on the earlier Portuguese maps of the Indian Ocean. Thus De Barros (ed. 1777) mentions that the Persian Gulf in the *"Geographica Universalis"* is based upon Arabic and Persian sources, while Alfonso de Albuquerque sent to King Manoel of Portugal an Arabic chart captured with a pilot at the Island of Socotra in 1507 (Aleem, 1968*a*). Ferrand (1928) adds that certain Portuguese technical terms in navigation are transcriptions of Arabic terms. In this respect we refer also to Delgado (1919-21) for the etymology of such words as: alfandega, algibeira, ceifa, aceifa, arratel and tariff, magazine, cheque, douane and many others which have strict Arabic origin.

Identity of the Pilot of Vasco de Gama from Malindi to India in 1498.

Popular accounts of Vasco de Gama's first expedition to India written by Portuguese historiographers tell us that he sailed from Portugal on the 25th of

March 1497, crossed the Cape of Good Hope on 22nd November of the same year and arrived at "Natal" on the New Year's day. In January 1498 he lost one of his 3 ships in north of Natal but continued his voyage hugging the East Coast of Africa and reaching Malindi in March 1498. At Malindi, he anchored for some weeks seeking information on the route to India. Meanwhile, he befriended the Sultan of Malindi and requested the services of a pilot to guide him to India. After some hesitation, the Sultan introduced a pilot to the Portuguese Admiral who was impressed by his knowledge, instruments and charts. The Admiral took off from Malindi in the company of this new pilot two days after their consultation i.e. on 24th April 1498 and reached Calicut, a small port on the West Coast of India, after 22 days.

It is to be noted that Vasco de Gama did not write his own memoirs of the expedition and this was described later on by the Portuguese historiographers such as de Basros (1553), Castenheda (1554) and Goes (1566). Besides, much of the original materials and charts kept in the archives of the Place of India in Lisbon were destroyed during the earthquakes of 1755.

For this reason, accounts differ on the identity of the pilot who guided Vasco de Gama in his first voyage to India, whether he was an Arab, a Moor or an Indian from Gujarat. He was referred to in Portuguese accounts as Muallim, Muallimo, Cana or Canaqua. The first two words are the Arabic name for a master or pilot and these were the popular names for all able pilots in the Indian Ocean irrespective of their nationality, in the same way as the earlier Arabs adopted the Persian words *"Nokhada"* for "Pilot" and *"Rahmang"* for "book of the route". The words Cana and Canaqua of Sanskrit origin signify an astrologian or a man who has knowledge of the stars.

It is also known that the Portuguese sent three expeditions to India as follows in succession during their early campaigns.

1 — Under Vasco de Gama in 1497 — 1498
2 — Under Pedro Alvares Cabral 1500 — 1501
3 — Under Joao de Nova 1501 — 1502

All these expeditions encountered difficulties and lost ships and men in the Bay of Delgao and sought the help of foreign pilots from Africa to India. Cabral was accompanied by two pilots of Gujarati origin to show him the way to India.

It was due to Ferrand (1922 *b*) that Ibn Magid was identified as the incumbent pilot of Vasco de Gama. Ferrand, an outstanding orientalist and a keen research worker based his identification on an Arabic manuscript of a book by Kotb el Din Al Nahrawaly written in 1577 under the name *"Al Bark al Yamani fil Fath el Osmani"* (on the Ottoman conquests in Yaman, etc.). Another manuscript of this book is found in the National Library in Cairo to which

I have also referred. Al Nahrawaly's story goes to say that the Portuguese used to face losses in men and ships in their attempts to reach India and it was not until an able pilot in the name of Ahmad Ibn Magid has shown them the way, because the Portuguese Admiral had made him drunk (with liquor).

In our view, this story seems unfounded for the following reasons.

1 — Al Nahrawaly's manuscript was written 79 years after Vasco de Gama's Expedition. Had the story been true, the author of "Muhit", a serious treatise on navigation in the Indian Ocean written in 1557 by the Turkish Admiral Sidi Ali should have noted it. Sidi Ali was more acquainted with Ibn Magid and his works.

2 — Ibn Magid was a pilot of high integrity and calibre, with deep respect for his religion. This is manifested in all his writings which reflect clearly the way of life he chose (Aleem, 1967 *b, c*). Thus he writes "a pilot should be clean in body and thought". He always started his voyages with prayers and with submission to God. His saying may be noted "On board the ship you are a guest of Allah, never fail to remember and obey him". Besides at the time of this expedition Ibn Magid must have been over 60 years old, an age in which one is not easily tempted to drink.

3 — It is rather naive to think that a man like De Gama would trust a pilot to guide him while drunk.

4 — Al Nahrawaly's book lacks accuracy in other places, for example the conquest of Harmuz by Albuquerque in 1507 was made before building the Citadel at Goa and not after.

5 — The most important evidence, however, that Ibn Magid was not the pilot of Vasco de Gama or of any other Portuguese ships is derived from his own works. Thus in 1957 Schomovsky in Leningrad published three new Urjuza's of Ibn Magid. One of these (over 500 verses) is entitled "Urjuza of Sofala" describes the routes from Gujarat, Sind, Malabar to Sing Coast, Madagascar and Comore Island.

I have read thoroughly this Urjuza and in spite of the numerous difficulties encountered in deciphering this manuscript, photo-printed in Schomovsky's book, it appears beyond doubt that Ibn Magid was not the pilot of Vasco de Gama.

Ibn Magid at this time was certainly aware of the activities of the Portuguese in the Indian Ocean whom he refers to as the "Francs"* in several places of his Urjuza. He speaks of their infiltration into the Indian Ocean, their seeking of information from pilots arriving from India, their conquest of islands and leaving their men to rule over. He also condemns their conquest to India. Ibn

* "Francs" is a popular name in Arabic for nonbelievers, mostly from Europe. It was used extensively during the Crusades.

Magid was unaware of the coast south of Sofala and round South Africa, but he had certainly heard of the arrival of the Portuguese from this route.

Ibn Magid's account of the first arrival of the Portuguese to India goes to say that it took their ships about two years to cross and reach the East Coast of Africa (in 902 *higra* = 1497-8) and then they "undoubtedly diverted their course to India, but they hesitated to attempt the voyage to China". From India they returned to the Zing Coast. "Then again in the year 906 Higra (= 1501-2) they returned to India along the same route. "This time they bought houses, settled and the Zamorines, the people (of India) were bewildered of these *Francs;* have they come with the intention to rule over, or are they crazy robbers?"

As a man of the sea, Ibn Magid does not refrain from admiring the knowledge of the Portuguese. He admits in places in this *Urjuza* that "You shall learn more about these routes from the *Francs*" (he means the routes south of Sofala and to the west of Africa). He was certainly impressed by their arrival from the south and west, the routes which he himself had not followed, but had many illusions about these.

In no place of this *Urjuza* had Ibn Magid either directly or indirectly admitted that he ever guided a Portuguese ship to India. In an earlier *Urjuza* which he wrote in 906 *higra* (1501-2), Ibn Magid did not seem to have been aware of the presence of the Portuguese in the Indian Ocean, for not a single reference has been made about them. There is therefore no reason to dispute the Portuguese accounts that the incumbent pilot was a Moslem pilot from Gujarat. Ibn Magid was an Arab pilot from Oman.

Sources of "Muhit", a Turkish Treatise on Navigation in the Indian Ocean

Prior to the Expedition of Vasco de Gama, the Portuguese were collecting information about the route to India from the traders, and special missions were sent for this purpose to the East.

One such mission headed by Alfonso de Paiva and Pero de Covilham sailed from Portugal to Egypt, ten years before Vasco de Gama. Disguised as a Moslem, de Covilham boarded an Arab ship from Suez to Aden, while de Paiva remained in Egypt. From Aden, de Covilham took another Arab ship to India where he visited Calicut and Goa and sailed back to Sofala before he returned to Egypt. Shortly afterwards, he sailed back to India once more and this time with two other Portuguese, the name of one was Abraham de Pia and of the other Jusef Lamigo. At Hormuz in the Persian Gulf, they dispersed and de Covilham returned to Portugal via Abyssinid and through the Nile. It is said that he brought back with him Arab maps for navigation in the Indian Ocean (Kammerer, 1935).

Following the Expedition of Vasco de Gama, sea cruises by the Egyptian and Turkish fleets on one hand and the Portuguese on the other, went on for about 50 years in the Red Sea and Indian Ocean. In one such cruise, 20 ships sailed from the Suez under the Turkish Admiral Sidi Ali Hussein and these encountered 34 Portuguese ships in the Arabian Sea.

Storms often created havoc and both sides suffered heavy casualities. The Turkish Admiral took refuge in Diu and Sorat in Sind with only 9 ships of his fleet left. From there he entered the Persian Gulf and stayed in Basra for 5 months waiting for the monsoons. During this time Sidi Ali came across the nautical books of Ibn Magid and Al Mahri, from which he derived his nautical instructions known as "Mohit", which he wrote in Turkish.

This book received wide recognition only towards the end of the 19th century, when it was translated into German language by Maxmillian Bittner under the title "Die Topographischen Capitel der Indischen Seespiegels "Muhit" and, commented upon by Tomaschek (1897). Hammer (1834) and Bonelli (1894) had earlier translated parts of this book. Tomaschek adds that "Muhit" is a rare book which discusses all problems of navigation and compares favourably with the best of the Portuguese accounts of its kind.

However, Ferrand (1928) who discovered the manuscripts of Ibn Magid at a later date and compared these with "Muhit" gives no credit to the Turkish Admiral. His criticism of the latter goes to say that "tous les renseignements nautiques et astronomiques contenus dans le "Mohit" ne sont quela traduction turke, *parfois mediocre*, des textes arabes faisants l'object de la presente publication".

This criticism seems unjustified, since Sidi Ali himself gives enough credit to the Arab pilots. In his introduction to "Mohit", Sidi Ali states that during his journey to Basra, he had ample opportunity to talk to these pilots on nautical matters. "I also collected books written by pilots as Ahmad Ibn Magid and Sulayman al Mahri such as *Kitab al Fawayed, Tuhfah,* Minhag and Kilada. I have gone through these books thoroughly and believe that navigation without them is quite difficult".

"I have found it necessary to translate them into Turkish, etc."

Sidi Ali Hussein also adds that "Ibn Magid was one of the best of pilots for the West Coast of India".

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THE FUTURE OF FISH PROCESSING INDUSTRY OF INDIA

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ABSTRACT

The fish processing industry in India, during the past ten years has been rather exclusively concerned with shrimps largely because of the easy market which the shrimps provide abroad. The impact of shrimp export has not been very healthy, as the industry failed to diversify itself to other fish and fish products. Shortage of Shrimps as raw material in some areas or in certain seasons has led to under utilization of the freezing and canning plants. Surely the future of the processing industry in India does not lie in shrimps alone, for these constitute only about 12% of the country's total catch. Therefore, all other fishes including the trash fish should be considered first as important by the industry.

The Central Institute of Fisheries Technology has made considerable advance on the economic utilization of many other varieties of fish. These include marketing of the entire fish, fish fillets and picked meat. Other products such as fish flour, fish protein concentrate, fish hydrolysate, fish soup powder, fish flakes and fish sausages seem to have great possibilities. Little known products such as bacteriological peptone prepared from trash fish are also important.

Of the export-oriented industries in India that have developed during the post independence period, the fish processing industry is of special significance. It made its beginning in 1954 and exclusively based on foreign market, within a span of about 19 years, it attained the status of a full-fledged industry—augmenting the national economy by way of foreign exchange to the tune of 450 million rupees, as in 1971-72. About 34100 tonnes of fish products were exported from India during this period. But almost all the developments in fishing and fish processing has been oriented towards a single commodity-shrimps-which constitutes only about 12% of the total landings of fish in the country. Easy market facilities for processed shrimp in foreign countries was the main reason for this rather one-sided development. More and more entrepreneur were attracted to the

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trade owing to this factor and as a result the need for processing facilities increased several folds than what the landed resources could sustain. Today the country as a whole has a daily freezing capacity of over 450 tonnes with cold storage facility of 8000 tonnes and a daily canning capacity of 95 tonnes. Considering that these plants operate for 200 days in a year, they are capable of processing 1,09,000 tonnes of food per year, which, in terms of the total raw material would amount to about 2,18,000 tonnes. As against this, the total production of processable varieties of prawns in 1971 has been 73,320 tonnes. Estimate shows that about 75% of the capacities of freezing plants and 82% of the capacities of canning plants are under-utilized. It is only natural that shore plants which depend on a seasonal raw material such as shrimps, which have glut and lean periods, have excess capacity so that they can handle most of the available material during the seasons of plenty. At the same time, it is very necessary that the average utilization should not fall below a minimum of say 50%, as accepted in some other nations, so as to safeguard the viability of the units.

With the unrestricted growth of processing establishments an intense competition has also emerged for the raw material. This has led to an increase in the cost of raw material. An analysis of the price during the past five years reveals that the cost of processable varieties of prawns has gone up by 200 to 300%. The total export, on the other hand, has remained more or less the same with fluctuations of about $\pm$ 10%. Critical analysis of the unit-value-realization for the different varieties of shrimp shows that a fair increase has occurred in bigger-sized shrimp prices, except in 1970, for the smaller sized prawns, which constitute the major portion of exports, the prices have been steadily falling except for the slight improvement in 1969. As the price of new material in the home market has been soaring high, the processing cost for frozen prawns showed a substantial increase from about Rs. 1.70 per kg in 1967 to over Rs. 2.70 per kg in 1971, mainly due to increase in labour charges, cost of packing materials and freight. Yet another factor that has affected the shrimp processing industry adversely is that the availability of raw material has not kept pace with the increased demands from the industry. The increase in the production of processable varieties of prawns in 1968 as compared to 1967, has been about 46,404 tonnes and in the years 1969, 1970 and 1971, the increase and decrease have been + 2619, + 17,492 and — 16,492 tonnes respectively, when compared to the previous year in each case. These figures clearly show that the production is on the decline. The catch per unit effort of the mechanised vessels, operating especially in the south-west coast has come down considerably during the past few years. A decrease in the quantity of shrimp landed by these vessels has affected the total cost of operation by the processing plants. All these have led to the inevitable conclusion that as far as shrimp processing and exports are concerned, a near saturation point has probably been reached.

It is evident from the foregoing comments that the future of the fish processing industry in India would depend on how best the fish component of the

total catch is utilised. Under normal fishing conditions about 70-80% of the catch of the vessels is composed of fish, the major portion of which belongs to lesser known varieties of bottom forms. The pelagic fish resources comprising mostly of sardines and mackerel include 25-30% and 6-10% respectively of the total fish production in the country. These offer promise for an expanding processing industry. It is estimated that by the end of the Fifth Plan period, i.e. by 1978-79, the total marine fish catch will increase to 1.954 million tonnes from its present level of 1.17 million tonnes. By that time about 0.35 million tonnes of oil sardines, 0.295 million tonnes of mackerel, 0.35 lakh tonnes of pomfrets, 0.114 million tonnes of Bombay duck, 0.94 lakh tonnes of tunnies and 6 lakh tonnes of miscellaneous types of fishes such as sole, cat-fishes, sciaenids, ribbon fish etc. would be available annually. It is under these circumstances that the need for working out ways and means for an effective utilisation of the fish component becomes necessary.

These problems have been anticipated by the Central Institute of Fisheries Technology, where investigations on both fundamental and applied problems have been going on for the past few years. Technical problems such as "belly bursting", development of rancidity and weight loss during preservation in ice or by freezing in the case of oil sardine can be successfully overcome. Suitable insulated containers have been developed for the transport of fish over long distances. Trial consignments could be successfully transported from Cochin to Calcutta and the fish could be marketed in excellent condition at the destination. The technical know-how available in this respect offers scope for the establishment of an industry for this transportation of fresh or frozen fish to distant markets in India. Yet another significant development has been made in the production of canned sardine products. Canning of the fish for export has not so far been attempted in large scale in this country. The efforts so far made has been to produce canned sardines mainly for the internal markets.

Recent investigations have shown that even with the high cost of the tin cans, sardine canning can be made economical by resorting to alternative methods. Of these, the most promising appears to be the "Sardine natural pack" in which the fish is packed in its own juice. This product has been found to be very attractive with excellent flavour, unparalleled in any other sardine pack. Methods have also been standardised for packing the fish in tomato and white sauces. There is growing demand in the world for sardine and sardine-products in view of the shortage caused either by a fall in the catches or because some of the areas used for sardine fishing have been declared unsuitable for fear of mercury contamination. There is thus immense scope for Indian sardine to enter the world market either in the frozen form to cater to the raw material requirements of the pet-food industry or canneries such as in Spain and Portugal which are reported to be lying idle.

Progress achieved in researches on the economic utilisation of several other varieties of fishes has also been very encouraging and sufficient information has been gathered on some of the important technological problems by the Central Institute of Fisheries Technology. The feasibility of transporting some of the selected varieties to distant inland markets in fresh, iced or frozen conditions, fillet or minced meat form, conversion or certain fishes into speciality products like fish sauce, fish paste, fish soup (in powder, tablet or frozen form), fish flake, high energy food preparations, etc. and conversion into commercially important products such as bacteriological peptone or conversion into ensiled feed materials for cattle and poultry, have been studied in great detail.

Marketing of the whole fish

Certain species like *Nemipterus japonicus* (thread fin bream, locally called 'kilimin') have been found to lend themselves well to preservation by icing or freezing in the whole form and this can be transported to distant markets. At times this species constitutes more than 50% of the trawl catches. Icing in 1:1 proportion is suitable for transportation involving 24 hours journey by rail or by insulated or refrigerated trucks. For longer distances freezing and subsequent packing in insulated containers has been found to be more economical. As there is a shortage of refrigerated rail wagons in the country, the method of freezing and packing in insulated boxes becomes very handy for the large scale movement of the fish to such markets where it is most needed. Field trials conducted under an All India Co-ordinated Project on Transportation of Fresh Fish, sponsored by the Indian Council of Agricultural Research, have shown that the North Indian Markets react favourably to species like *Nemipterus,* offering an average price of Rs. 2,000/- per tonne. Considering an expenditure of approximately Rs. 900 per tonne on processing, packing and freight charges, the above price still leaves a minimum of Rs. 1,100/- per tonne to the sender to cover the price of the fish and profit.

Fish fillet and Picked meat

Trials carried out by the Indo-Norwegian Project have indicated the possibility of marketing cat-fishes, ribbon-fish and some of the deep sea bottom fishes in frozen filleted form. The possibility of extracting the meat from cheaper varieties of miscellaneous fish by using meat picking machines and freezing into blocks has also been encouraging.

Speciality products

(a) One of the effective means of utilising cheap fish is by the conversion into edible fish flour or fish protein concentrate (FPC) which can be blended, in suitable proportion with protein-deficient food materials such as cereals. India is among the few world countries which have perfected the preparation of FPC. The product has excellent colour, with an average protein content of 78.8%.

(b) Fish hydrolysate incorporated with high energy food

Another important product on which considerable work has been done at the Central Institute of Fisheries Technology is the malt and fish hydrolysate incorporated with high energy food. The product is readily soluble and can be consumed direct by mixing it with beverages, hot milk or water. Trials carried out by the Institute show that it has a consumer acceptability of 95%. It has great possibilities simply because it is highly acceptable and is free from fish-odour.

(c) Fish soup powder

Fish soup powder is another readily acceptable product which can be prepared from miscellaneous fish. The product can be readily mixed in boiling water to a consistency which is acceptable to more than 95% of the consumers, as revealed in a recent acceptability survey.

(d) Fish flake

Another product for which the method has been standardised is fish flake. It contains about 20% protein and has been found to have good cookers properties. The product has already become popular.

(c) Fish sauage

Experiments carried out have revealed the possibility of using jew fish, kilimin etc. for the preparation of fish sausages. Work is being undertaken at the Fisheries College, Mangalore, under the All India Co-ordinated Project on the utilisation of trash fish sponsored by the ICAR to evolve the most suitable synthetic casings for the product and to extend its shelf life.

(f) Other products from trash fish

Experimental studies have shown that good quality bacteriological peptone can be prepared from trash-fish-meat. The product is comparable in quality to imported peptone processed from several other sources. Yet another product that holds a good scope for commercial production is fish ensilage for cattle and poultry feeds. It is a good protein supplement.

As mentioned earlier, the future of the fish processing industry in India depends on an effective utilisation of all types of fish. With the available technology on a variety of products one can safely say that the industry will take the right step forwarding its various stages of development.

HYDROGRAPHY IN RELATION TO TUNA FISHERIES IN THE INDIAN OCEAN

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ABSTRACT

Tuna fishing grounds in relation to hydrographic conditions were studied from the data obtained during the IIOE (1960-64). The most abundant catch of the yellowfin tuna was found in the equatorial countercurrent area and in the south equatorial current areas. The Indian Ocean central water area and subtropical convergence area (75°E) formed good ground for albacore tuna. The big-eye tuna occurred in subtropical convergence area with the maximum concentration of fishes along the marginal areas. The results indicate that the upwelling areas are favourable for tuna fishing in the equatorial zone.

INTRODUCTION

Subpolar intermediate waters coming from the higher latitudes to lower subtropical and tropical latitudes have potentialities to enrich the upper euphotic zone through the physical processes such as upwelling or upward flow, convectional mixing, overturn or turbulent mixing due to the transport of nutrient-rich water. Gales such as hurricanes, cyclones and strong monsoons also cause upwelling, convection and turbulent mixing. Accompanying eddies along the boundaries of major oceanic currents may result in mixing of deeper nutrient-rich-water in the upper sun-lit layer of the above mentioned storm-breeding vorticity zone. The cyclonic eddies in particular of the northern hemisphere and anti-cylonic eddies of the southern hemisphere give rise to highly fertile water respectively from the deep layer in their cores.

As usual, intense photosynthetic activity of phytoplankton starts, in the euphotic zone, which leads to grazing of zooplankton and successive prey predators interactions in the food-web at each tropic level and consequently results into

the successful abundance of commercial fishes. In this way, a productive zone is established in the equatorial belt of the Indian Ocean, similar zones can also be recognised as a result of equatorial undercurrent and equatorial countercurrent in the open sea of the Indian Ocean.

From the data obtained during the IIOE (1960-1964), we have studied tuna fishing grounds in relation to hydrographic conditions and some of the results have been reported below :

Tuna Fishing Grounds In Relation To Hydrography In The Eastern Indian Ocean

The Japanese participation (1960-1964) of the IIOE included 4 fisheries training and research vessels (*Umitaka Maru, Koyo Maru, Kagoshima Maru* and *Oshoro Maru*). During the northern winter, we found a remarkable zone of discontinuity at the meridional sections of the Indian Ocean near the latitude 15°S. In the northwestern offing of the Australian continents, wherein a conspicous cold and fertile upwelling area is located, the mixed subantarctic intermediate water in the upper layers, south of Sunda Islands can be recognised. This is intercepted by the north Indian saline water having its origin in the

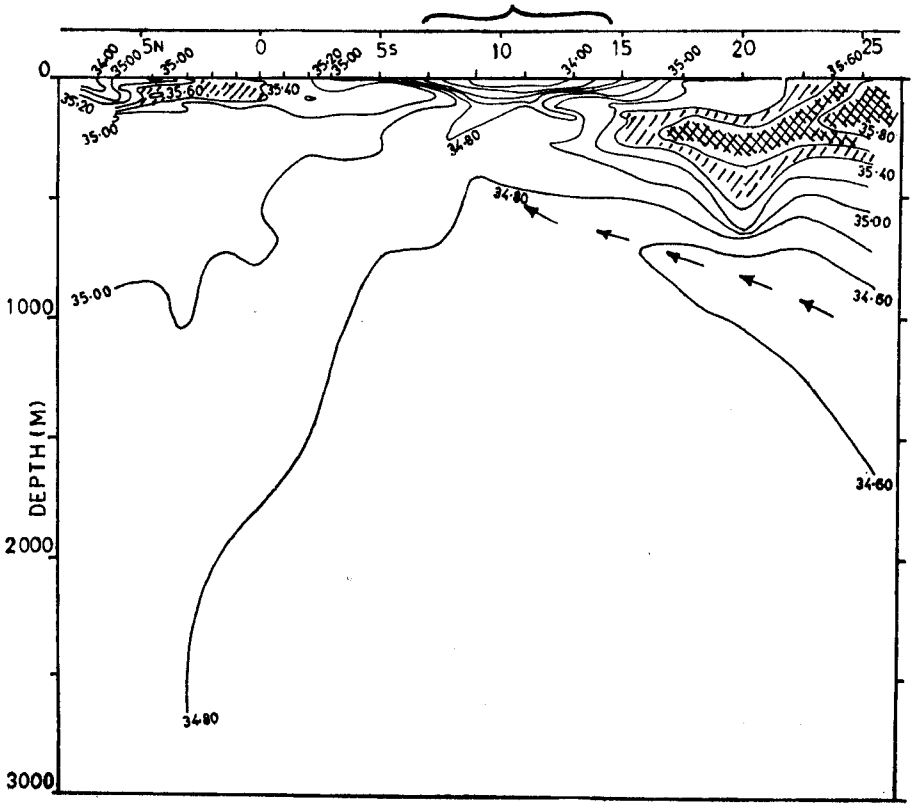


Fig. 1. Vertical distribution of salinity (‰) along the maridional line 78°E (1962/'63)

Arabian Sea and the south Indian saline central water (Figs. 1 and 2). In the northern summer, the line of discontinuity (equatorial oceanic front) still existed and continued till winter. (See the result of the Australian survey CSIRO, 1963-65). The productive zone coincided with the intertropical convergence zone (a train of atmospheric anticyclonic eddies or the breeding zone of cyclones and hurricanes) which corresponded to the above upwelling zone.

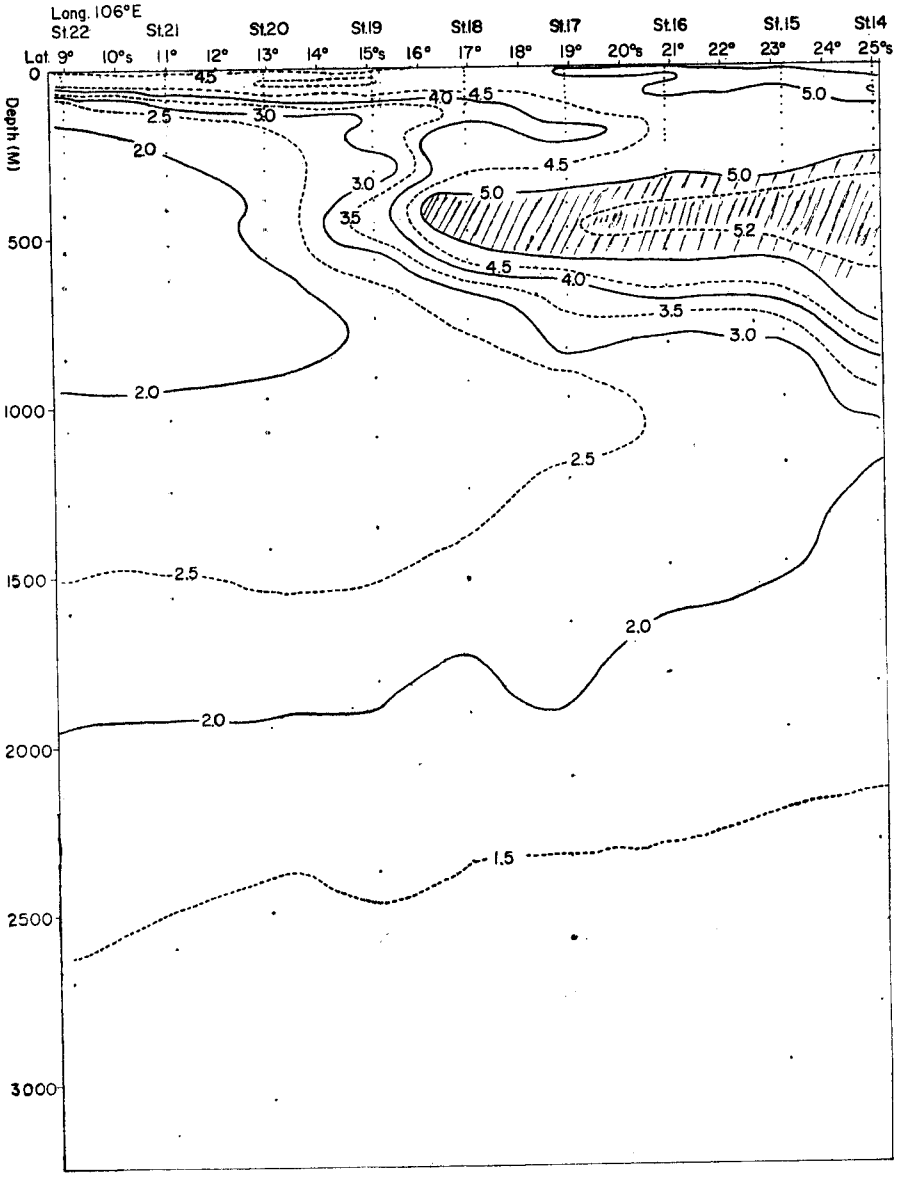


Fig. 2. Distribution of dissolved oxygen (ml/l) along the meridional line of 106°E.

We have noticed considerable variation in the distribution patterns of water temperature, salinity etc. between the winters of 1962/'63 and 1963/'64. This indicates the general northern shift of the current systems and the upwelling area of the above-mentioned cold water in the eastern Indian Ocean, in response to changes in meteorological conditions, e.g. a contrast in the distribution of salinity at 100 m depth in both years. (Figs. 3a and 3b). The world-wide abnormal climatic year 1963 is noted by the prevalence of northeast monsoon with abnormal coldness in the southeast Asian region in response to southerly invasion of jet-stream (planetary development of three waves pattern).

The biosphere was closely related to the above oceanographical structure and variation. The distribution maps of primary production prepared by Sugawara and Saijo, sea-birds and fishes by Ozawa and total tuna catch by Uda (Nat. Comm. for IIOE, Japan, 1966) agreed with the distribution of salinity-minimum belt (upwelling zone of the subantarctic intermediate water) as shown in Figs. 1 and 2.

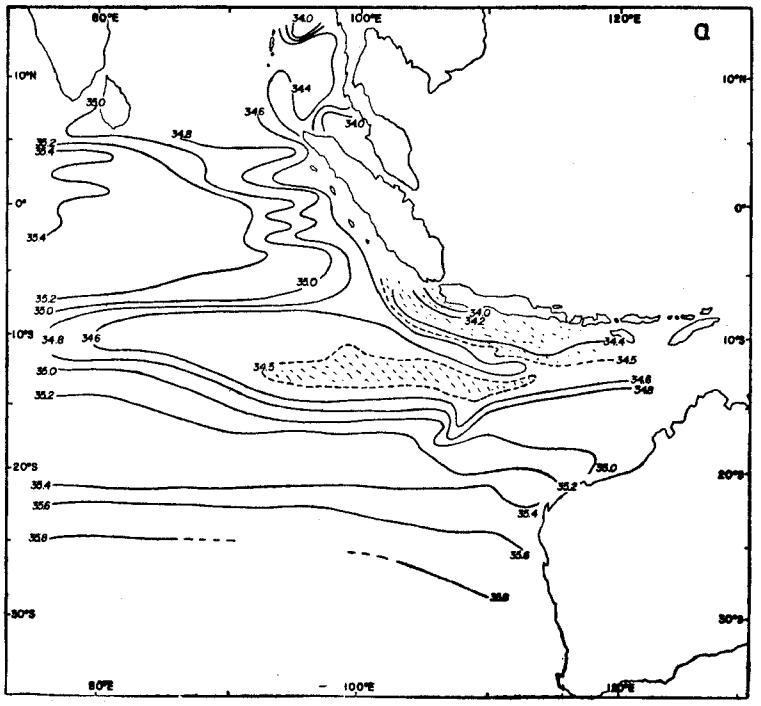


Fig. 3a. Horizontal distribution of salinity (‰) at the depth of 100 m in the winter of 1962/'63.

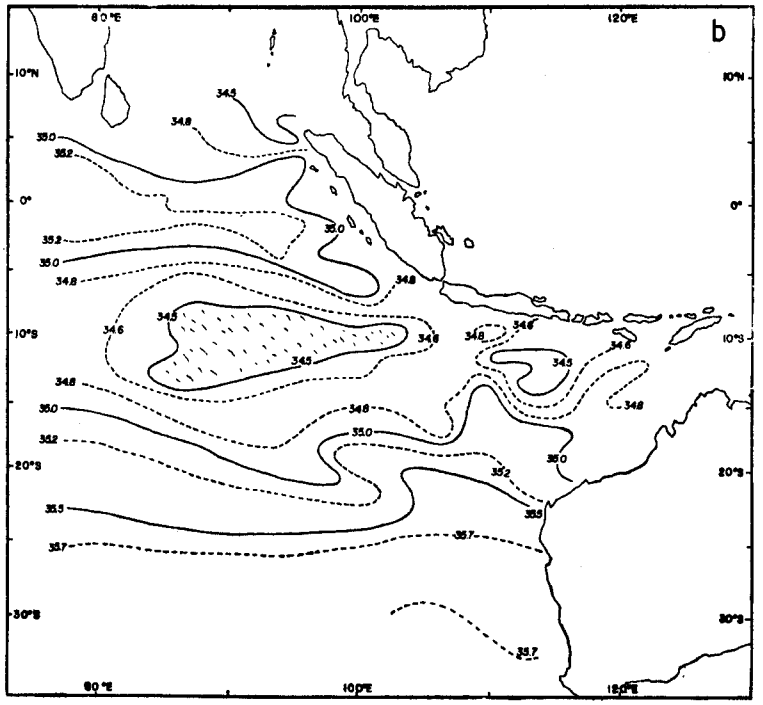


Fig. 3b. Horizontal distribution of salinity (‰) at the depth of 100 m in the winter of 1963/'64.

Water masses in the eastern Indian Ocean were analysed as indicated in Fig. 4 and the following areas were identified:

A .... South Indian Ocean central water (highly saline)
B .... Arahura sea water (low saline, high temperature)
C .... Arabian Sea origin north Indian water (highly saline)
D .... North Indian Ocean origin of waters in the Bay of Bengal (low salinity)
E .... mixed water, upwelled in the area, south to Sunda Islands
F .... mixed water, flowing to west in the south equatorial current.

Summarizing the above, we can conclude that the most favourable tuna fishing grounds are located mainly around the marginal areas of the above mentioned upwelling zone. We recognize similar oceanographic and fisheries conditions in the western Indian Ocean as described later (IIOE-Japan, 1966; Suda, 1971; Ramanathan, 1969). In conclusion, it seems that from the west to the east belt, located along 10°S-15°S in the Indian Ocean, has the zone of demarcation, which is a highly productive area. It has water of relatively low salinity due to the mixing of upwelled subantarctic intermediate water, with the highly saline watermasses of the north and south Indian Ocean (see above A and C).

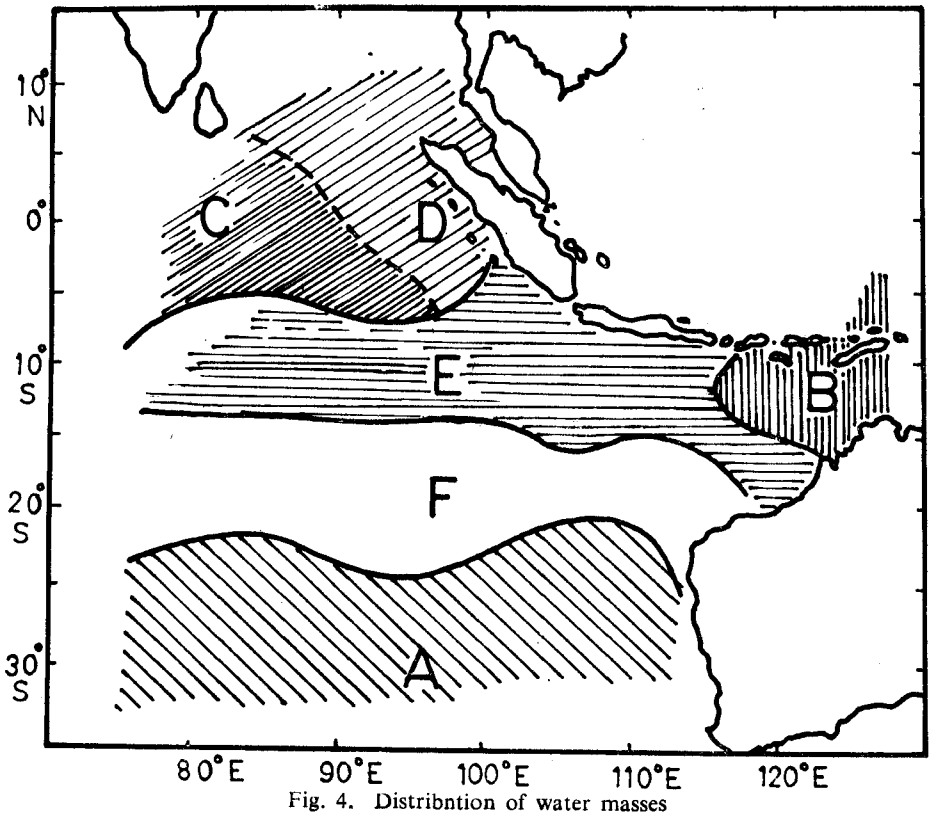


Fig. 4. Distribntion of water masses

The southward expansion of the lower salinity water in the surface layer, west of Sumatra, changes from year to year. The variation in the core pressure which is low in summer is also important. Variability in the oceanic climate was illustrated by isotherms and isohalines at the meridional sections and along the horizontal levels above 600 m depth. Seasonal oceanic changes—the most remarkable one in the pre-monsoon period, from April to May, and the year by year changes induced by the incoming monsoon—are very well pronounced. These may be responsible for the dominant year-classes of tunas and consequently to their abundance.

Tuna Fishing Grounds and Oceanic Fronts in the Western Indian Ocean, Basing on the Data by the *Anton Bruun's* Survey.

The surveyed areas by the *Anton Bruun* (Cruise 5, January 26-May 4) during the US Program in Biology of IIOE, can conveniently be divided into the following three regions : i) Arabian Sea (January 27-February 3), ii) 10°N-36°S along 55°E line (February 5-March 9), and iii) 43°S - 5°N along 75°E line (April 4-30), (Fig. 5). Experimental fishing using Japanese tuna long-line was carried out at 38 stations (5 along i, 17 along ii, 16 along iii) with 45 baskets at each station and 6 hooks per basket on the average.

(a) *Hydrographic results of the survey along 55°E and 75°E*
55°E (Fig. 6 a, b, c, d)

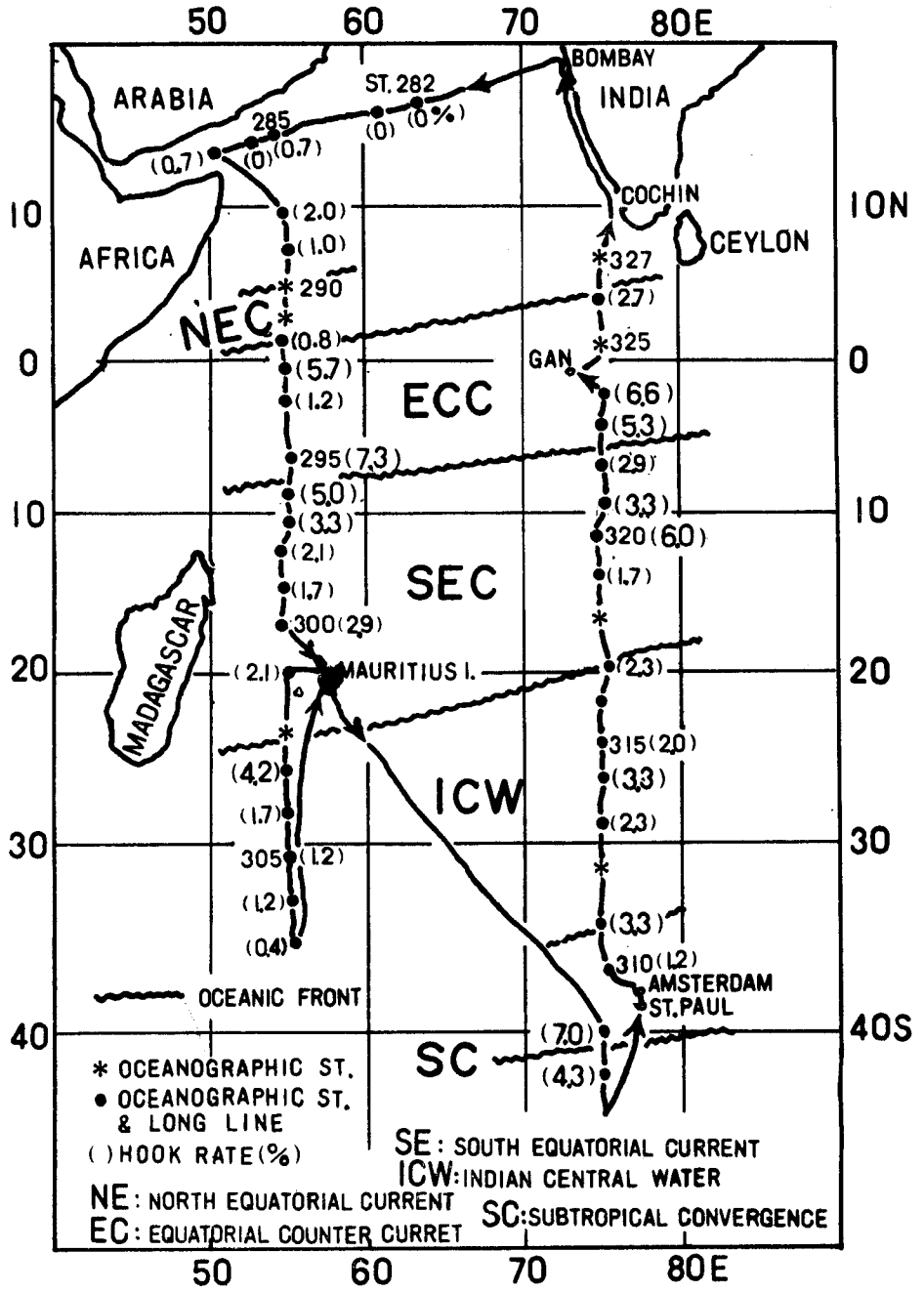


Fig. 5. Cruise track and station positions by the *R. V. Anton Bruum* Cruise 5, Jan. 26–May 4. 1964 Figures indicate the mean hook rate (%) by the long-line and current system based on data by the *R. V. Anton Bruum* Cruise 5.

Temperature and salinity profiles are shown in Fig. 7. Dissolved oxygen profile denotes a discontinuity layer at about 50-100 m, similar to thermocline indicated in the figures. From these figures we can notice the north equatorial current area (5°N-1°N), the equatorial counter-current area (1°N-8°S) and the south equatorial current area (8°S-23°S). Consequently the existence of oceanic fronts are evident at about 1°N between north equatorial current (most developed in north-east monsoon season) and the equatorial counter-current, at about 8°S between the equatorial counter-current and south equatorial current, and also at about 24°S, as a line of convergence between the south equatorial current and the south Indian Ocean central water.

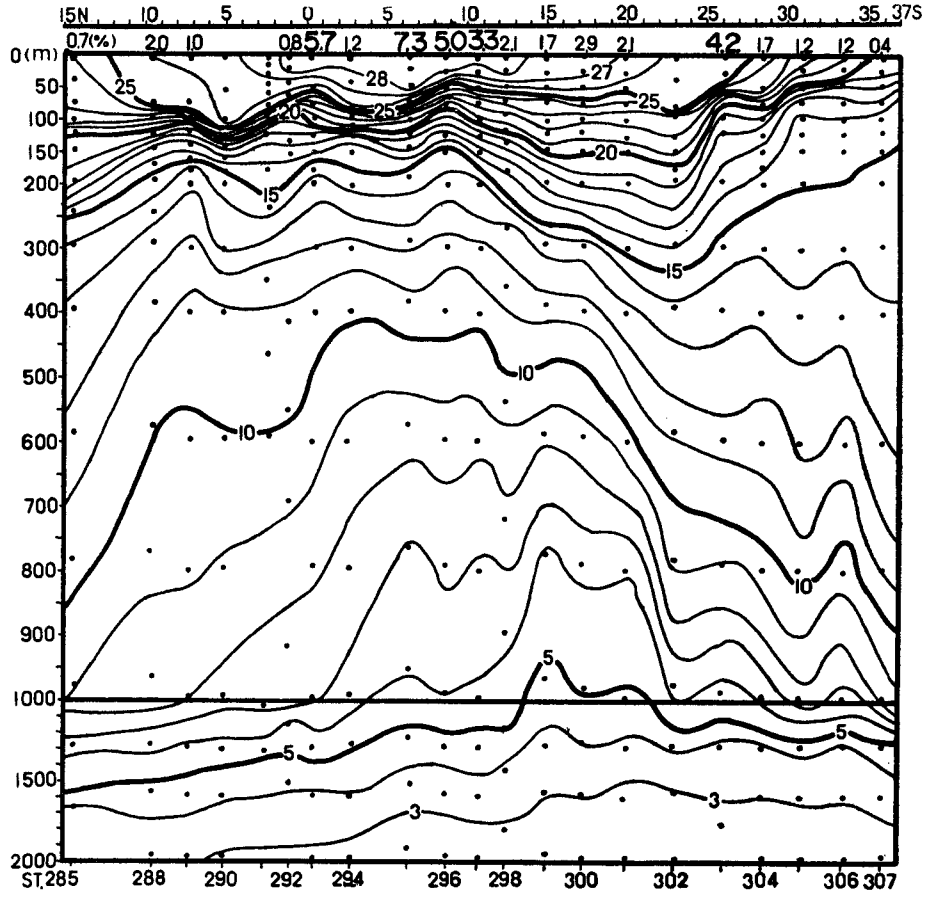


Fig. 6a. Vertical distribution of water temperature (°C), along 55° E.-line, Feb. 5- Mar. 9, 1964. Figures along 0 m-line indicate hook rate (%) by the long-line at each station (See Fig. 1)

Further, we can remark thermal spreading pattern of isotherms below the equator, suggesting the existence of equatorial undercurrent at about the depth of 150 m near about 1°N and also upwelling pattern under the equator, 75°E profiles (Fig. 7 a, b, c, d).

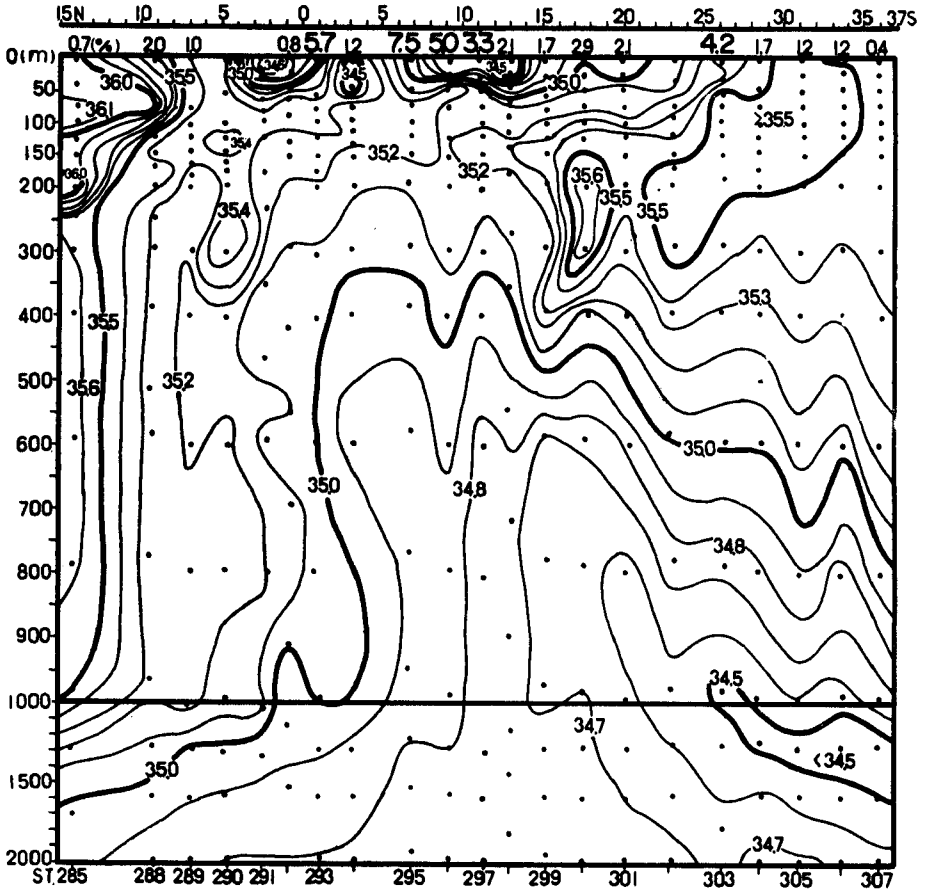


Fig. 6b. Vertical distribution of salinity (‰), along 55° E.-line, Feb. 5- Mar. 9, 1964. Figures along O m-line indicate hook rate (%) by the long-line at each station.

Temperature, salinity and oxygen profiles commonly indicate the sharp spring layers. The existence of water boundaries were observed at about 4°N between the north equatorial current (table north-east monsoon current in the surface layer) at about 6°S between the equatorial countercurrent and the south equatorial current, at about 20°S between the south equatorial current water and the south Indian Ocean central water, at about 35°-40°S between the Indian Ocean central water and the west drift water as the line of subtropical convergence.

It is hard to distinguish clearly the peculiar thermal spreading feature characteristic of the equatorial undercurrent on this profile.

(b) *The experimental result of longline fishing* (Anton Bruun *cruise 5*) *in the western Indian Ocean* (Fig. 8, 9 and Table 1)

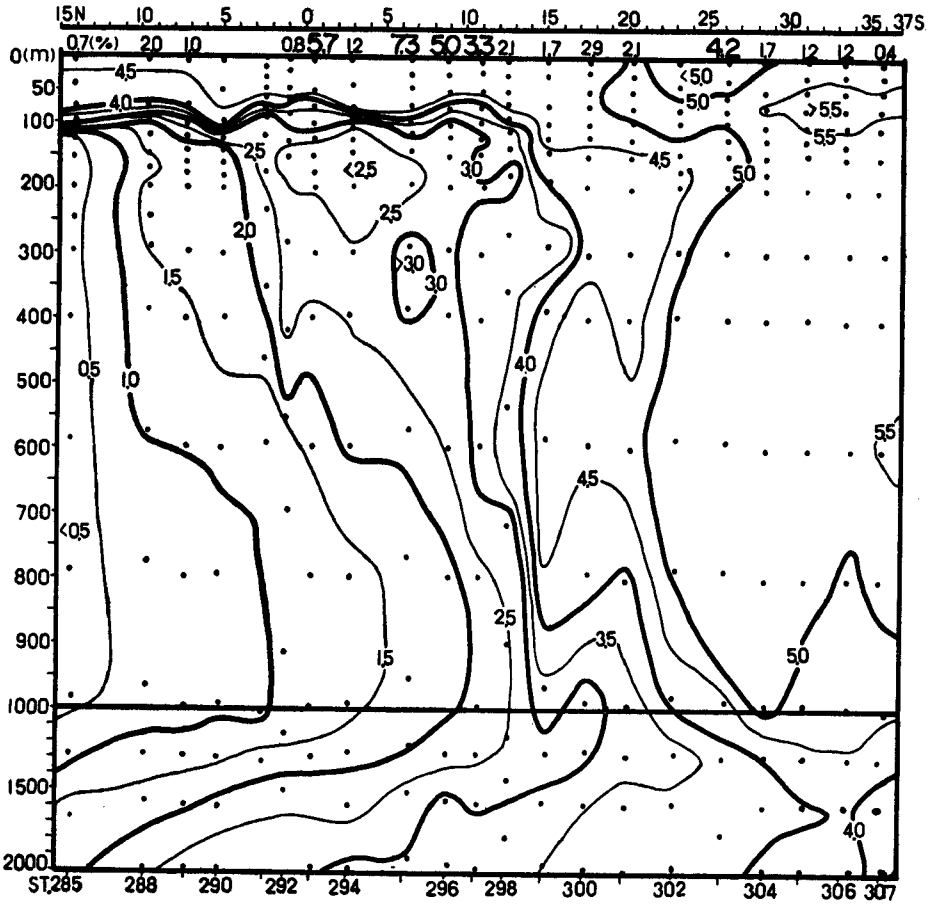


Fig. 6c. Vertical distribution of dissolved oxygen (ml/l), along 55° E.-line, Feb. 5- Mar. 9, 1964. Figures along O m-line indicate hook rate (%) by the long line at each station.

The hook-rate shown in the figure presents higher values around 8°-11°S and 26°S along 55°E line, and from the equator to near 3°S, 8°-11°S, near 26°S and near around 40°S-42°S along 75°E line. The appearance of tuna catch in the latitudal zones for each meridional profiles along 55°E and 75°E lines respectively has been indicated in Table 1-a and 1-b. Figs. 8 and 9 give the species composition of the tuna catches on each meridional profile. In the tuna catch along 55°E line, yellowfin was the highest, and the next were the big-eye and albacore, nearly of the same order. Along 75°E line, the albacore catches were most abundant, and the yellowfin and big-eye catches were nearly the same. Accordingly, we can see that the yellowfin was relatively more abundant in the western part and in the lower latitudes. In the south Indian Ocean,

the more abundant catch was of albacore (20°-40°S) and there was no catch of this tuna north to 5°S.

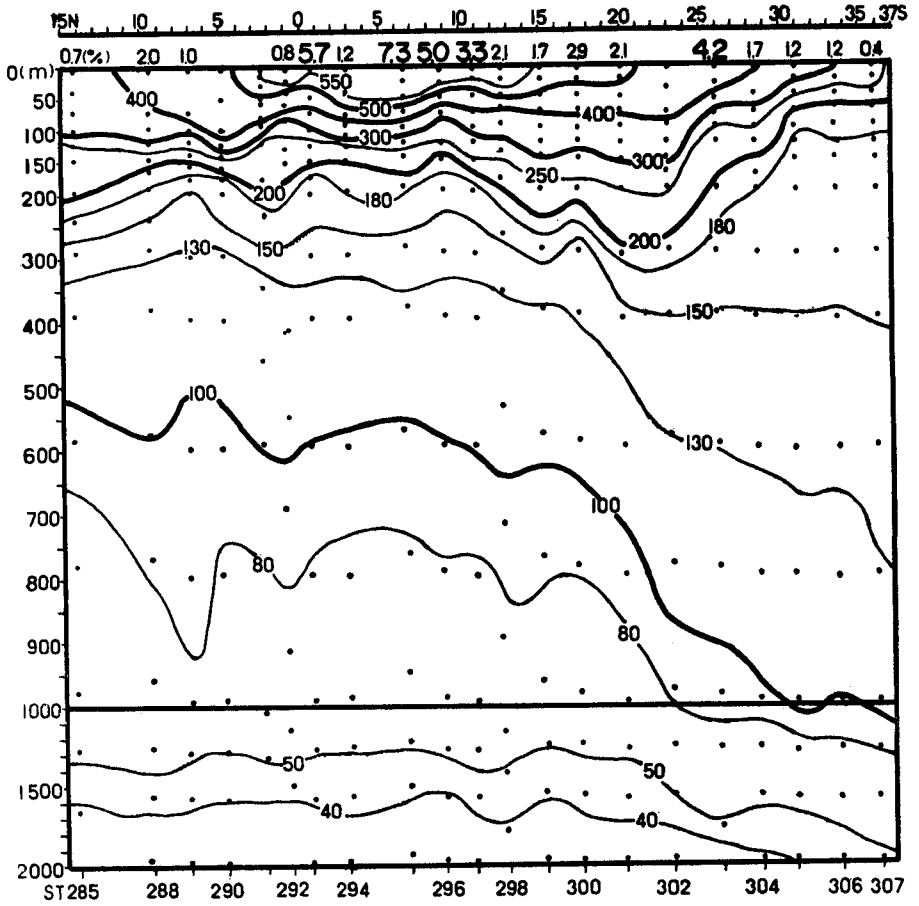


Fig. 6d. Vertical distribution of thermosteric anomaly ($\delta\tau$, cl/ton), along 55° E-line, Feb. 5-Mar. 9, 1964. Figures along O m-line indicate hook rate (%) by the long-line at each station.

(c) *Tuna fisheries in relation to hydrography of the western Indian Ocean*

Almost 55°E line in general, higher hook-rate were found around the oceanic fronts, i.e. between north equatorial current and equatorial counter-current; between equatorial counter-current and south equatorial current, and in the zone of convergence near the southern boundary of such equatorial current.

Similarly, along 75°E line higher hook-rate were recorded around or adjacent to the oceanic fronts, i.e. around the water boundary of the equatorial counter-current and south equatorial current; near the water boundary (convergence)

between the south equatorial current and the Indian Ocean central water; near the subtropical convergence in the southern hemisphere. However, the hook-rates of tunas along the 75°E line around the oceanic front, between the north equatorial current and the equatorial counter-current (near 4°N) appear to be lower as compared to that of 55°E line.

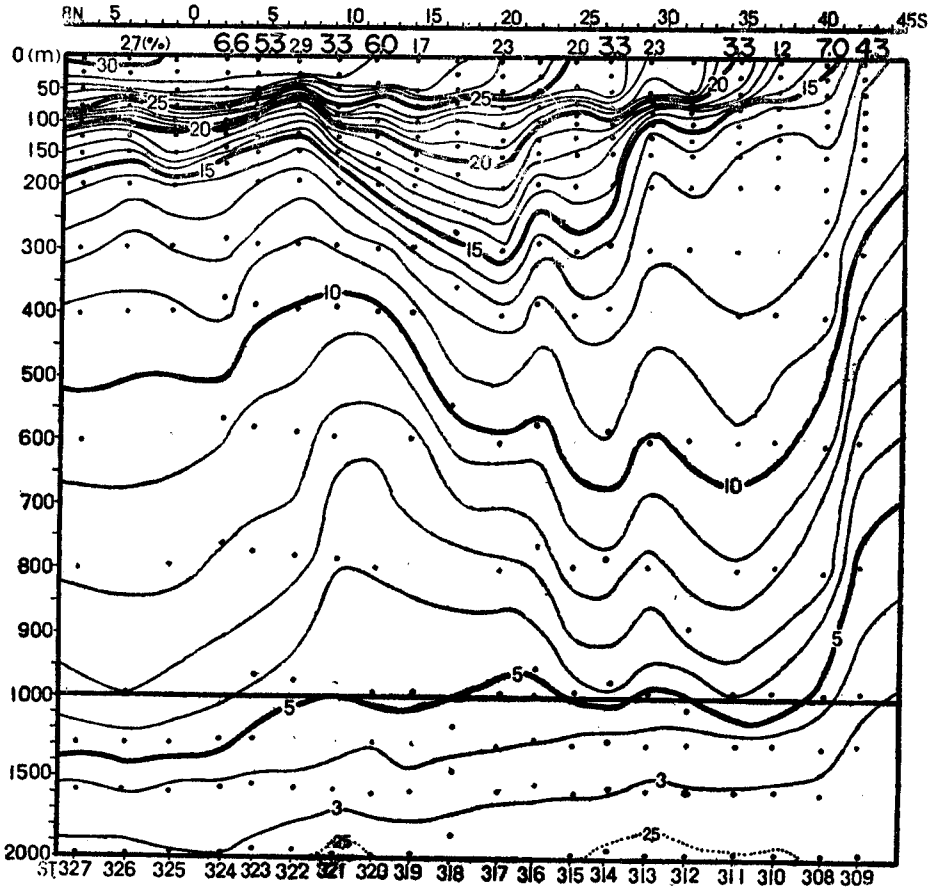


Fig. 7a. Vertical distribution of water temperature (°C), along 75° E.-line Apr. 4-30, 1964. Figures along O m-line indicate hook rate (%) by the long-line at each station (See Fig. 1).

It should be noted that particulary favourable catches along both the profiles of 55°E, and 75°E lines were found near the water boundary between the equatorial counter-current and the south equatorial current.

The hook-rate on an average along 55°E and 75°E lines, show a shift of the peak in the equatorial waters 8°-9°S, 55°E, near 6°S and on 75°E, which

may be due to the shift of oceanic fronts. The peaks on both the profiles lie along the equatorial counter-current area or north of its southern boundary. The favourable tuna fishing grounds, therefore, are located along the oceanic frontal region.

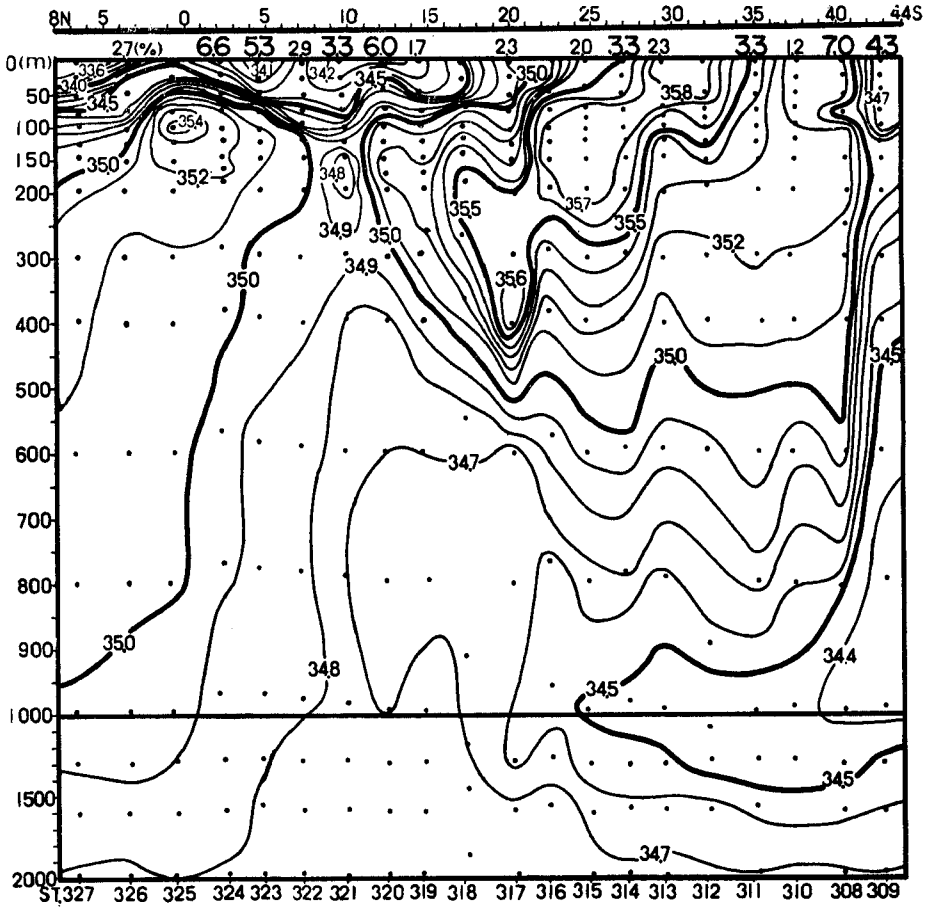


Fig. 7b. Vertical distribution of salinity (‰), along 75° E-line, Apr. 4-30, 1964. Figures along O m-line indicate hook rate (%) by the long-line at each station.

The prevalence of the Red Sea water is recognised more along 55°E down to 8°N, (having salinity above 35.5‰) and less along 75°E. It is extended more to the south (near 1°N having salinity of 35.4‰). In general, the region of maximum hook-rate appears to localize in the marginal area or water boundaries or along the oceanic fronts.

We can thus conclude that the most abundant catch of the yellowfin tuna is found mainly in the equatorial counter-current area and in the south equatorial current area, that of albacore-tuna in the Indian Ocean central water area and subtropical convergence area (75°E), and that of big-eye tuna particularly in the subtropical convergence area with the maximum concentration of fishes along the marginal area.

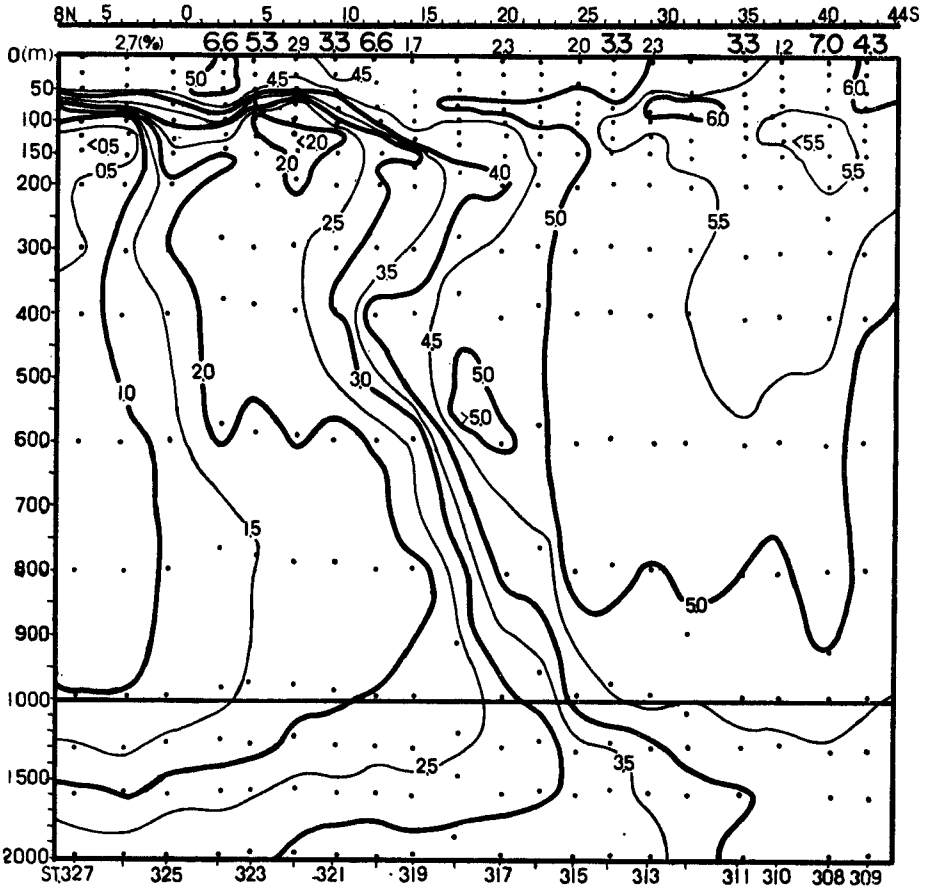


Fig. 7c. Vertical distribution of dissolved oxygen (ml/l), along 75° E.-line, Apr. 4-30, 1964
Figures along O m-line indicate hook rate (%) by the long-line at each station.

Panikkar and Jayaraman (1966) have pointed out the biological and oceanographic differences between the Arabian Sea and the Bay of Bengal with reference to upwelling areas and the fisheries of the oil sardine and mackerel in India. Our results of the IIOE (1966) confirm that upwelling areas are also favourable for tuna fishing in the equatorial zone.

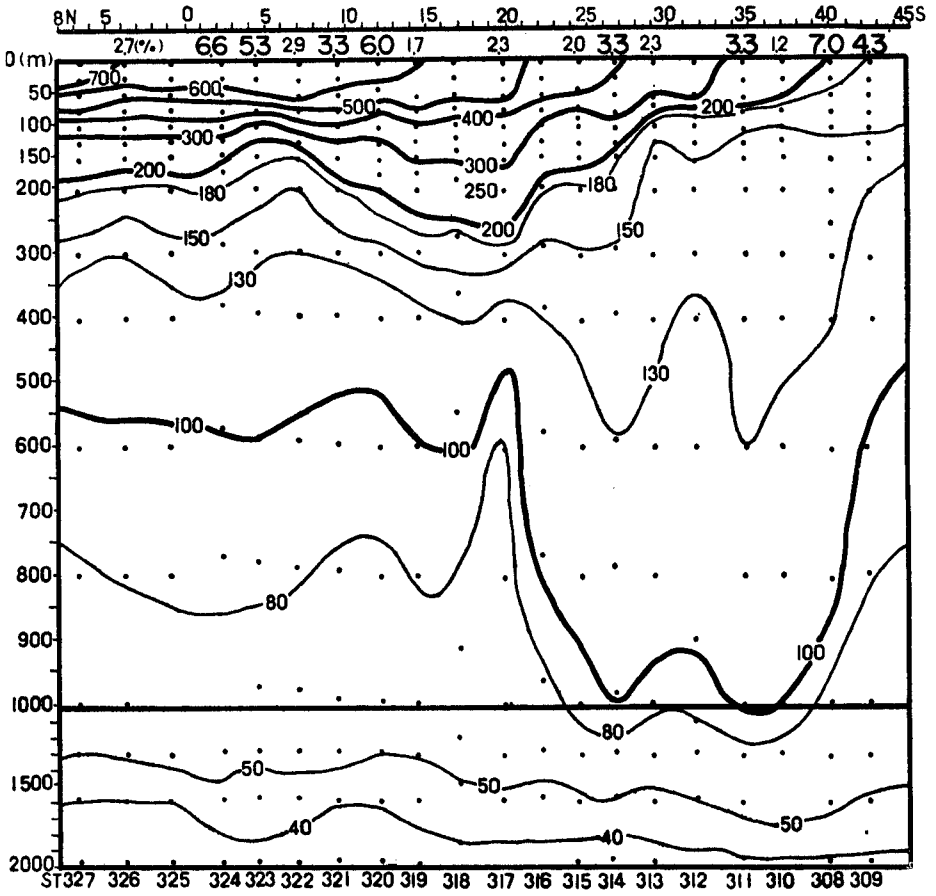


Fig. 7d. Vertical distribution of thermosteric anomaly ($\delta\tau$, cl/ton), along 75°E.-line, Apr. 4-30, 1964. Figures along O m-line indicate hook rate (%) by the long-line at each station

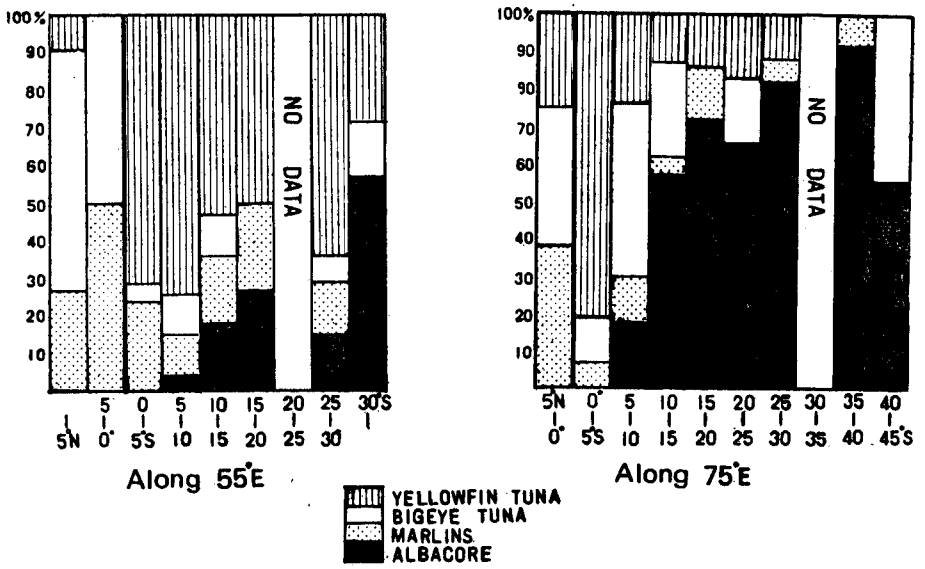


Fig. 8. Fish composition of Tunas at the intervals of 5° latitude.

TABLE 1. *A final result of longline-fishing by the R. V. Anton Bruun Cruise 5 in the Indian Ocean. Mean hook rate means arithmetical mean at the intervals of 5° latitude*

a. Along 55° E.-line (Feb. 5-Mar. 9, 1964)

Position of fishing round	No. of hooks	No. of operations	Fish Species				Total catch	Mean hook rate
			Yellowfin	Bigeye	Albacore	Marlins		
— 5°N	1208	4	1	7	0	3	11	0.93%
5° — 0°	242	1	0	1	0	1	2	0.80
0° — 5°S	484	2	12	1	0	4	17	3.45
5° — 10°	544	2	25	4	1	4	34	6.15
10° — 15°	725	3	9	2	3	3	17	2.37
15° — 20°	484	2	6	0	3	3	12	2.50
20° — 25°		NO DATA						
25° — 30°	484	2	9	1	2	2	14	2.95
30°S —	720	3	2	1	4	0	7	0.93
TOTAL	4891	19	64	17	13	20	114	2.33

b. Along 75°E.-line (Apr, 4-30, 1964)

Position fishing round	No. of hooks	No. of operations	Fish Species				Total catch	Mean hook rate
			Yellowfin	Bigeye	Albacore	Marlins		
5°N — 0°	302	1	2	3	0	3	8	2.70%
0° — 5°S	544	2	26	4	0	2	32	5.95
5° — 10°	544	2	4	8	3	2	17	3.10
10° — 15°	604	2	3	6	13	1	23	3.85
15° — 20°	302	1	1	0	5	1	7	2.32
20° — 25°	302	1	1	1	4	0	6	2.00
25° — 30°	604	2	2	0	14	1	17	2.80
30° — 35°		NO DATA						
35° — 40°	544	2	0	0	12	1	13	2.25
40° — 45°S	602	2	0	15	19	0	34	5.65
TOTAL	4348	15	39	37	70	11	157	3.61

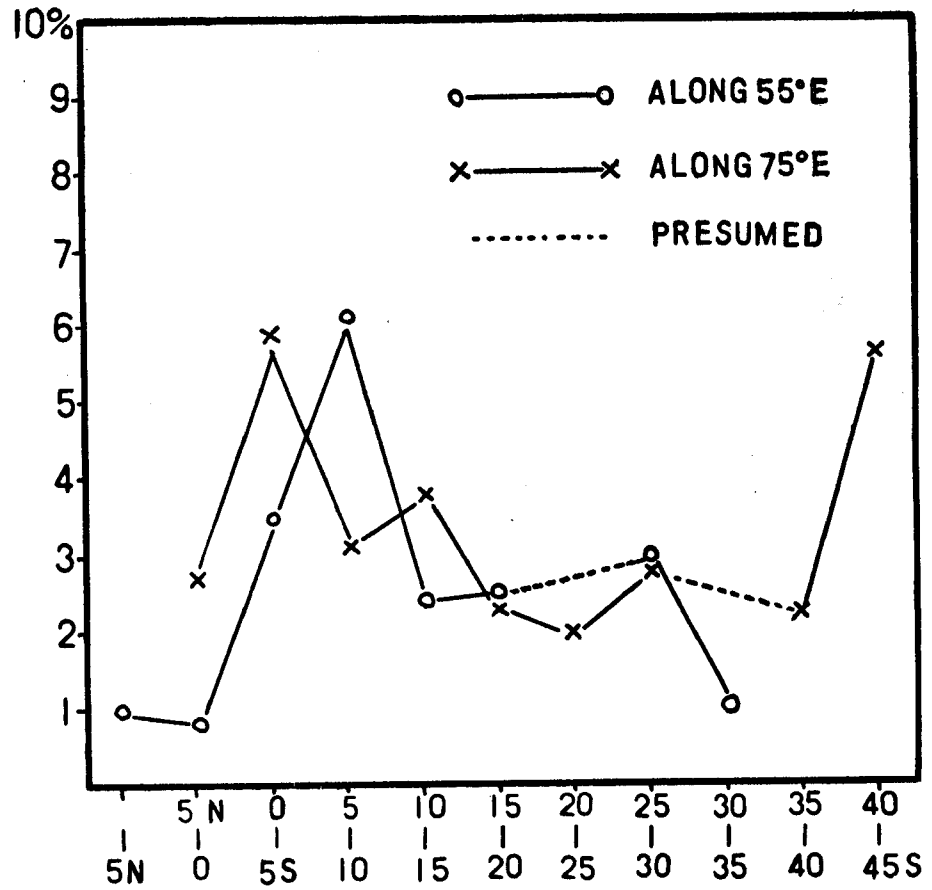


Fig. 9. Arithmetical mean hook rate (%) of Tunas at the intervals of 5° latitude.

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THE ATTACHMENT AND EARLY DEVELOPMENT OF THE TETRASPORES OF SOME CORALLINE RED ALGAE

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INTRODUCTION

Corallina officinalis L. and *Jania rubens* (L.) Lamour, are both members of the Corallinaceae; until fairly recently their similarity led to their being placed in the same genus, as, for instance by Newton (1932) but the separation is now accepted and Johansen (1970) has shown that important differences exist, particularly in the reproductive structures. Ecologically there are additional differences : *Corallina officinalis* is a lithophyte occurring on a wide range of shores, both sheltered and exposed, throughout the cooler waters (0°C-20°C surface temperature) of the Northern Hemisphere. It is common on all coasts of the British Isles in littoral pools, on lower littoral rock and extends into the sub-littoral. *Jania rubens* is found in warmer waters (10°C-30°C) and in the British Isles is common only on the more temperate coasts, including the Channel Islands, Southern England west of the Isle of Wight, Ireland and northwards to Anglesey on the coast of Wales. The species is less common in Scotland and eastern England. Unlike *Corallina, Jania* is invariably epiphytic on other algae in pools or in the immediate sub-littoral on fairly sheltered shores. It has a restricted range of hosts; on Anglesey these are *Furcellavia fastigiata* (L.) Lamour., *Laurencia pinnatifida* (Huds.) Lamour, and most frequently, *Cladatephus verticillatus* (Lightf.) C. Ag. and *C. spongiosus* (Huds.) C. Ag.

Previous work on the morphology, life history and taxonomy of both species has appeared in publications by Rosenvinge (1917), Suneson (1943), Von Stosch (1969) and Johansen (1970). Cabioch (1966) has investigated the early development of some coralline spores but did not specify her culture conditions.

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Preliminary observations suggested that there might be differences in the settlement and rate of development of the spores which might be related to their habitats and a closer examination of these topics is the subject of the present paper. During the course of the work, observations were also made on a third coralline alga, *Melobesia minutula* Fosl. which occurs as a small epiphyte on *Jania rubens* and, to a lesser extent, on *Corallina.*

Development Rate of Tetraspores

Materials and Methods.. Fertile material of both species was collected during July and August 1970, at Rhosneigr and Treaddur Bay on the west coast of Anglesey and transferred without delay to the laboratory. Plants were maintained in a healthy condition in the re-circulating sea water system described by Jones and Dent (1970). Tetrasporic plants were more readily available than cystocarpic and tetraspores were therefore used exclusively. The spores are produced in conceptacles which were examined for the presence of mature spores before the material was used in experiments. In order to do this, selected conceptacles were first de-calcified in dilute hydrochloric acid.

To obtain spores, fertile plants or portions of plants were cleaned of obvious epiphytes and placed on glass microscope slides in shallow dishes containing a 2 cm depth of sea water. These were left undisturbed for 18 hours during which spores were shed naturally from conceptacles. The fertile fronds were then removed but, in order to allow the spores to attach themselves to the slides, the dishes were left undisturbed for a further period. This was 24 hours in the case of *Jania* but it was found that *Corallina* required longer and 48 hours was therefore allowed for this species. After attachment the slides could be handled for examination or placed in running sea water without risk of accidental detachment.

Three temperature regimes were employed :—

1) 10°C in a temperature - controlled tank of re-circulating sea water.
2) 15°C in a temperature-controlled cabinet in filtered sea water which was changed every other day.
3) 17-20°C in the laboratory's circulating sea water system. This temperature was not controlled and was subject to seasonal and some daily variation.

Illumination was provided for a daily period of 12 hours by means of Atlas 'Daylight' fluorescent tubes producing 1300-1500 lux at the position of the experimental material. This was the same for all temperature regimes.

Batches of 30 slides were used in each experiment, ten being placed in each temperature regime. A record was kept of the course of development and its

rate by examination of the slides under the microscope. Whilst the spores were being observed and photographed each of the slides bearing them was held in a shallow 'Perspex' tray into which it fitted closely and which contained sufficient sea water to cover the spores and prevent their desiccation.

In order to detect the onset of calcification, sodium alizarin sulphonate, which stains calcified tissue red, was employed. Dilute hydrochloric acid was also used, calcification being indicated by the appearance of a bubble of carbon dioxide which could be observed under the microscope.

Development of tetraspores of Jania rubens

In running sea water at a temperature of 17°–20°C the course of development was similar to that described by Cabioch (1966a). At the time of release the tetraspores were spherical; on becoming attached they flattened somewhat against the substratum with an increase of diameter of about 20%. Newly attached spores were found to measure from 35 m to 100 m in diameter with a modal value of 75 m. At this stage the light microscope revealed a halo of refractive material, presumably an attaching substance, around the spore. Division began within a few hours of attachment, the first wall being more or less upright but not apparently orientated in any particular direction related to external stimuli. A second division divided the spore into four approximately equal

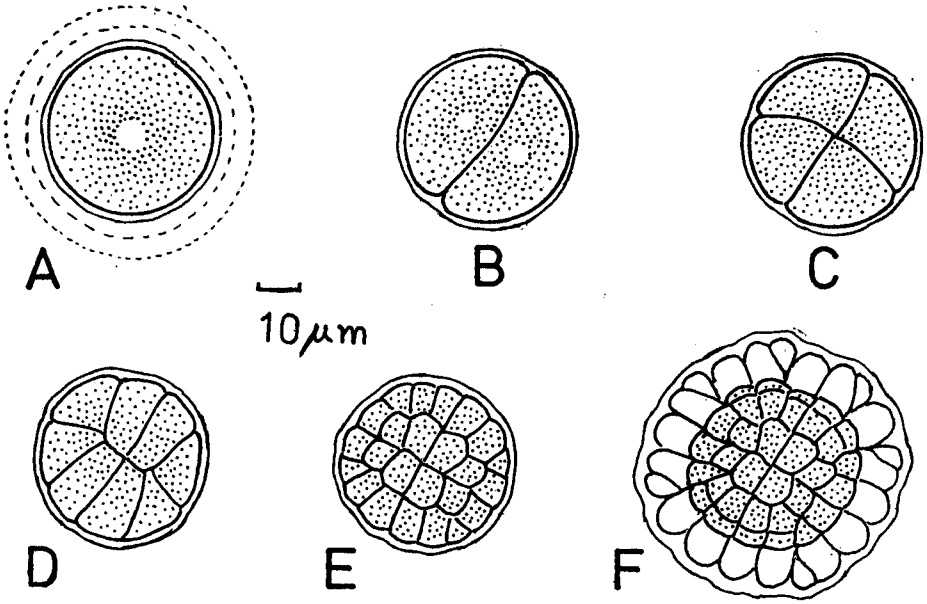


Fig. 1. Stages in the early development of tetrasperes *Jaina rubens* at 17°C - 20°C
A, Newly attached spore showing 'Hale' of mucilaginous material. B, 2-celled stage, 9 hours after attachment. C, 4-celled stage. D, 8-celled stage. E, 24 cells visible at surface of spore, 1-2 days after attachment. F, Initiation of marginal growth, 2-3 days after attachment.

segments; these four cells were found, as Cabioch (1966a) reported, to behave as 'primordial cells'. Subsequent division (see Fig. 1) resulted in the formation of a 24-celled stage, as seen in surface view. Frequently additional divisions occurred in the periferal cells to give a 36-celled stage. Up to this time no enlargement of the spore could be detected but subsequently growth began, appearing first in the marginal cells which acted as the primordial cells of the basal crust. Each of these apical cells cut off cells of the crust by tangential divisions, also undergoing frequent oblique divisions which served to increase the number of marginal apical cells and kept pace with the expanding circumference.

Calcification was first detected at the 24-or 36-celled stage when red staining could sometimes be obtained with sodium alizarin sulphonate; the production of a gas bubble by dilute hydrochloric acid could not be observed earlier than the initiation of the basal crust.

By the 6th day the basal discs had grown to a diameter of 70—120 m. Beyond this, there was little increase in diameter but the initiation of the upright axis was observed on the 7th day. Groups of elongated, colourless cells were cut off at the surface of the sporeling, either on the central portion formed by the original spore or on the marginal disc. These uncalcified cells constituted the basal geniculum which reached 40-50 μ in height within 24-48 hours. In a further 24 hours the darker cells of the first intergeniculum had appeared and the cells of the second geniculum were being cut off at its distal end. Thus, within 10 days, the tetraspore had grown into a recognisible plant with a well marked upright axis and a fully formed basal attachment disc. By the 13th day the first intergeniculum was up to 200 μ m long and 50 μ m broad; its cells had become calcified very quickly.

Hairs of the type usually seen in the Rhodophyceae developed on the first intergeniculum of most sporelings in cultrue at 150°C. These hairs were unicellular, up to 200 μ m long and 10 μ m wide. They were deciduous and were shed after about three weeks.

In subsequent development, sporelings were often observed on which one or two additional axes developed from a single basal disc.

Development of tetraspores of Corallina officinalis

The tetraspores of *Corallina* were also spherical but smaller than those of *Jania;* newly attached spores had diameters ranging from 35 μ m to 100 μ m with a modal diameter of 58 m. Their development in running seawater at 17°C —20°C was as follows:

The halo surrounding the newly attached spore was considerably smaller and had a more distinct margin than in the case of *Jania. Corallina* spores

were more densely pigmented and this made cell divisions more difficult to observe. This difficulty was increased by the earlier calcification of the sporeling which could be detected at the 4-celled stage. Within 48 hours of attachment, a 24- or 36-celled sporeling similar to that of *Jania* was produced and growth of the basal crust began within the next 24 hours. The crust was organised in four segments, each originating from one of the four primordial cells. If any of these failed to develop, the crust would at first be deficient of the corresponding segment(s) but this became less obvious with the continuing spread of the crust. The expansion of the crust continued as in *Jania* and as described by Cabioch (1966a) but there was no early cessation of growth; the crust continued to grow to exceed 1.5 mm in some cases. Coalescence of sporeling crusts similar to that reported by Jones (1956) in *Gracilaria verrucosa* (Hudson) Papenfuss was often observed but the position of the original spore was marked by the presence of a dome of cells which reached an average height of 70 μm and a diameter of 150 μm in four weeks. The production of upright axes occurred much later than in *Jania;* only after 13 weeks was the first intergeniculum visible. The axes developed only from the sporeling domes and were never observed to do so from the crust in these cultures. If a dome was damaged, as sometimes occurred during the removal of epiphytic diatoms, no axis developed. However, in earlier experiments, when *Corallina* spores were grown for a long period at a lower light intensity, very extensive crusts were produced which covered the full width of a microscope slide and extended over the edges; these produced upright fronds at the edges after many months of growth.

As in *Jania,* hairs were observed. These grew from the basal crust in cultures at 15°C and 10°C.

Development of spores of Melobesia minutula

This species was identified growing epiphytically on *Corallina* and *Jania.* Spores were presumably shed by fertile plants on the experimental material since *Melobesia* sporelings appeared on the slides. The thallus of *M. minutula* is a thin fan-shaped encrustation which grows from spores similar to those of *Jania* and *Corallina. Melobesia* spores were measured as having diameters of 28—30 μm. Development began very soon after attachment. The first two divisions gave rise to four primordial cells, which each divided tangentially to give rise directly to a crust initial or, sometimts, a second cell which again divided to give the crust initial. In either case a rapid development of the creeping thallus began. Fronds corresponding to both *f. typica* Fosl. and *f. lacunosa* Fosl. were observed, both were monostromatic, bright pink in colour and lightly calcified.

Effects of temperature: Results

1) *Corallina officinalis.* Growth was measured as the expansion of the basal crust taking the average of 10 sporelings in the 17°C—20°C regime and 5 each at 15°C and 10°C. The results are shown in Table 1. In this the maxi-

mum individual size attained at the end of 40 days at 17—20°C and 48 days in the others is shown together with the average growth of the 5 or 10 sporelings measured at each temperature.

TABLE 1. *Growth of Corallina sporelings measured as diameter of basal crust in the first 40-48 days*

Temperature	17°C — 20°C	15°C	10°C
Maximum size recorded	651 μm	412 μm	230 μm
Average growth per day	13.6 μm	3.7 μm	3.0 μm

The initiation of the upright axis showed differences of the same kind. At 17—20°C the first segment was formed in 12 weeks. At 15°C only the basal cellular dome was formed by this time and at 10°C no more than a slight rise could be seen at the position of the original spore.

2) *Jania rubens.* Growth in *Jania* was not measured by the expansion of the basal disc which was of limited growth. Table 2 shows the time taken to reach various stages at the two higher temperatures.

TABLE 2. *Time taken in days to reach successive stages in the development of Jania sporelings*

Temperature	17°C–20°C	15°C
24 cell stage	1–2	2–3
Crust initials	2–3	4
Basal geniculus	7	8
1st. segment	8–9	10

At 10°C few sporelings developed beyond the 24—36-celled stage; loss of pigmentation and death occurred at this stage or earlier.

3) *Melobesia minutula.* This species grew equally well under all three temperature regimes and development was considerably faster than that of *Jania.* Fronds, 2 or 3 cells broad, were formed within 24 hours and grew into well developed encrusting thalli recognisable as *Melobesia* plants in 3 days.

ATTACHMENT OF SPORES

Sinking Rate. The sinking rate of spores in still water is, to some extent, a measure of the time for which they can remain suspended. This rate was measured in *Jania* and *Corallina* by timing the sinking, through a measured distance (15 mm) of spores which had already been sinking long enough to reach their terminal velocity. Spores could be readily observed through a stereobinocular microscope when illuminated from the side by a beam of light at right angles to the line of vision.

The average sinking rates were 0.7 mm. sec $^{-1}$ for *Jania* tetraspores and 0.33 mm. sec $^{-1}$ in the case of *Corallina.* These differences are in accordance

with Stoke's law on the basis of the relative radii of the spores and providing that their denisities are similar.

Time required for attachment. It has been mentioned that it was found necessary to allow *Corallina* spores a longer period for attachment. This is a matter with interesting ecological implications and it is also important to know if the process is a gradual one extending over hours or if it is a comparatively speedy process which is subject to a mechanism which delays its occurrence. It seemed advisable to investigate this more fully.

Method. The apparatus shown diagrammatically in Fig. 2 was designed to subject settled spores to an oblique force which could be duplicated exactly for each test.

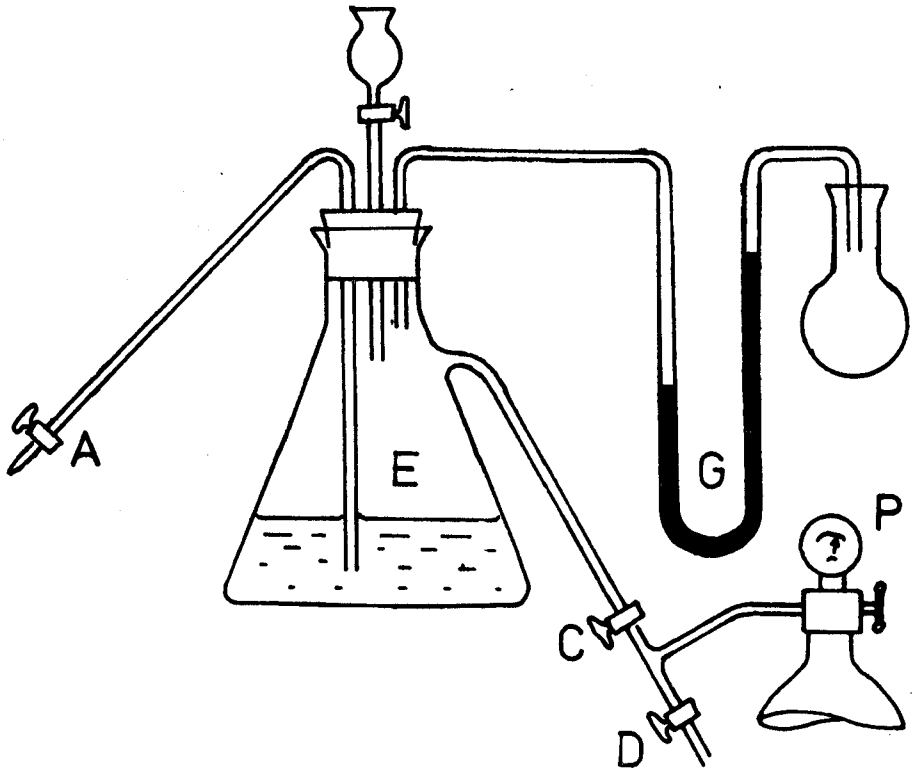


Fig. 2. Apparatus used to determine numbers of spores successfully attached. For explanation, see text.

A cylinder of compressed air was connected via a reducing valve at P. With taps C open and D closed, the pressure in the Buchnar flask E could be adjusted by the reducing valve and read on the mercury manometer G. On opening tap A, water was forced through the capillary tube. The pressure in E remained constant by the action of the reducing valve regardless of the changing volume.

In use the capillary tube was directed towards the spores on a slide held at 45° to the direction of the jet and 3 cm. away from it. The pressure was maintained at 122.4 gm. cm $^{-2}$. Fertile material was set to shed spores on to slides and was removed after one hour. Then at suitable intervals batches of three slides were removed from the dish. On each in turn the spores were counted, the slide subjected to the jet and the spores remaining counted again.

Results. Table 3 gives the percentage of spores of *Jania* and *Corallina* respectively which remained after treatment based on the totals from three slides in each case.

TABLE 3. *Percentage survival of spores under standard jet treatment*
Numbers given are totals from three slides

A. *Jania rubens* tetraspores

Hours after shedding	Number of spores before test	Number of spores after test	% Attached
0–1	36	0	0
1–2	33	4	12.5
2–3	37	10	27
3–3.5	38	33	80
3.5–4	22	18	82
4–4.5	45	44	98

B. *Corallina officinalis* tetraspores

Hours after shedding	Number of spores before test	Number of spores after test	% Attached
2–3	73	0	0
5–6	81	4	5
8–9	96	12	12
23–24	80	43	54
25–26	89	56	60
27–28	128	107	76
31–32	116	98	80
47–48	94	94	100

In the case of *Jania,* no attachment occurred in the first hour but subsequently the number surviving each successive test rose rapidly until after 4-4½ hours, 98% of the spores were attached. *Corallina* spores, on the other hand, attached themselves much less readily; only 5% had done so after 5-6 hours, 54% after a day and only after two days was 100% attachment observed.

Conclusions. Assuming that the attachment process is similar in all spores of a particular species, it appears that some spores can complete the process in under 2 hours in *Jania* and 5 hours in *Corallina.* However, some spores have not done so after 4 hours in *Jania* and 32 hours in *Corallina.* It seems more probable that, in these late attachments we are dealing not with a long drawn-

out cementing process but with a comparatively speedy one, the onset of which is delayed for a period which varies between individuals but is generally longer in *Corallina* than in *Jania.*

Examination of newly settled spores

Since the delay in attachment was so different in the two species and since differences could easily be seen in the appearance of newly settled spores, it was decided to investigate this aspect in more detail.

Methods. Observations by means of the light microscope was supplemented by examination under a Cambridge 'Stereoscan' electron microscope for which the spores were prepared as follows : Settlement of tetraspores was obtained onto cover glasses. Twelve hours were allowed for attachment in *Jania* and 48 hours in the case of Corallina. Fixation was effected in 4% gluteraldehyde solution buffered to pH7 with Cacodylate and with sucrose added to 0.25 M concentration. Overnight fixation was followed by three 30 minute washes in buffer with successively smaller sugar concentrations. The coverglasses were then passed through liquid Arcton to liquid Nitrogen and freeze dried. A carbon film was then deposited followed by a film of 60:40 gold/ paladium.

Observations. The attached spore of *Jania* was seen, under the light microscope, to be surrounded by a light halo of material spreading as much as 20 μm from the spore and apparently of more than one concentric band of refractive material. Under the Stereoscan microscope the surface of the spore appeared to be covered by a substance which spread into a rim around the spore. Under a higher magnification, the rim appeared to consist of at least 3 layers, the lowermost spreading farthest outwards, which had a distinctly stranded appearance. The inference drawn was that a considerable quality of some (? mucilaginous) substance had been produced in a series of discharges from the spore and spread outwards cementing it to the glass.

Under the light microscope, *Corallina* spores lacked the extensive halo and had a much more restricted and clearly defined rim resembling a cell wall. Under the Stereoscan, the exudation from the spore was much less copious than in *Jania* seemed less stranded and to be one layer only. The well defined outer edge of the rim suggested a material of greater viscosity than in *Jania.*

Chemical nature of the cementing substance

Methods. Some preliminary tests were made on the attached spores using the following stains and reagents : 1) Gurr's negative stain, the particles of which adhere to mucilage; 2) Methylene blue as a general stain for mucilage; 3) Alcian blue as a stain for acidic mucopolysaccharides; 4) Sodium alizarin sulphonate as a stain for calcified material; 5) Dilute hydrochloric acid as an indicator of calcification.

Observations. Negative stain particles adhered to the surface of newly attached spores of both species and to the halo of *Jania* indicating the presence of mucilage. Blue coloration obtained with Methylene blue and Alcian blue, indicated that the attaching material was probably a mucopolysaccharide.

In Jania spores, sodium alizarin sulphonate produced no colour, indicating no calcification at this stage; hydrochloric acid had no obvious effect. In *Corallina* spores, however, the stain produced a red coloration, indicating some calcification and hydrochloric acid caused the spores to become detached. In view of the early calcification of the spore, it appears that this process is also involved in the attachment of the *Corallina* spore at an early stage but not in the case of *Jania.* Possibly the cementing mucilage is less important in *Corallina* and the cell wall itself plays a part in early attachment.

Other observations

1) *Tolerance of desiccation.* Both species required continuous immersion for successful attachment. After this, young, uncalcified spores of *Jania* could not survive 30 minutes out of water in the laboratory but spores of *Corallina* of the same age could survive a longer period of desiccation.

2) *Spore production.* When the rate of release of tetraspores from receptacles was investigated, it was found that *Jania* shed an average of 9 spores per receptacle (range 5-14) in 12 hours. In the same period, *Corallina* shed an average of 25 spores per receptacle (range 10-38).

General Discussion

The differences described in this paper between the development patterns of *Jania rubens* and *Corallina officinalis* correlate well with the ecology of the species.

The more southerly distribution of *Jania* and its greater prominence in Anglesey shores in summer, together with its short, summer fruiting season, are reflected in its failure to develop beyond the 24-36 cell stage at 10°C. It is interesting to note that development to a similar stage, which involves cell division without growth, can take place readily in the dark in some red algae such as *Gracilaria verrucosa,* presumably at the expense of stored food reserves. The division of the *Jania* spores under unfavourable conditions which will not permit growth is analogous. *Corallina* has a more northerly distribution and a much longer fruiting season on Anglesey, reflected in its slow, but otherwise normal, development at 10°C.

Other characteristics may be related to the epiphytic habit of *Jania* contrasted to that of the lithophytic *Corallina.* Thus the more rapid development of *Jania* correlates with its growth on a living and, therefore, short-lived sub-

stratum. In this connection the still more rapid development of *Melobesia,* an epiphyte on *Jania,* seems entirely appropriate.

Jania's smaller spore output, faster sinking rate and short delay before attachment argues a reduced need for wide distribution. Where there is one suitable host plant, there will probably be another nearby and the chance of successful settlement is likely to diminish with increasing lapse of time. Suitable habitats for lithophytes are more widespread. Similarly the small basal attachment disc of *Jania* seems appropriate; an extensive basal crust as seen in *Corallina* would have no great survival value on a narrow cylindrical substratum.

In *Corallina* the long delay before attachment in the majority of its spores is arguably an advantage in a lithophyte. Such plants are more often found growing in cracks and depressions than on smooth rock; presumably initial fixation in such places has the advantages of protection against dislodgment by water movement, grazing by browsing molluscs and, in littoral situations, against desic cation. A spherical, non-motile spore is more likely to lodge in such a position if there is a period during which water currents can roll it across a rock surface. A short delay would be no disadvantage in *Jania* but here the limited range of its host plants suggests that there may be some kind of chemical stimulus triggering the attachment process when contact is made with the appropriate hosts. We have no evidence on this point, however, but have noted that, following the formation of its basal disc, *Jania* adheres much less securely to glass than does *Corallina.* Glass is much more similar to the natural substratum of *Corallina* and it may be that the attachment chemistry of *Jania* is better adapted to fixation to plants. Our observations suggest that the cell wall of *Corallina* is more directly concerned in the attachment of the plant than in the case of *Jania.*

Although we cannot conclude that the attachment process in *Jania* is essentially different from that of *Corallina,* it seems that there are at least differences of degree. A reasonable conclusion would be that there may be differences as large or greater in the attachment process of other Rhodophyceae and that the investigation of these mechanims should be a fruitful field for study.

SUMMARY

The growth rate of tetraspores of *Jania rubens* (L.) Lamour and *Corallina officinalis* L. at different temperatures correlates well with their geographical distribution. *Corallina* grows slowly at 10°C whereas *Jania* will not develop beyond an early stage at this temperature. Subjection of settled spores to a standardised water jet showed 98% of *Jania* spores securely attached after 4½ hours, but the same result in *Corallina* was obtained only after 2 days. Examination of spores showed that *Jania* spores produced more mucilage than those of *Corallina.* Dilute acid caused the detachment of *Corallina* spores but not those of *Jania.* Development after attachment was faster in *Jania* where an axis grew from a basal disc of limited size in 8 days. In *Corallina* broad basal crusts

produced axes only after 12 weeks. *Corallina* sporelings became calcified at an early stage; *Jania* considerably later. It is suggested that *Jania's* more rapid development, its limited basal development and shorter delay before attachment are related to its epiphytic habit, while the longer delay in *Corallina's* attachment allows wider dispersal and its wide basal spread and slower development are not disadvantageous on a longer lasting stony substratum. It is also postulated that similar or greater differences may be found between the attachment processes of other red algae.

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ZONATION OF INTERTIDAL ORGANISMS ON THE ROCKY SHORES OF BOMBAY

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ABSTRACT

Zonation of intertidal organisms on the rocky shores of Cuffe Parade, Chowpathy, Breach Candy and Mahim around Bombay was studied. In all the four shores it was possible to recognise the following general pattern of zonation.

(i) Upper littoral zone dominated by littorinids-four littorinid species were abundant in all the four localities. Major species showed definite vertical zonation.

(ii) Mid littoral zone characterised by barnacles and oysters, was divisible into three or four belts-dominated by distinct set of animals.

(iii) Lower littoral zone (wide zone), had a large number of species and maximum number of animals-trochids in general dominated this zone.

INTRODUCTION

The study of biotic divisions of the intertidal region is very fascinating. The environment is subjected to interaction between the sea, land and atmosphere and is covered and uncovered every day by the flood and ebb tides, with the result that the organisms inhabiting the intertidal region acquire the capacity to endure the variations in temperatures and desiccation during the exposure which continously changes from day to day and from season to season. The striking feature of such an environment is reflected in the vertical zonation of the organisms. The zones where the animals of one type predominate are named after them. This is because that these organisms are generally restricted to definite limits and concentrate at levels where optimum living conditions exist. One characteristic feature of the shore fauna is that the composition and the order of the communities are almost the same everywhere; thus the littorinids inhabit the higher levels of the shore throughout the world, but the individual species are different in different parts of the world. Barnacles are found on the midlittoral rocks in the cold as well as in tropical seas. The algae dominate the lower levels. Similarly the members of Trochidae are also found at about the same levels in many places.

Stephenson (1939) visualized the possibility of evolving a universal system for zoning the intertidal regions of the world. Stephenson and Stephenson (1949) recognised three zones viz. (1) Supralittoral fringe extending from the upper

limit of the barnacle line to the upper limit of littorinids, (2) Midlittoral zone and (3) the Infralittoral fringe at the point where the large algae such as the laminarians cease to become dominant. These authors have also pointed out that the limits of these zones and the indicator organisms vary from place to place as these get modified by the various environmental factors. Other investigators in the field such as Womersley and Edmonds (1952) and Chapman and Traverthan (1953) have given different names to different zones of the intertidal regions. Bhatt (1959) has shown from his studies on distribution of the organisms on four rocky shores around Bombay i.e. Cuffe Parade, Chowpatty, Breach Candy and Mahim that the three zonation present support the scheme drawn by Stephenson and Stephenson (1949). However, it is felt that the terminology proposed by them and subsequently adopted by many workers needs certain modifications and this aspect has been mainly discussed in this paper.

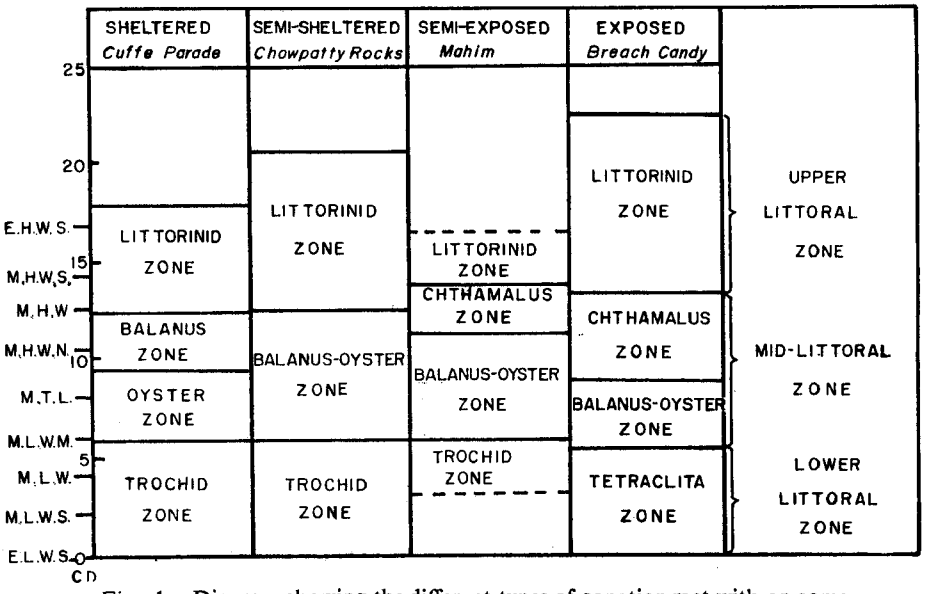


Fig. 1. Diagram showing the different types of zonation met with on some rocky shores at Bombay.

EHWS - Extreme High Water of Springs - 5.2 meters
MHWS - Mean High Water of Springs - 4.4 meters
MHW - Mean High Water - 3.8 meters
MHWN - Mean High Water of Neaps - 3.2 meters
EHWN - Extreme (lowest) High Water of Neaps - 2.7 meters
ELWN - Extreme (Highest) Low Water of Neaps - 2.6 meters
Local Mean Sea Level of Survey of India Levelling or MTL - Mean Tidal Level - 2.5 meters.
MLWN - Mean Low Water of Neaps - 1.9 meters
MLW - Mean Low Water - 1.3 meters
MLWS - Mean Low Water of Springs - 0.8 meters
ELWS - Extreme Low Water of Springs - 0.0 meters above Chart Datum
C.D. - Chart Datum

CUFFE PARADE SHORE

The Cuffe parade is a sheltered boulder beach, facing north-west. It lies in a small shallow bay and is bounded on one side by a sea wall which is parallel to the shore and acts as a breakwater. This sea wall and the boulders at the entrance to the bay reduce the wave action. To the south of this is a mangrove swamp, separated by a uniformly 3 meters wide storm-water-drain. The wall of this drain is about 2.2 meters high with its top situated at the level of MHWS.

The shore is 457.5 meters long of this about 305 meters is exposed at ordinary spring tides. The rocks extend down to the level of MLWS, below this the bottom is of soft sand and clayey mud. Most of the Bay gets uncovered at the lowest spring Tides (Plate I, Fig. 1). It is divisible into three sections. In the first section one finds sloping embankment of stones and extending from over a 0.3 meters above the EHWS to about MHW. The stones chiefly harbour littorinids and the Isopod (Ligia). In the next section which is about 183 meters wide, there are large boulders and rocky ledges parallel, to the shore with mud deposits in between them. Most rocks are from 1 to 1.5 meter high. Small pools also exist as a result of the construction of fish-traps. The boulders are covered with oysters and along with these *Planaxis, Nerita* and *Cerithium* are also found. Trochids and muricids are often found near the base of the boulders. In the third section which is near the low water, there are rocky platforms, boulders and stones largely covered with borers. In some parts the substratum is made of gravel. The beach in general is very irregular. The deposition of mud and sand, over the rocks limit the distribution of animals. Thus although no clear zonation of some of the common species was found, the following four zones could possibly be recognised (1) Littorinid zone upward, (2) Balanus zone, (3) Oyster zone and (4) Trochid zone.

Littorinid zone : This was the uppermost zone, extending from the level of EHWS to the barnacle line. The population of the littorinids was rather sparse. *Tectarius malaccanus* was present from EHWS to MHW on the exposed rocks which were dry due to sunlight. When the temperature was high, they moved into the crevices or along the shaded sides of the stones. *Littoriana intermedia* was the most abundant species of the littorinids. It had its maximum density from EHWS to MHW. *L. ventricosa* and *L. subgranosa* were in fewer numbers and formed a horizontal zonation, the former being present along the stones nearer the storm water drain and the latter which was rare was found on the stones exposed to the wave action near the adjacent sandy beach. Other animals associated with the littorinids in this zone were *Ligia exotica* in small numbers, a few *Balanus amphitrite* upto MHW and *Planaxis sulcatus* with its upper limit at MHWS. *Neritina pulchella* was common in the rock pools which had brackish water.

Balanus zone : This zone was a narrow belt largely composed of *Balanus amphitrite var. communis* on stones. The barnacles were predominant from

about MHW down wards upto MHWN. They also extended upto MLW but were absent along the sheltered sites. Their maximum density was on rocks which were not shielded by the seaward rocks. Deposition of mud and sand over the rocks adversely affected their settlement and growth. Wherever the wave action was less, they were replaced by the oysters. The barnacles were absent in permanent pools. A negative correlation was noticed between the barnacles and the oysters. The lower boundary of the barnacles here in the storm-water-drain was MHWN. Below that the oysters were present. The upper limit where the barnacles occurred in greater density was recognised as the boundary separating the midlittoral from the supralittoral zones.

Neritina pulchella predominated the brackish water pools from MHW to ELWN. *Planaxis sulcatus* also was abundant in this zone. At the base of the embankment where there was black and foul smelling mud, the polychaete *Onuphis*, the bivalve *Coecella*, and many sea anemones, chiefly *Anemonia* and some anthopleura were common (from MHWN to MHWN). *Crossostrea cucullata, Nerita polita, N. Oryzarum* and *Cerithium morus* were fewer in numbers as this zone was their upper limit.

Oyster zone : This zone extended from MHWN to MLWN. At its lower limit pronounced change was noticed in the fauna and flora, even though the rock oyster, *Crossostrea cucullata* was abundant upto MLWN with its lower limit at MLWN. Thick encrustations were found over boulders and rocks at MTL. Dominant forms were *Planaxis sulcatus, Nerita polita* and *Cerithium morus*, while *Nerita oryzarum, Thais tissoti* and the black algae, *Caloglossa* were only subdominant; the last mentioned species was found mostly in patches covering the side and the top of boulders and very often over the oysters themselves. The alga, *Ulva lactuca* appeared seasonally in this zone. It was seen in November in rock pools and in the next two months it grew fast and covered the entire muddy area and the rock pools. However, it disappeared fast towards the end of February, from the zone. Below MLWN, *Ulva* was replaced by several brown algae, many of which occurred throughout the year.

Along the seaward side there was a small mud flat at MTL, where the snail *Potamides cingulatus*, the mud skipper *Boleopthalmus* and fiddler crabs of the genus *Gelasimus* occurred. Here polychaetes belonging to the families Nereidae and Glyceridae were also common.

The negative correlation between barnacles and oysters, was again noticed in this zone. The slopping seaward sides of the rocks were covered with barnacles while the landward sides had thick deposits of oysters and *calog!ossa*.. However, there were places where both these animals occurred together. Among other typical inhabitants of this zone were the crabs *Ozium rugulosus, Leptodius crassimanus, Lytocheria angustifrons* and *Metagraspus messor* which tended to hide under the rocks. The bivalve *Trapezium vellicatum* was common in rock crevices in between the oysters.

Some of the inhabitants of the next zone (Trochid) were also found in this zone. There were the ascidians and molluscan (*Calliostoma scobinatum, Oncidium verruculatum, Cerithium rubus, Cellanaradiata, Bursa tuberculata* and *Aplysia cornigera*). The eel *Pisodonophis* and the brittle star *Ophiactis* were sometimes found in the rock pools. Spat-falls of oysters and the cyprids of barnacles occurred in this midlittoral zone during late May and early June indicating that both these groups spawn at the same time. The spat settlement commenced at the lower levels and of barnacles at the higher levels.

Trochid zone : This extended from MLWN downwards and merged into the sublittoral zone. The main species of the oyster zone were regularly present upto the lower limit of the MLWS. Its upper limit was about MLWN, for at this level there was a pronounced change in the composition of fauna. The animals from the understone increased enormously both in types and numbers.

Of the molluscan family Trochidae, *Calliostoma scobinatum* which is an endemic species, was abundant between MLWN and MLWS, along with other species such as *Trochus radiatus, Clanculus depictus, Euchelus asper, E. indicus, E. tricarinatus* and *Gibbula swainsonii.* Among other molluscs were *Bursa tuberculata, Cellana radiata, Scutus unguis, Cypraea pallida, Astrea stellata, Aplysia cornigera, Bursatella leachii, Onchidium verrauculatum* and *Lithophagus cinnamonea. Aplysia* and *Bursatella* were seasonal in their appearance and occurred in December and January. Among the other animals of this zone were *Tethya lyncurium, Balanus tintinabulum, Dendrostomum spinifer* (Sipunculoidea), *Harmathoe ampullifera* (Polynoid) and *Petrolisthes boscii* (Anomura). small encursing algae were present in all the months while those with bigger thalli were common only in the winter months (December and January).

T. vellicatum and some ascidians were also abundant here. Some members of the family Zoanthidae were present in the rock pools between MLWS and MLWS. *Ophiactis savighvi,* some chitons and nudibranchs were very common under the stones and in rock pools. Some of the stones and rocks were bored by *Lithophaga* and *Martesia.* This region extend from MLWS to MLWS. In the same region some species of corals were also seen. In general the fauna here was very rich and varied. Most of the animals present were small in size and generally lived in protected situations. some forms were also found at higher levels in rock pools. *Tethya* was found in pools upto MLWN. Members of this zone could often be collected from the sublittoral zone and a few from below the tidal range occasionally moved into this zone.

CHOWPATHY SHORE

The area surveyed was about 488 meters located at the foot of the Malabar Hill where boulders and stones are resting on a substratum of sand and gravel. (Plate I, Fig. 2). The shore towards the land has a high stone-wall for the protection of the road. This wall had many littorinids. Most boulders

were covered with animals, barnacles and littorinids were found along the upper half of the stones and trochids and muricids towards the bottom. The gravel and stones also had holothurians. At the bottom the echiuroid, *Ochaetostoma bombayensis* was also found. Other animals such as *Martesia striata* and *Perineries* spp. were seen burrowing into the rocks.

The vertical limits of the faunal distribution was not as clear here as at the Cuffe Parade Shore. The lower limit of the midlittoral zone could not be found as a distinct belt of any one dominant species. However, the following three zones could still be distinguished. (1) Littorinid zone, (2) Balanus-oyster zone and (3) Trochid zone. The zonation here was at about the same level as in the earlier shore except that the midlittoral was not divided into separate Balanus and Oyster zones.

On the seawall along Bay, the oysters were seen as 1.5 meters belt from MLW to MTL. Above this upto MHWS (1.5 metres height), the barnacles were predominant. The height of MTL coincided with the level at which the *Balanus* and oyster zones were identified at the Cuffe Parade shore. The topmost littorinid zone was followed by a belt of oysters and *Balanus*. Below this was the zone of *Polydora* and *Anemonia*.

Littorinid zone : Was at the same level as at the Cuffe Parade. *Littorina intermedia* was very plentiful. The lower limits of distribution of these species was greater than at Cuffe Parade.

Balanus-Oyster zone : The barnacles had a slightly bigger belt than that of the oysters. *B. amphitrite* was represented by three subspecies *communis*, *hawaiiensis* and *cochinensis*, of these, the first was more abundant. On some rocks the barnacles were present only on the sheltered fronts. The upper and lower limits of *Crossostrea cucullata* were greater by two feet than that of their distribution at the Cuffe Parade. *C. lacerata* and *C. bicolor* were also seen. *C. bicolor* was often found on the underside of the stones. The distribution of the other faunal elements in this zone was very much the same as at Cuffe Parade. The trachytes had *B. amphitrite* on top along with a few oysters. Below this there was a band of *Caloglossa*. *Martesia* and *Perineris* burrowed into the soft substratum while *Arca* and *Bundosoma* occurred in the crevices and clefts. The animals in the Trochid zone, such as *Drupa*, *Bursa* and *Calliostoma* extended over a much greater area than at the Cuffe Parade.

Trochid zone : The fauna was rich both by species and in numbers. Trochids were fewer than in the previous locality and occurred on the underside of the stones. Among the non-cryptic forms of this shore were *Balanus tintinabulum*, *Thias ,Bursa, Crossostrea, Drupa* and *Cantharus*. The understone inhabitants were *Scutus, Arca, Cyprea, Cancellaria* and *Astrea*. The two bivalues, *Gafrarium divaricatum* and *Chione imbricata* were often found buried in the subs-

tratum. Ophisthobranchs, Patellids and oysters were at the same level as in the previous locality. Here *Crossostrea madrasensis* occurred below the lower limits of *C. cucullata.* Egg capsules of *Thais* and other muricids occurred on the under sides of the boulders. Among the crustaceans the usual crabs, the alphields and isopods were commonly seen. Holothurians were found in isolated areas of stones and gravel on the sandy bottom with puddles. Some polychates such as *Dasychone* and *Spirographis* were present in muddy sand below MLWS.

Breach Candy Shore

The area studied was aout 366 meters along the coastline which was almost entirely rocky with only a few sandy patches found above MHW and below MLWS (Plate II, Fig. 1). Sewage outlets were very few. Here the water was cleaner than that of the other localities. About 304 meters was exposed at the spring low tides. The first belt of sand was lying above MHW. It was bound by halophytic plants and mangroves. Below this was the area of stones, gravel and boulders followed lastly by big boulders and raised terraces on the seaward side. These reduced the wave action considerably on the shore. The littoral region could be divided into four zones viz. (1) Littorinid zone, (2) Chthamalus zone, (3) Balanus-Oyster zone and (4) Tetraclita zone.

Littorinid zone : Was dominated by *T. malaccanus* which was plentiful between MHW and EHWS. *L. intermedia* was common here and occurred upto EHWN. Other littorinids and *Ligia exotica* had a similar distribution as in the other localities.

In the *Chthamalus* zone, *L. challengeri* replaced *Balanus amphitrite communis,* and occurred from MHWS to MLWN, with a maximum between MHWS and MTL. Its extreme lower limit coincided with the upper limit of another barnacle, *Tetraclita.* There was a negative relation between *Chthamalus* and *Balanus.* The former genus occurred where the wave action was maximum along on the seaward sides of the boulders. *B. amphitrite hawaiiensis* also occurred in fewer numbers along with *C. Challengeri, Caloglossa, Planaxis* and *Cerithium.* Some Neretids and sea anemones were also present. Almost midway along the gravely substratum where there was a mixture of sewage water and sea water, *Neritina* and *Potamidis* were seen.

In the *Balanus-oyster* zone which was narrow in between MSL and MLWN there was a preponderence of *C. cucullata* and some times of *B. amphitrite communis,* depending upon the extent of the sheltered area available on the rocks. Oyters in this locality were not abundant at this shore. Along with *C. cucullata* there were *C. bicolor* and *C. madrasensis* in fewer numbers.

Caloglossa, Planaxis, Nerita and *Bunodosoma* were common here. *N. oryzarum* and *C. radita* were also found. *Thais tissoti* was abundant on rocks. *Gafrarium, Drupa, Arca, Trapezium, Perineris, Nudibranchs* and *Spirorbis* were also present in this zone.

Here Tetraclita zone corresponded with the Trochid zone of the other localities and extended lower than MLWN. The barnacle *Tetraclita purpurascens* which was present along the sides of the rocks and on the under surface of the over-hangs, was the dominant species in this zone. The other species *Cellana radita* was also abundant. The trochid molluscs *Euchalus, Clanculus, Trochus* and *Calliostoma* were also common. The crevice dweller such as *Arca symmetrica* were also commonly seen. *Lima lima* was seldom seen. The gasrotpods *N. polita* and *Drupa* and numerous other organisms so characteristic of this zone were also present at the lower levels. The zoanthids formed a thick mat on the rock platform with their associate fauna.

Mahim Shore

About 305 meters long shore line off the Mahim Causeway, located between Bandra and Mahim and facing west was selected for study. The rocks here were smaller and occurred between MHWN and MLWN levels. These covered with *B. amphitrite* and *C. cucullata.* (Plate II, Fig. 2). The numerous rockpools had numerous sea anemones (*Anemonia*) in them. The landward side of rocks had littorinids and *Chthamalus,* but these rocks did not extend above EHWS. On its landward side at the highest level, there was strip of sand. Below the rocks there where sand-bars which harboured *Katelysia* and *Meretrix.* These were exposed at low water spring tides. The adjacent mud flats and sandy areas were inhabited by the crab *Dotilla. K. marmorata* and *K. opima* were abundant below MLWN. *A. granosa* and some sea anemones were also present. The seaweed *Ulva* and *Enteromorpha* were common during the winter months. *Natica* sp. were also found in this locality.

Four zones were recognised in this locality i.e., the (1) Littorinid zone, (2) Chthamalus zone (3) Balanus-oyster zone and (4) Trochid zone.

These zones had fauna characteristic of similar to those of other shores described earlier. In the littorinid zone, *L. intermedia* was most abundant. The *Chthamalus* zone was dominated by *C. withersi* unlike *B. amphitrite* of which was so abundant at the Cuffe Parade and Chowpatty shores and *C. challengeri* of the Breach Candy shore. In the *Balanus*-oyster zone *B. amphitrite* and *C. cucullata* were predominant on the rock platforms. In the trochid zone the trochidae were represented by a number of species which were not very abundant excepting *Euchelus tricarinate.* Most of the species were found attached to the under surface of the stones.

General Considerations

By taking all the above four shores into account, it is possible to recognize a general pattern of zonation (1) the upperlittoral zone was dominated by littorinids, (2) the midlittoral zone by barnacles and oysters, (3) the lower-

littoral zone by a rich variety of fauna of which the trochids generally dominate.

Upperlittoral zone : In all the four localities, four littorinid species were found. These were *L. ventricosa, L. subgranosa, L. intermedia* and *Tectarius malaccanus.* The last species was widely distributed and was the most abundant member of the group. *L. ventricosa* was rare and was found only in sheltered areas. *L. subgranosa* was sparse everywhere except at the Breach Candy. All the major species showed a definite vertical zonation. *T. malaccanus* was abundant and occurred as high as EHWS *L. intermedia* had an upper limit but not higher than EHWS. Its lower limit was even below MLWN. All the littorinids and *Ligia exotica* present in this zone, were generally seen in rock crevices. This habit according to Stephenson (1943) was not so much for shade as for the protection from the wave action. Penetration of species belonging to the midlittoral zone into this zone was a common feature. The animals concerned were *Planaxis sulcatus, C. cucullata* and *balanids.*

Midlittoral zone : In all the shores, this zone was dominated by barnacles and oysters and was usually divisible into three or four belts. Each belt was dominated by a distinct set of animals. Except for the Chowpatty shore, it could be divided into two recognizable bands at the three other shores, each having a set of indicator animals. In the Cuffe Parade Shore this zone could be divided into *Balanus* and oyster belts and at Mahim and Breach Candy into *Chthamalus* and *Balanus*-oyster belts.

A greater wave action was found to increase the settlement of barnacles and decreased the oysters in numbers. Thus at the Chowpatty rocks *Balanus* occupied the entire width of the zone mixed with oysters, and formed the *Balanus*-oyster belt. The very striking belt of *Balanus* and *Crossostrea* at the Cuffe Parade was not there, because of competition for space as it was due to the severity of surf action at different levels. With an increase in the wave action, Balanus was replaced at higher levels by *Chthamalus.* It is interesting to note that *Chthamalus withersi* formed a narrow belt upto about MHW, thus raising the upper limit of the barnacle distribution. C. *withersi* were found on the leaves and bark of *Avicennia,* this feature suggests that thus species had a preference for mangrove swamps or similar marshy or swampy conditions. *Avicennia* were plentiful at Mahim but no barnacle were seen on its leaves.

Lowerlittoral zone : This zone had the larger number of species and the maximum number of animals. It was a wide zone extending from ELWS to MLWN and had the presence of trochids. Various algae were found in this zone during winter in sheltered areas. With an increase in the wave action trochids decreased both in the numbers and species. At the Breach Candy shore trochids were fewer in numbers and did not extend higher than MLWN. The fauna at the Breach Candy was restricted as compared to the other places. The belt of *Tetraclita purpurascens* occurred at very low levels. Previous accounts on its vertical distribution indicate that the species is confined to midlittoral zone along the Australian and Tasmanian coasts.

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Plate I. 1. Cuff Prade (Bombay) photographed at low water spring tide.
2. Exposed rocks at Chowpathy during the ebb tide.

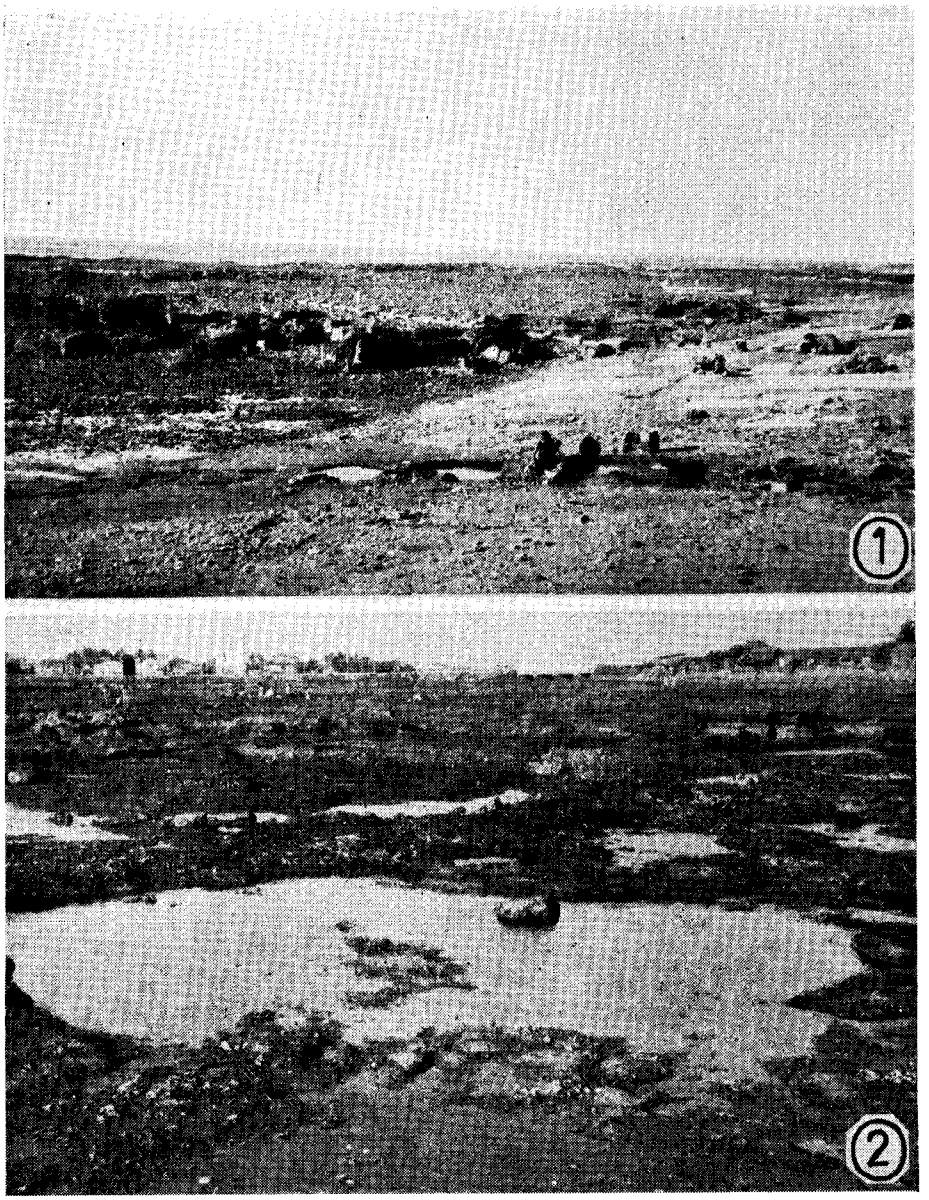


Plate II. 1. A view of the Breach Candy Shore at the ebb tide.
2. A view of the Mahim Beach at the ebb tide.

SOME CONCEPTS ON THE PRODUCTIVITY OF TROPICAL SEAS

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ABSTRACT

The paper gives a critical review of the different environmental factors which may be responsible for the differences in the productivity of the lower and higher latitudes. The various factors which contribute to the low productivity in the tropical and subtropical seas as compared with the temperate and polar seas are analysed. The reasons for limited high productivity zones in the coastal waters of the tropical and subtropical regions are explained as due to upwelling in coastal waters and divergence in offshore waters. The need for intense exploration and location of high productivity zones in the typically tropical and seasonal 'Monsoon type' of upwelling in the seas bordering India is emphasised as also the adoption of modern craft and gear to exploit the seafood resources.

The productivity in any area is a measure of the rate at which carbon dioxide is photosynthetically fixed as plant material. The plant material in its turn is converted to pelagic fish through various trophic levels. The lower trophic levels representing the phytoplankton and zooplankton provide food for the fish larvae and juvenile fish. A number of studies have established a direct relationship between productivity at lower trophic levels and fish production.

The production of phytoplankton which are the primary producers is limited by the availability of some essential nutrients such as nitrates and phosphates which may be in short supply in the upper illuminated photic zone. There is always a larger amount of nutrients in the deeper waters below the photic zone which in the polar and temperate seas are brought to the surface in winter by extensive vertical mixing or turbulence. In summer the warming up of the surface water prevents mixing owing to thermal stratification and when the available nutrients are used up production may come to a stand still in the photic zone. For optimal production there should be an optimal depth and speed for vertical turbulence. If its range is too short all the available nutrients are quickly depleted and the photic zone is isolated from further supplies. If it goes too far down below the photic zone, there is a danger of the phytoplankton carried down below the range of light for effective photosynthesis and ultimately a loss to total production

if kept under these conditions too long. Turbulence in shallow waters is also not conducive to production owing to the churning action of bottom particles which are held in suspension reducing light penetration.

The statement that tropical waters are comparatively poor in nutrient salts and that they cannot support a rich plankton is a gross over simplification of the matter according to Hart (1953b). Hart (*loc. cit.*) states that there are at least three vital factors, nutrient concentration, light penetration and the degree of stabilisation of the surface layers that provide a sound working hypothesis to account for the comparative poverty of warm seas as a whole in contrast to the rich plankton of most (not all) temperate and polar waters. However, while the open sea in lower latitudes is relatively sterile owing to thermal stratification which precludes any complete or rapid renewal of nutrients from the nutrient rich deeper layers, the situation is quite different in the coastal areas with upwelling or in offshore region of divergence. For example along the Californian coast (Moberg, 1936); in the region of divergence along the equatorial counter currents and along the west coast of Africa (Hentschel, 1928) there is rich production. The Peru Current in tropical and subtropical regions brings to the surface an abundant and continuous supply of nutrients which results in heavy phytoplankton production mainly near the coast but in some sections this intensity is maintained to a distance of 320 km seawards (Gunther, 1936). In one small island of the Chinchas group there are estimated to be some five or six million marine birds, such as cormorants, pelicans and garnets which daily remove at least 1000 tons of small fish from the surrounding water and the great guano deposits on the shore of these regions may be as much as 30 m in thickness (Schott, 1932).

While some limited areas in the warmer seas such as the upwelling regions off the coast of Africa and South America are exceptionally rich and may maintain substantial quantities of nutrients at the surface, over vast areas of the tropical seas there is a very strong discontinuity layer at a depth of 60 to 150 m as a result of thermal stratification. Any nutrient brought to the surface is immediately synthesised and this may account for the low and very often undetectable level of nutrients in the tropical surface waters. The deeper layers may have ample nutrients for rich production but the light energy is greatly reduced with depth being only about 25 per cent of the surface value. It seems to follow rationally from this that such rich plankton production as is known to occur in warm seas is limited to times and places where turbulence breaks down the thermocline and enriches the upper layers of the euphotic zone with nutrients. The great upwelling regions such as the Peru Coastal Current, Benguela Current (Hart, 1953a) and Canary Current show some upwelling activity throughout most of the year except near the equatorial limits. The upwelling regions of the Californian Current is more seasonal (Sverdrup and Allen, 1939). The typically tropical and seasonal "Monsoon Type" of upwelling along the coast of India and southern Arabia are well known as rich areas of plankton production (Ryther

and Menzel, 1965; Panikkar and Jayaraman, 1966; La Fond, 1955; Murthy and Varadachari, 1968; La Fond and La Fond, 1968). Because of the high degree of stability of the surface layers through most of the year in the tropical seas, turbulence in its beneficient aspect has to be looked for as a pre-requisite of rich production in them (Hart, 1953b).

While the general view that production in the sea tended to increase with latitude, the work of Riley (1929) has divided opinion on the matter. Working on a range of stations in north Atlantic and measuring the production of oxygen by phytoplankton at different depths, Riley (1939) came to the conclusion that as much or more production was going on at the tropical stations owing to greater depth of light penetration than those further north. Steeman-Nielsen (1952) experimenting with the rate at which radio-active carbon is taken up by the photosynthetic organisms, supports the thesis of somewhat poorer production in the tropics and he has criticised Riley's methods.

The plankton observations made on deep-sea expeditions in the last few decades have also indicated a somewhat varying standing crop with a tendency to show higher values at the higher latitudes. Lohman (1920) in the "Deutschland" expedition to the Atlantic in 1911 found that in tropics, the microplankton per litre of sea water could be counted in thousands, in temperate oceanic waters in tens of thousands, and in temperate coastal waters in hundreds of thousands. The above observations made by the expedition have also been borne out by counts of diatoms made throughout the annual cycle in coastal waters at different latitudes. At Low Isles in the tropics the average daily number of diatoms counted in a liter was 5,753 (Marshall, 1933); off Plymouth 14,282 (Lebour, 1915); at La Jolla 39,994 (Allen, 1927) and at Loch Striven 1,009,400 (Marshal and Orr, 1927).

Ascending the various levels of production to the point of annual fisheries yield, Wimpenny (1953) has taken figures of the commercial fish landings, in thousands of metric tons, of some important countries north of 30°N Lat and others between 30°N Lat. and 30°S Lat. The corresponding landings for the same countries have been given by me from the FAO yearbook of Fisheries statistics for the year 1970 (Table 1). While the figures for y950 and earlier years show a substantially lower yield in the tropical and subtropical countries as compared with the countries in the higher latitudes, the figures for 1970 show a markedly increasing trend of catches for the same countries. The phenomenal increase in the catches off Peru is due to a change in the fishing regulations in 1955 which permits taking of anchovies for fish meal and oil. Peru today tops the list of fish production in the world.

TABLE 1. *Annual commercial fish landings in thousands of metric tons in countries north of latitude 30°N and those between 30°N and 30°S* (FAO Yearbook of Fishery Statistics for 1950-51 and 1969-70

North of 30°N			*30°N to 30°S*		
	1950-51	*1970*		*1950-51*	*1970*
Russia	1,800	7,250	Africa	800	4,150
Europe	3,900	11,970	India &		
Japan	3,796	9,309	Pakistan	905 (1950)	2,166
Korea (N)	1,326 (1938)	800	Ceylon	37	100
Korea (S)	628 (1938)	934	Indonesia	420 (1949)	1,249
Canada	948	1,378	Malaya	177	365
U. S. A.	1,583 (1946)	2,714	Indo-China	410 (1949)	2,472
			Australia	46 (1950)	140
	13,981	34,355	Philippines	266	989
			Mexico	55 (1950)	353
			Brazil	155 (1950)	493
			Peru	84 (1950)	12,612
			Venezuela	78 (1950)	114
				3,433	25,203

Wimpenny (1953) has given a number of reasons which operate in favour of inferior production in lower latitudes. Among these high temperature is likely to increase the respiratory rate of phytoplanktonic organisms more than the photosynthetic rate, resulting in reduced production. The deeper photic zone in the lower latitudes results in a wider dispersal of plankton food, involving more energy in its pursuit and leaving less for building up body tissues and food reserves. In warm seas the communities of commercial fishes and their food organisms are more complicated and divided into a larger number of species. The species may get linked together in long food chains with special food organisms and consequent wastage of considerable effort in the pursuit of food. These result in wastage of potential production in the use of extra kinetic energy. The higher metabolic rate in tropical and semi-tropical fish find it more expensive in food to maintain the same unit weight as in cooler seas. The mortality rate is also likely to be higher when food is sparse owing to greater break down rate.

In conclusion it may be said that while there is a concensus of opinion that the higher latitudes are more productive than the lower latitudes, there are vast areas in the tropical and subtropical regions which are highly productive. These are areas subjected to upwelling in the coastal areas and divergence in the offshore regions.

It is well known that the seas bordering the tropical and subtropical countries have not been as well or as extensively exploited as some of the European countries and when this is done with modern methods of fishing the disparity in production is likely to narrow down further.

The urgent need for the exploration and location of productive areas in the tropical and subtropical seas and a rational exploitation of the fishery resources to supply a cheap source of protein for the chronically protein deficient food of the developing countries bordering the warmer seas cannot be over emphasised.

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ON DENDRONOTACEAN NUDIBRANCH GASTROPODS OF THE GENERA *HANCOCKIA* AND *DOTO* FROM THE GULF OF MANNAR

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ABSTRACT

Hancockia papillata (O'Donoghue) has been redescribed, based on an examination of living material obtained from the Gulf of Mannar along the Indian Coast. As compared with other species under the genus, *H. papillata* is devoid of jaws. Tubercles and branched papillary processes over the surface of the rhinophores and the dorsum are very characteristic of this species. The radula is triseriate as in other members under the genus. The spawn and early developmental stages have been described. The larva has an elongated spirally coiled shell and the excretory organ is reddish brown. The larval shell bears a pair of small denticulations at the base of the aperture.

The general structure and early development of a dotonid species, also obtained from the Gulf of Mannar, have been described and compared with some of the known species under the genus *Doto*. This species is characterised by the presence of an abbreviated oral veil, nonbranchiate cerata with tubercles in 3 to 4 circlets and rhinophore sheath with spoon-shaped extension in the anterior margin. The dorsum and the sides are without papillary processes. The larval shell is a short spire. The veliger when hatched is without the pigmented eye spots and the excretory organ is colourless.

Two dendronotacean nudibranch molluscs *Hancockia papillata* (O'Donoghue) and *Doto* sp found among the brown algae and colonial hydroids attached to the submerged rocks in the Gulf of Mannar at a pier close to the Central Marine Fisheries Research Institute at Mandapam Camp (Southern India) have been described in the present paper. The descriptions are based on living material examined by the author. It may be pointed out that the earlier accounts on *Hancockia papillata* were from preserved material only, which could not show many of the external and internal morphological characters in a satisfactory manner. The specific indentification of *Doto* obtained was found difficult in the absence of any marked diagnostic features underlying a generalised structural pattern of the genus. When these animals were kept in small aquaria in the laboratory, they deposited spawn out of which hatched the veliger larvae. Hence it was possible to observe and record here the nature of the spawn and some of the early developmental stages.

The Suborder Dendronotacea of the Order Nudibranchia under the Opisthobranchiate gastropods includes a mixed assemblage of different families namely Tritonidae, Dendronotidae, Fimbridae, Bornellidae, Hancockidae, Dotonidae, Mirianinidae, Scyllidae, Lomanotidae and Phylliroidae. The one common character to all these families is the presence of rhinophore sheaths into which the rhinophores are retractile. The head usually bears an enlarged frontal sail with digitate processes. Paired cerata are usually present in the members, but they are without cnidosacs except in *Hancockia*. In some, the lateral notal ridges also bear much branched gills and the dorsal surface is beset with papillae and tubercles. The midgut gland may be branched or unbranched. The jaws are usually present and the radular structure is very varied, being uniseriate, triseriate or even multiseriate. The reproductive organs are of varying complexity and the penis may be armed or unarmed. The anus and the genital openings are antero-lateral on the right side. They are usually found creeping among the sedentary organisms, but some are pelagic.

The family Hancockiidae is represented by a single genus *Hancockia* Gosse 1877. It is characterised by a limaciform body with a bilobed frontal veil and palm-shaped paired cerata laterally arranged. The rhinophores are club-shaped and retractile into well developed rhinophore sheaths. The radula is triseriate, the median tooth denticulate and the lateral teeth smooth. The penis is unarmed.

The genus includes five valid species, viz., *H. uncinata* Hesse (Plymouth, Torbay), *H. californica* MacFarland (California), *H. ryrca* Marcus (Brazil), *H. burni* Thompson (Queensland, Australia) and *H. papillata* (O'Donoghue) (Indian coast of the Gulf of Mannar). The distribution of the members of the genus is along the coasts of the Atlantic, Pacific and the Indian Oceans.

HANCOCKIA PAPILLATA (O'DONOGHUE)

A specimen collected from the Krusadai Island (Gulf of Mannar) and wrongly reported as *Doto indica* Bergh was reexamined and named *Iduliana papillata* Gen. et. sp. nov., by O'Donoghue (1932), but Odhner (1936) has established that *Iduliana* being synonymous with *Hancockia* Gosse the species should be named *Hancockia papillata*.

External Features: Two specimens were obtained by the present author one measuring 19 mm and the other 14 mm long (Gulf of Mannar, 18th February, 1969). The body is limaciform and elongated. The broadest region of the body at one third the length from the anterior end is 2 mm in width excluding the cerata. It is 9 mm in width with the cerata of the first pair fully expanded in the horizontal direction. The head bears in front a large flattened, bilobed oral veil or the frontal sail, each of the two lobes bearing peripherally six finger-like processes, which are unequal in length, those in the middle being comparatively larger than the ones on either side. The mouth

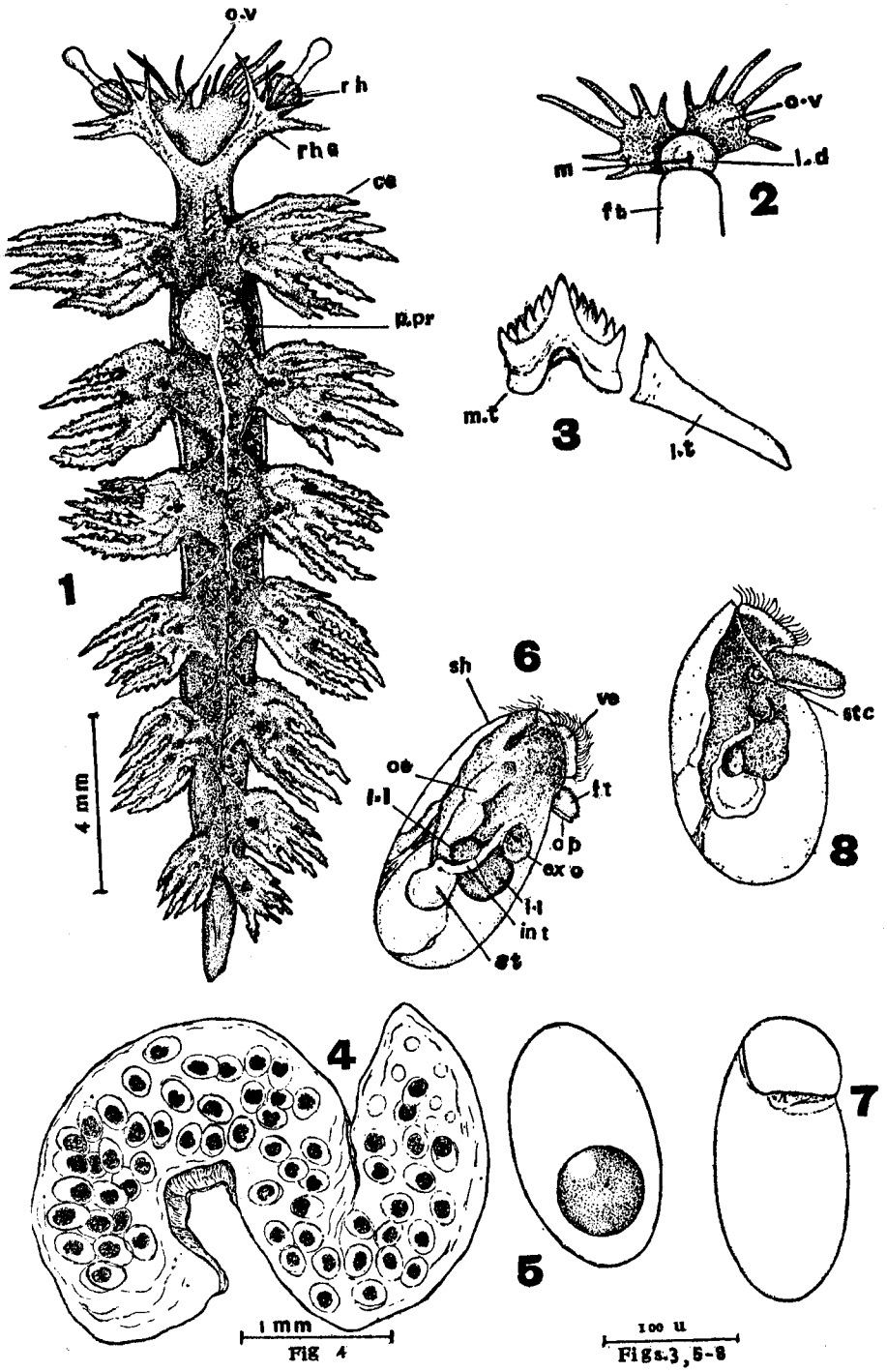
is median and antero-ventral, surrounded by labial thickenings, one on each side, but are confluent in front and behind, with the result that the mouth when viewed ventrally appears to be situated in a roundish fleshy disc anterior to the frontal margin of the foot. The oral veil overhangs this fleshy disc.

The head has dorsally two funnel-shaped rhinophore sheaths, the free margin of each of which bears six finger-like processes. On the surface of the sheaths there are sparsely scattered minute tubercles. Internally penetrating into the rhinophore sheaths are the ramifications of midgut gland. The rhinophores which are retractile into these sheaths are club-shaped; the basal region of each is longitudinally lamellate and the distal half is narrow and cylindrical terminating in a slightly bulbous swelling. The rhinophore lamellae are eight in each. In the earlier descriptions of this species by O'Donoghue (1932) and Satyamurti (1952) the presence of these lamellae was lost sight of in the preserved material they examined. In all other species of *Hancockia* reported earlier the rhinophores have been found to be lamellate. At the bases of the rhinophore sheaths the head bears a pair of minute dark pigmented eyes seen through the transparent integument of the body wall covering them (Figs. 1 & 2).

The elongated body bears laterally thick, paired cerata. In the first four pairs, they are placed right opposite to each other whereas in the first and sixth pairs, the arrangement is slightly oblique, those on the right side being placed more forwards than the corresponding ones on the opposite side. Behind the sixth, there is a small unpaired cerata on the right side. The cerata are of peculiar shape, like a partially closed human hand with several digitate processes, varying from six to nine, pointing outwards. The latter are contractile; when the animal remains undisturbed, they are relaxed. The midgut gland ramifications penetrate the cerata including the digitate processes. At the base of each cerata, there is a distinct cluster of roundish tubercles (Fig. 1). On the surface of the cerata, the integument bears numerous microscopic cnidosacs. Such cnidosacs are found scattered in the integument of the rhinophore sheaths also. In the Nudibranchia, outside the eolidacean group, *Hancockia* is the only genus which possesses the cnidosacs.

The number of cerata observed in other species is 5 on each side in *H. uncinata,* 4-7 in *H. californica,* 4-5 in *H. ryrca* and 5-6 in *H. burni.* The maximum number of ceratal digits observed in the above species has been 14, 16, 8 and 11 respectively (Thompson 1972). In respect of the cerata in *H. papillata* the earlier description (Satyamurti 1952) states that they are "club-shaped", arranged in 7 pairs, each bearing laterally 8-9 "tubercles".

Behind the first pair of cerata, at about a third of the distance from the anterior extremity, the dorsum shows a conspicuous roundish bulging, the pericardial prominence (Fig. 1). There is a median ridge along the length of the dorsum. Below this ridge and seen through the integument is a blood



Figs. 1–8: *Hancockia papillata*: 1. Dorsal view of the entire animal; 2. Ventral view of the anterior region; 3. Median and lateral teeth; 4. Spawn with developing embryos; 5. Uncleaved egg in capsule; 6. Veliger larva; 7. Apertural view of the larval shell; 8. Another view of veliger larva. *ce.* cerata; *ex. o.* excretory organ; *ft* foot; *int.* intestine; *l. d.* labial disc; *l. l.* left midgut gland lobe; *l. t.* lateral tooth; *m.* mouth; *m. t.* median tooth; *oe.* oesophagus; *op.* operculum; *o. v.* oral veil; *rh.* rhinophore; *rh. s.* rhinophore sheath; *r. l.* right midgut gland lobe; *sh.* shell; *st.* stomach: *st. c.* statocyst; *ve.* velum.

vessel starting from the pericardial bulging and running upto the last pair of cerata. A similar, but shorter median vessel is seen running forwards. The dorsum on each side has a lateral ridge between the cerata of the same side; it takes slightly a zig-zag course behind the second and the successive cerata. The lateral ridge extends to some distance forwards also on the head region. The median and the lateral ridges bear papillate processes, the larger of which are distinctly branched. The surface of the dorsum also bears similar, but smaller scattered papillate processes.

The foot is elongate, rather roundish behind the mouth (Fig. 2); and posteriorly behind the cerata it terminates in a slightly obliquely truncated tail.

The genital orifice is on the right side between the rhinophore and the first cerata. The anus is lateral on the right side between the first and the second cerata. The nephridiopore is close behind the anus.

Colouration : The general colouration of the entire animal on the dorsal surface is greenish brown. The oral veil and its peripheral digitate processes are pinkish. In the younger of the two individuals, the pinkish colouration of the oral veil is of lighter hue. The papillae and the tubercles over the body and the cerata are of a deeper brown. Like the body, the cerata are also greenish brown, but the tip of the digital processes are almost colourless. The fleshy labial thickenings surrounding the mouth opening and the entire foot are colourless or pale white. The midgut gland diverticula entering the rhinophore sheaths and the cerata are deep brown.

In the preserved material of this species as reported by Satyamurti (1952) the colouration is pale green throughout without signs of any distinct colour pattern. In O'Donoghue's original description, the colouration is stated to be "dirty gray" in material preserved in alcohol.

Internal Organs

The mouth opening leads into buccopharynx into which open the ducts of clusters of buccal glands and those of the paired salivary glands. *H. papillata* bears no jaws. The radula is triseriate, the radular formula being 59 x 1.1.1. The central tooth is denticulate, the middle denticle being larger than the lateral denticles of which there are six on each side. The lateral teeth are elongate and without denticles. (Fig. 3).

In *H. uncinata, H. californica* and *H. burni* well developed denticulate jaws are present. Those in *H. ryrca* are small and delicate (Thompson. 1972). The radular teeth observed by the author in *H. papillata* are similar to those figured and described by Satyamurti (1952). In a 4 mm long specimen he observed 51 rows of teeth; in the median tooth the central denticle is followed by 5 sharp denticles on either side.

A narrow oesophagus arising from the buccopharynx is followed by an enlarged stomach, the inner wall of which bears chitinous ridges. Communicating with the stomach is the midgut gland which bears two anterior and one posterior branches. Each of the anterior branches further divides and enters the rhinophore sheath and the first cerata of the corresponding side. The posterior branch of the midgut gland gives off minor branches to the second pair and the succeeding pairs of cerata.

Communicating with the minute ramifications of the midgut gland branches in the rhinophore sheaths and the cerata are numerous microscopic cnidosacs, which open to the exterior on the surface of the integument by minute pores. They are not situated at the free extremities of the cerata as is the case with eolidacean nudibranchs; in *Hancockia* they are located in groups along the slender ramificatons of the midgut gland and open to the outside laterally on the surface of the digitate processes of the cerata and the rhinophore sheaths. The cnidosacs contain numerous nematocysts. Thompson has observed in *H. burni* the discharge of nematocysts from the cnidosacs when the animal is disturbed.

The central nervous system shows the usual paired cerebropleural ganglia, the pedal ganglia, the rhinophoral ganglia, and the buccal ganglia with the associated commissures and connectives. The paired statocysts and the eyes comprise the sense organs. The numerous papillary processes and the general integument respond to tactile sense. The heart, the central organ of propulsion of blood, is enclosed in the pericardium. Its pulsations could be seen through the pericardial bulging behind the first pair of cerata.

Prominent among the reproductive organs are the hermaphrodite gland, the hermaphrodite ampulla, the seminal vesicle, the spermatheca and the mucoalbuminous gland with the associated passages. The penis is unarmed. The penial and the oviductal openings are close to each other in the genital orifice on the right side of the body between the first and the second cerata.

Spawn and Early Development : The spawn was like a flat ribbon when it was deposited on the wall of the glass aquarium. It was S-shaped and measured 6 mm in length by 1 mm in width (Fig. 4). It was colourless or pale white. In one spawn there were over 55 well formed egg capsules and a few empty small partially developed ones. The egg capsules were oval measuring 190 μ in the long axis and 100 μ in the short axis (Fig. 5). The yolk-laden eggs contained in the capsules were spherical with a diameter of about 70 μ In *H. burni* the eggs are slightly larger being about 82 μ in diameter. The early cleavages, the formation of the blastula, gastrulation, the early and late veliger stages followed in quick succession as in other opisthobranchs (Rao, 1961). The veliger larvae were fully formed in 50 hours after the deposition of spawn, but they were not liberated free until 72 hours. The salinity of the waters in the finger bowls in which they were reared was 32‰ and the temperature ranged from 27° to 28.4°C.

The veliger larva (Figs. 6 & 8) is characterised by a narrow, much elongated spiral shell 230 μ long. There are two denticulations, one on each side at the bases of the aperture (Fig. 7) as have been described for *Eolidina* (*E*) *mannarensis* (Rao and Alagarswami 1960). The velar lobes, the foot and the operculum are well developed. The oesophagus is long and fairly stout. The left digestive gland is very large and the right one very small. The stomach is small and roundish. Paired statocysts are present as in other opisthobranch larvae. The excretory organ, situated close to annus, is light reddish brown. The larvae lived in the aquaria for a few days in the finger bowls but they did not undergo metamorphosis.

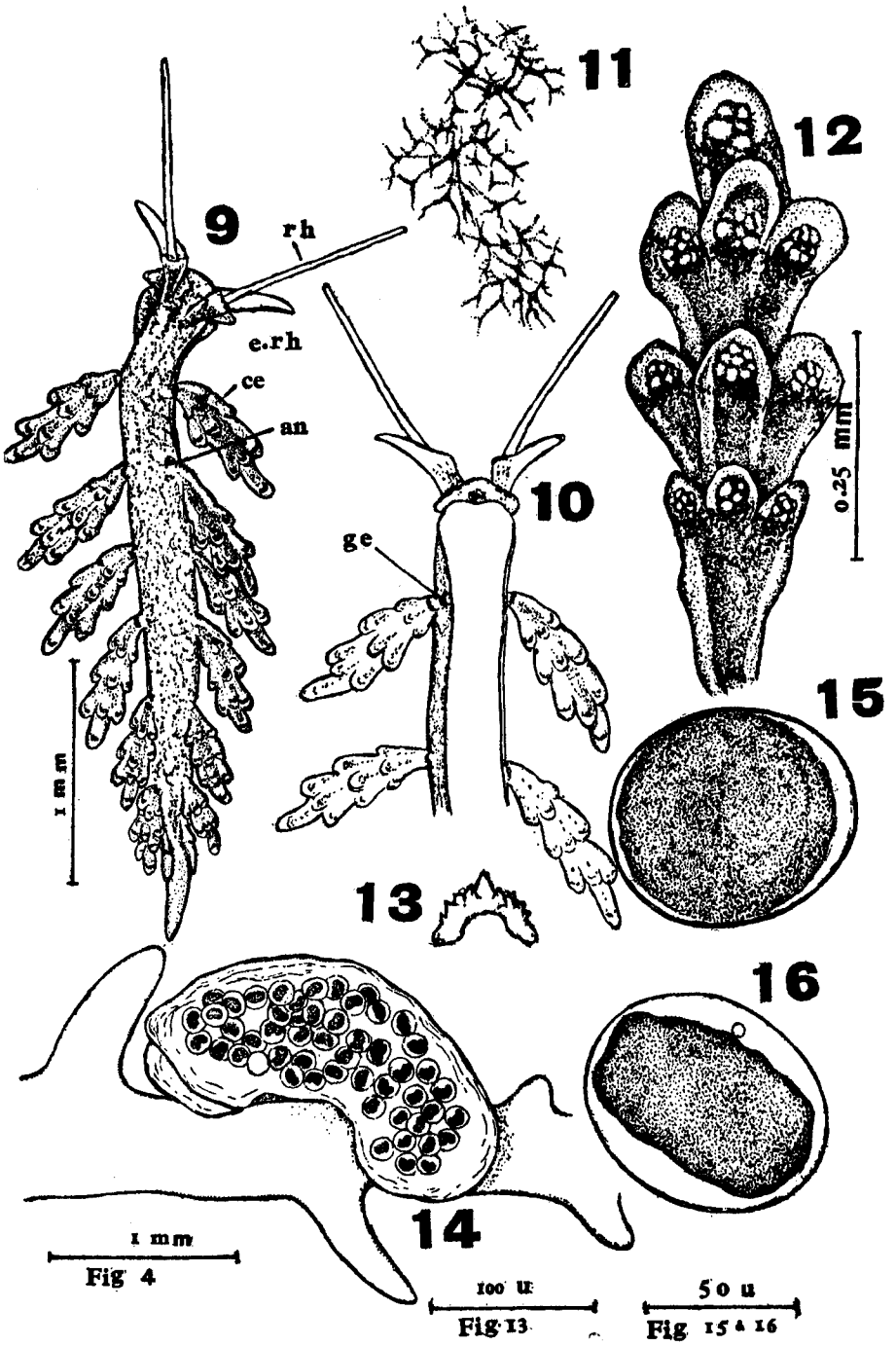
Doto SP.

There is practically no information on the dotonid nudibranchs occurring along the coasts of India. Hence the author considers it worthwhile to include the following descriptions of an as yet unidentified species of *Doto*. Two specimens of this were obtained with *Hancockia papillata* simultaneously from the same locality.

Members of the family Dotonidae are limaciform animals, possessing rhinophore sheaths into which the rhinophores are retractile as in other dendronotacean nudibranchs. The rhinpohores here are smooth, the anus and the genital orifice are anterolateral on the right side; the cerata are fairly stout and bear circlets of tubercles one above the other; midgut branches enter the cerata; cnidosacs are absent; radula is uniseriate and the penis is unarmed. They are widely distributed in all seas. The genus *Doto* includes numerous species. Some recognise several subgenera under the genus.

External Features

Of the two specimens observed one was 3 mm long and the other 2.8 mm. The body is elongate. The head is a little broader than the dorsum, which bears laterally paired cerata. The tail is moderately long terminating in a blunt point (Fig. 9 & 10). In the head, overhanging the ventrally situated mouth is a small expansion of a fold of skin which is produced into tiny blunt lobes one on each side. This structure, though much abbreviated and without any digital processes, is homologous with the oral veil met with in members belonging to allied families of Dendronotacea. The region of the head with the rudimentary oral veil measured 0.45 mm across and the width of the dorsum is 0.25 mm. The rhinophoral sheaths are well developed bearing terminally large spoon-shaped expansions, one to each rhinophore, extending forwards and outwards. The rhinophores which are retractile into the sheaths are slender, cylindrical and long, terminating rather bluntly at their free ends. At the bases of the rhinophore sheaths, seen through the integument covering the head is a pair of dark pigmented eyes. The head is smoothly arched at the sides behind the rhinophore sheaths. The cerata are in 7 pairs. The first 5 pairs are well developed, the sixth pair is very small and the seventh pair is rudimentary.



Figs. 9-16: *Doto* sp. : 9. Dorsal view of the entire animal; 10. Ventral view of the anterior region; 11. Pigment network over dorsum; 12. Cerata with tubercles magnified; 13. radular tooth; 14. Spawn deposited on weed; 15 & 16. Top and lateral views of blastula. *an.* anus; *ce.* cerata; *e. rh.* spoon-shaped extension of rhinophore sheath; *ge.* genital orifice.

Each cerata has generally 3 circlets of minute tubercles and each circlet has 4 to 5 tubercles. At the tip of the cerata there is a single apical tubercle. This apical tubercle and the tubercles in the third circlet just below the former are much larger than those in the first and the middle circlets. The midgut gland ramifications penetrate into the cerata and also the tubercles. These ramifications bear vesicular terminations in the tubercles, the function of which is little known. In one of the two specimens in the third pair of cerata there were four circlets of tubercles (Figs. 9, 10 and 12).

The genital orifice is on the right side of the body at the base of the first cerata (Fig. 10). The anus is on a distinct elevated papilla in front of second cerata of the right side (Fig. 9). The foot is broadly ovate in front and sightly notched in the middle (Fig. 10). It is a little narrower than the dorsum and terminates posteriorly in the blunt tail.

Colouration

There is a dark greyish patch on the head and it extends forward on the outer faces of the rhinophore sheaths. Over the dorsum is a network of dark greyish pigment (Fig. 11). The intervening spaces in the network are pale white or light yellow. The upper surfaces of the cerata and the anal papilla are greyish. The cerata appear to be carmine in colour due to the digestive gland ramifications of the same colouration entering them. The tips of the tubercles are whitish, but immediately below there is a zone of grey. The sides of the body are irregularly splashed white and grey. The foot is colourless.

Some Internal Structures

No jaws have been found in the buccopharynx. The radula is uniseriate. In a 3 mm long specimen, the radula had 21 rows of teeth, each having a small median denticle and 4 lateral denticles (Fig. 13). The penis was found to be without armature.

Spawn And Early Development

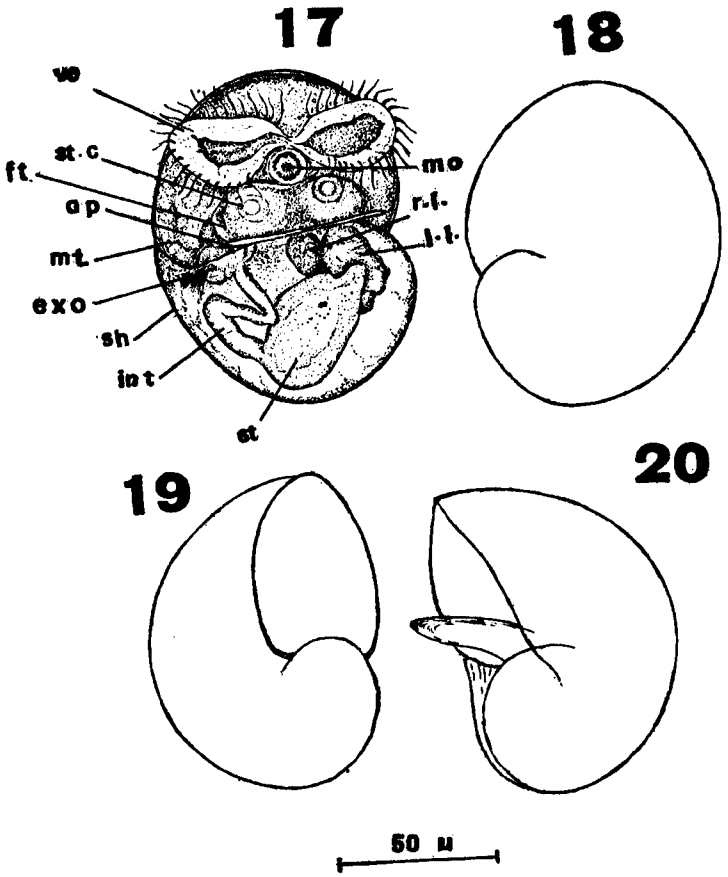
The spawn which was deposited on an algal weed was about 2 mm long and cylindrical with a diameter of about 0.7 mm (Fig. 14). The egg capsules were about 80 μ in the long axis and the egg itself which was spherical had a diameter of about 70 μ. The blastula was circular when viewed from above but somewhat flattish in a lateral view. (Figs. 15 & 16). In the fully formed veliger the shell was broadly stout and spirally twisted.

The aperture was large and wide (Figs. 17 to 20). The velar lobes were moderately large and each lobe was provided with a subvelum a little below the level of the velar cilia. The foot was thin and ciliated bearing a short wide operculum. Between the velar lobes and the foot was a circular mouth opening leading into a fairly stout, short oesophagus. The latter communicated with

the stomach which in a ventral view of the larva was prominently placed in an oblique horizontal position. The midgut gland lobes were unequal, the left one being the larger of the two. The intestine showed a short loop and the anus opened into the mantle space close to an almost transparent colourless excretary vesicle. The just-hatched veliger was blind. A pair of statocysts containing each a statolith was present. Retractor muscles for the velar lobes and the foot were present as in other opisthobranch larvae.

Comparison With Other Dotonids

In the Australian species *Doto yongei* Thomson the cerata have each 3 rings of tubercles and some of those in the region of the peduncle are slightly modified but have not reached the condition of gills met with in some other species. The tip of each of the cerata is drawn into an elongated digital process and the margins of the rhinophore sheaths are entire (Thompson, 1972).



Figs. 17-20: *Doto* sp.: 17. Veliger larva; 18–20. Different views of larval shell. *ex. o.* excretory organ; *ft.* foot; *int.* intestine; *l. l.* left midgut gland lobe; *mo.* mouth; *mt.* mantle; *op.* operculum; *r. l.* right midgut gland lobe; *sh.* shell; *st.* stomach; *st. c.* statocyst.

Some of the Japanese species described by Baba (1949) are also distinct from the present one. In *Doto japonica* Odhner there are well developed ceratal gills and the rhinophore sheaths have wavy margins. In *Doto bella* Baba and *Doto rosacea* Baba no branchial folds or gills are present in the cerata and the margins of the rhinophore sheaths are entire. *Doto purpurea* Baba is also without branchial folds on the cerata but with characteristic digitiform processes on the anterior margin of the rhinophore sheaths. *Doto (Gellina) pacifica* Baba is distinguishable from other species by the presence of inflated, fusiform non-tuberculate cerata.

There are dotonid species in which in addition to the paired lateral cerata, tubercles and papillae on the middle of the back and the sides of the body are present: *Doto fragilis* (Forbes) figured by Alder and Hancock (1851) has dorsal tubercles; *Doto pinnatifida* has rows of papillae, one row in the middle of the back and two rows one on each side of the body. Baba's (1971) subspecies *Doto fragilis nipponensis* has seven pairs of cerata with 4 to 5 circlets of elongated conical tubercles, and some papillae along the mid dorsal line and along the sides of the body. *Doto chica* Marcus (1972) from southwest Greenland and Florida has an arched veil, rhinophore sheaths with scalloped margins, cerata with rings of tubercles and branched gills and papillae several on the head and on rhinophore sheaths as also in mid-dorsal and lateral rows. In the present species, mid-dorsal and lateral tubercular or papillary processes are altogether absent.

Conclusion

Recorded information on this interesting group Dendronotacea in particular and the nudibranchiate gastropods in general occurring along the Indian coasts is much scattered in the early publications not easily accessible to the interested scientific worker. Many of the first descriptions are based on preserved materials only. The taxonomic findings of the earlier workers needs revision in the light of more recent findings. A systematic compilation of the available information on the subject, if attempted in a monographic form, will be extremely useful as a reference work not only to those interested in this country but also elsewhere, for a fair number of the Indian species have a wide range of distribution in the Indo-Pacific.

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THE ECOLOGY OF TWO SANDY BEACHES IN SOUTH-WEST INDIA: IV. THE BIOCHEMICAL COMPOSITION OF FOUR COMMON INVERTEBRATES.

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INTRODUCTION

In three previous papers in this series (Ansell *et al.*, 1972 a, b, c,) we have described for two beaches in south-west India, a) the seasonal changes taking place in the macrofauna as a result of seasonal climatic and hydrographic fluctuations; b) the biology of the mole crab, *Emerita holthuisi;* and c) the biology of the bivalves *Donax incarnatus* and *D. spiculum;* three species which together account for much of the macrobenthic biomass of the beach. The study of the trophic processes taking place on tropical beaches, of which these contributions formed a part, was initiated during the period of the International Biological Programme as a cooperative venture involving the Marine Laboratory, Aberdeen, and the National Institute of Oceanography of India, together with individuals from other institutions. Dr. N. K. Pannikar was closely associated with the inception of this project, and has taken a lively interest in the progress, and it seems appropriate therefore that part of the results of this study should appear in a volume dedicated to the celebration of his 60th birthday. It is a pleasure to acknowledge the contribution which Dr. Pannikar's interest made to this joint project.

We are grateful to Dr. J. Steele, Marine Laboratory, Aberdeen, for the original invitation for one of us (A.D.A.) to take part in this joint study, and to the Royal Society for funds and support for travel to India (A.D.A.) and to

Britain (P.s.). Mrs. Margaret Leftley carried out the lipid analyses at Dunstaffnage, and further valuable technical assistance was provided by Miss Janet Mackay and Mrs. Linda Robb.

Material and Methods

Individuals of the crab, *Emerita holthuisi*, Sankolli the bivalves *Donax incarnatus* Gmelin and *D. spiculum* Reeve and the gastroped *Bullia melanoides* Deshayes, were collected non-quantitatively during various visits to beaches at Cochin and Shertallai during 1968. The four species involved were among the most abundant on the two beaches (Ansell *et al.*, 1972a) and are all tidal migrant forms (Ansell and Trevallion, 1969). Aspects of the behaviour and general biology of the gastropod, *Bullia melanoides*, were described by Ansell and Trevallion (1969; 1970), Trevallion and Ansell (1969) and Ansell *et al.* (1972a); of the mole crab, *Emerita holthuisi,* by Ansell *et al.* (1972b); and of the two bivalves *Donax incarnatus* and *D. spiculum* by Ansell and Trevallion (1969) and Ansell *et al.* (1972c).

Following collection, the animal were returned in fresh condition immersed in seawater to the laboratory and a sample was used for the determination of wet and dry percentage tissue weights and, in the case of the molluscs, shell weight. For the bivalves, the shell was first blotted dry. The shell length and the total weight was determined, the shell was then opened by severing the adductor muscle, and the flesh removed to a weighed dish. The wet weight of the tissues, and the dry weight after drying in an oven at 80°C for 24 h, were determined. The shell was allowed to dry in air and then reweighed. The wet and dry weights of the tissues, and the shell weights are expressed as a percentage of the total weight of the intact animal. In the gastroped, *Bullia melanoides*, the foot is a large expanded organ and its withdrawal takes place only after severe stimulus. In this species, the foot was stimulated to complete withdrawal, resulting in loss of the extrapallial fluid (see Brown, 1961), and the spire height of the shell and the total weight were then determined after the shell had been blotted dry. The tissues were removed by cracking the shell using bone forceps and severing the columellar muscle, taking care to remove the finest whorls of the gonad from the spire of the shell. Animals which were too badly crushed in this process were rejected. Again the wet tissues were weighed into a weighed dish, and reweighed following drying in an oven at 80°C. For *Emerita,* the carapace length and total wet weight were determined, and the intact animal then dried, in a weighed dish, for determination of dry weight.

The tissues were removed from separate groups of the bivalves and gastropods, and these, together with separate groups of *Emerita*, were freeze-dried. The freeze-dried samples were stored in a dry condition in air-tight sealed cans, until the analyses were made. The freeze-drying and canning of all samples

was carried out using the facilities of the Central Institute of Fisheries Technology, Cochin by kind permission of the Director, and all analyses have been carried out at the Dunstaffnage Marine Research Laboratory.

Carbon and nitrogen, carbohydrate, lipid and ash were determined on aliquots of the freeze-dried material, which was first ground to a homogeneous fine powder in a pestle and mortar. Carbon and nitrogen determinations were made with a Perkin-Elmer model 240 elemental analyzer. Carbohydrate was determined using the method of Dubois *et al.* (1956), as in previous studies of the biochemical composition of bivalves (Ansell and Trevallion, 1967; Ansell and Trevallion, 1967; Ansell, 1972), and lipid was also determined by the method used in these studies, which was a slight modification of the method of Bligh and Dyer (1959). Ash was determined by igniting an aliquot of the freeze-dried material at 600°C in a muffle furnace. Total nitrogen multiplied by a factor of 6.25 has been taken as an estimate of protein, and the calorific content of the tissues has been calculated using the factors Nx6.25x5.65; carbohydrate x 4.1, and lipid x 9.45.

In temperate and boreal species, where mature individuals may be present in the population for several years during which time cyclical processes of gametogenesis and storage of reserves take place on a seasonal basis, it is appropriate to represent seasonal biochemical changes on the basis of a standard animal (Barnes, Barnes and Finlayson, 1963; Ansell and Lander, 1967; Ansell and Trevallion, 1967). Such a concept is not applicable to the shorter-lived tropical species, such as the two species of *Donax* and *Emerita,* where rapid growth accompanies these processes, and where, as a consequence, different stages of the cycle may be invariably associated with animals of different size. In these species therefore, only percentage composition is considered. The concept of a standard animal, however, may apparently be applied to *Bullia,* for which species individuals of all sizes were represented in the population throughout the year.

Results

Donax incarnatus

Donax incarnatus was present on both Shertallai and Cochin beaches in the early part of the year, but disappeared from samples from Cochin during the monsoon. On both beaches, two groups of animals were present, deriving from separate recruitment during 1967 and 1968. Ansell *et al.* (1972c) have already described the changes in body weight of animals from these two groups on the two beaches. There was little difference between the mean percentage wet and dry weights of the 1967 and 1968 year groups from each beach, and since freeze-dried material was not available separately from all collections the mean wet and dry weights derived by combining the two year groups are used here to compare with the results of analysis. The results are summarised in Table 1 for Cochin and Table 2 for Shertallai.

There seems to be no consistent trend in the biochemical composition either at Cochin or Shertallai. When animals from the two beaches are compared however, there are consistent differences. Most important is that the lipid content of the tissues was higher in animals from Shertallai than in animals from Cochin. As a result the percentage carbon was greater in Shertallai animals and the total calorific content higher. Ansell *et al.* (1972c) have previously noted that the mean percentage dry weight of tissues from animals from Shertallai was greater than that of animals from Cochin, and that the maximum size reached by *D. incarnatus* at Shertallai was greater than at Cochin. All these differences are consistent with the generally higher levels of particulate organic matter in the surf water at Shertallai throughout the year (Ansell *et al.*, 1972a) indicating generally better conditions of nutrition for this species on this beach.

Donax spiculum

Although *D. spiculum* was present on both beaches, at Cochin prior to the monsoon and at Shertallai after the monsoon, freeze-dried material of this species was collected only from Cochin. The results of the analyses of the four samples are given in Table 3. The results of the four analyses are closely similar, and like *D. incarnatus,* show no seasonal trends. The mean percentage dry weight rose steadily between February and June, and this rise was associated with development and proliferation of the gonad which in February was undifferentiated and sexually indistinguishable, but in June was well developed, apparently ripe, and with a distinctive orange-brown colouration in the female. However, this change in sexual maturity was not reflected by any change in percentage composition; rather there appeared to be a gradual accumulation of lipid, protein and carbohydrate in roughly equivalent proportions.

Comparison of the mean values for these four determinations with those of *D. incarnatus* from Cochin show that the composition of the soft tissues of the two species was very similar, although *D. spiculum* had a somewhat higher lipid content, resulting in a slightly higher value for the total calorific content. In both bivalves the carbohydrate content showed the greatest variation between samples. In bivalves generally, the carbohydrate reserves may be rapidly utilized under unfavourable conditions, and the great variation found in carbohydrate in the samples perhaps indicates that in these tropical species the level of mobilizable carbohydrate reserves may fluctuate widely and rapidly in response to short-term fluctuations in conditions affecting the nutrition of the animal.

Bullia melanoides

B. melanoides was found only on the beach at Shertallai, where it was present throughout the year, although samples suggested that the population was not homogeneous, and perhaps consisted at different times of different groups moving throguh the sampling area.

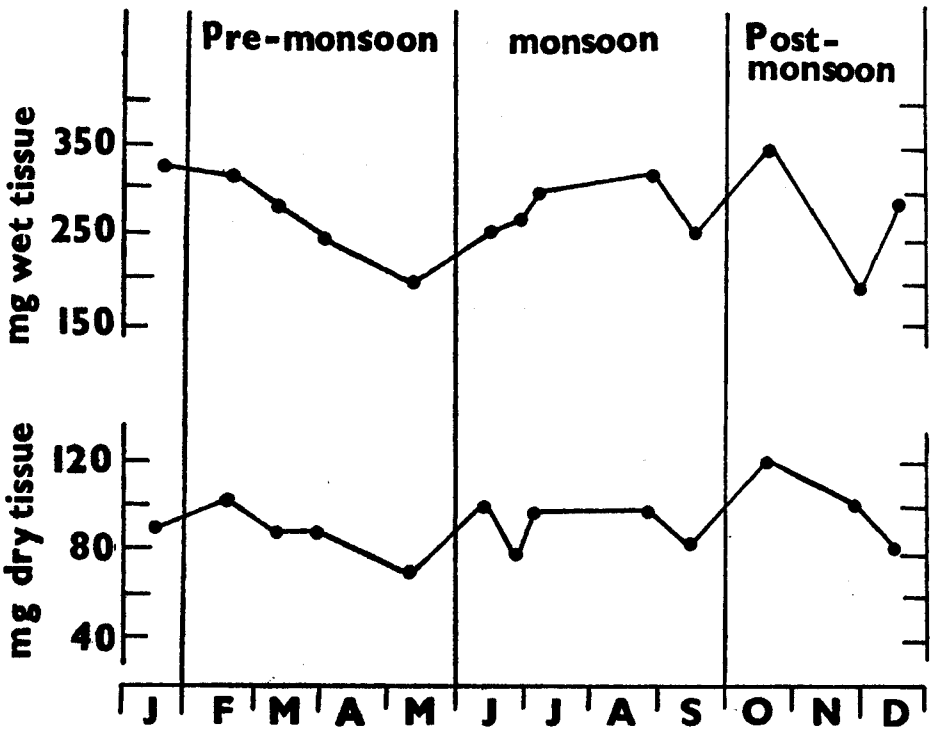


Fig. 1. *Bullia melanoides*. Changes in the wet and dry tissue weight of a standard animal of 1g total weight at Shertallai beach during 1968.

The results of analyses of *Bullia* are shown in Table 4, and summarised in Figs. 1, 2 and 3 which show the composition of a standard animal of 1 g total weight (spire height approx. 25 mm). There is an indication of some seasonal trend in the results which indicate that the highest values for lipid and nitrogen content of the standard animal were reached immediately after the monsoon season while the lowest values were reached just before the start of the monsoon. *Bullia melanoides* is mainly a scavenger on cast-up animal remains on the beach, and these seasonal changes may reflect changes in the seasonal availability of food, although it is possible too that they reflect seasonal gonadal changes. The species produces egg capsules which are attached to the foot of the adult until they hatch (Ansell and Trevallion, 1970) and Ansell *et al.* (1972a) considered that there might be two main periods of recruitment to the beach population from spawnings in the pre-monsoon and monsoon periods.

Compared with the two bivalves, *Bullia melanoides* had a consistently higher ash content, and lower carbohydrate content. The lipid content of the tissues was lower than that of *D. incarnatus* from Shertallai, but similar to that of the *Donax* species from Cochin. As a result of these differences the total caloric content of the *Bullia* tissues was lower than that of the bivalves.

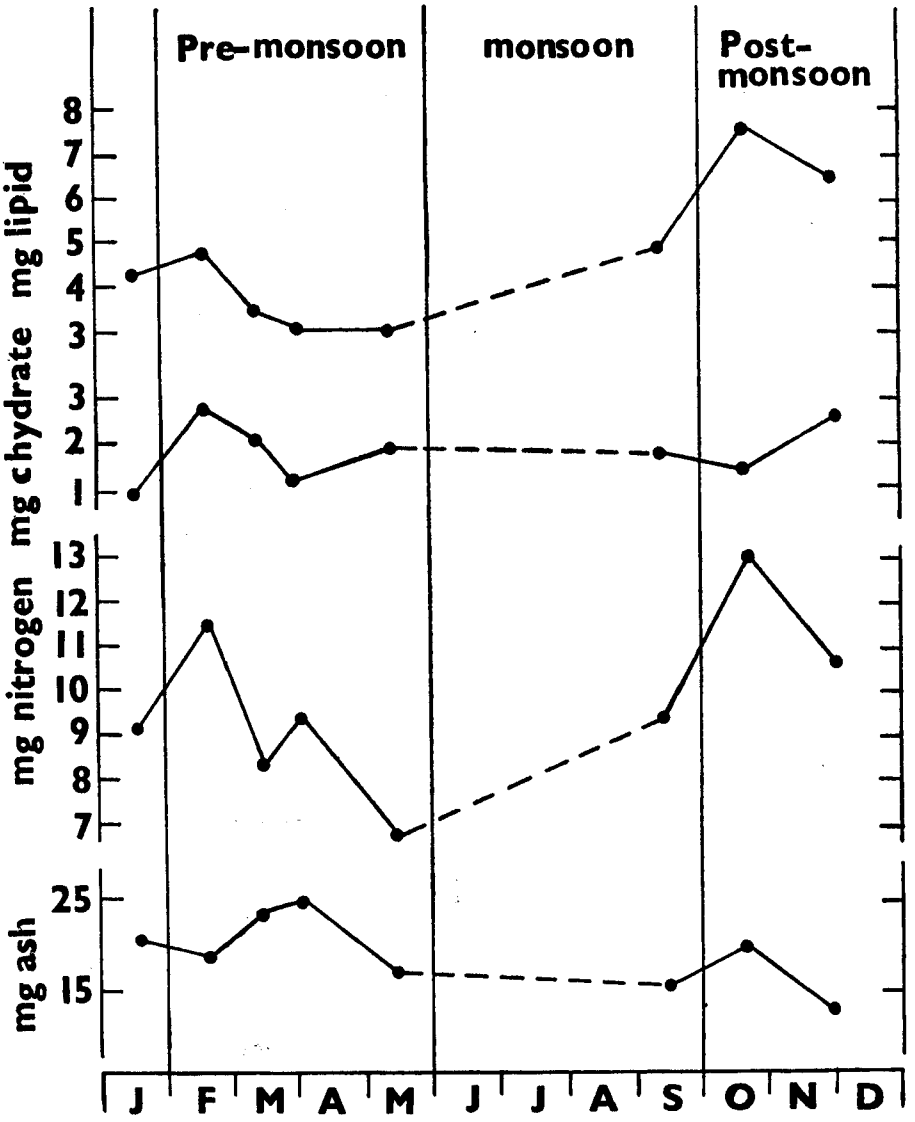


Fig. 2. *Bullta melanoides*. Changes in the chemical composition of a standard animal of 1g total weight at Shertallai beach during 1968.

Emerita holthuisi

This mole crab was found on both beaches throughout the year, although it reached its maximum numbers at different times in the two areas. Two samples from Cochin and five from Shertallai were analysed and the results are shown in Tables 5 and 6 respectively. The samples from the two beaches

show no consistent differences, apart from a higher nitrogen content of the Cochin samples. The seven samples include animals ranging from mostly small, newly-recruited, young to large gravid females carrying eggs and when these differences in size are considered there is a tendency for the larger animals to have a higher nitrogen content, a higher total carbon content, and greater caloric content. The differences between the Cochin and Shertallai animals are probably the result of these size differences.

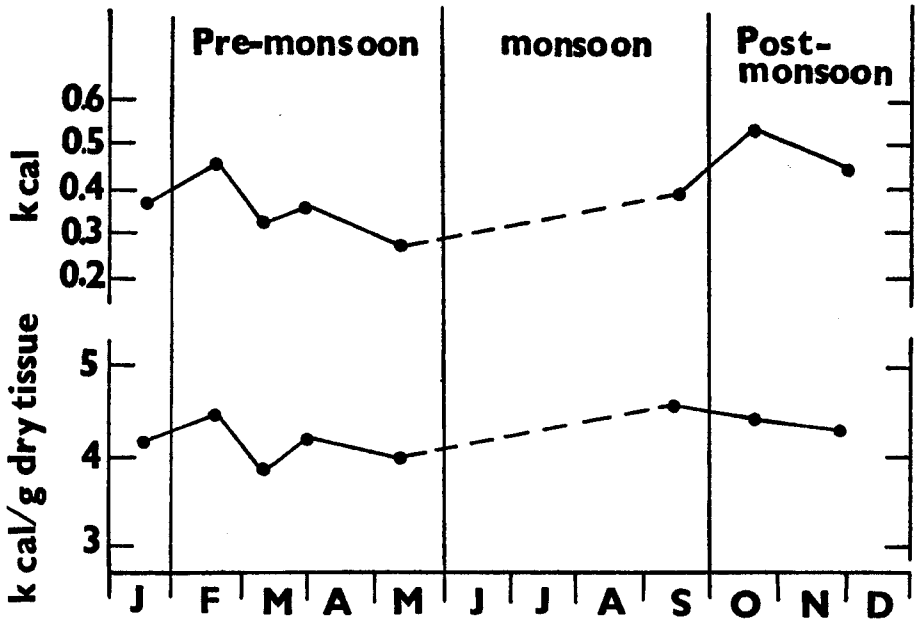


Fig. 3. *Bullia melanoides*. Changes in the calorific content of the tissues, and of a standard animal of 1 g total weight at Shertallai beach during 1968.

The composition of *Emerita holthuisi* apparently differs markedly from that of the bivalves. In particular, the ash content is high, and as a consequence the percentage of all other constituents is low. These differences result from the inclusion of the shell of the mole crab in the freeze-dried material, and a more meaningful comparison would involve ash-free dry weights (Table 7). However, this comparsion indicates that even taking into account the contribution of ash, there is still a difference between the crustacean *Emerita* and the molluscs, which affects particularly the calculated calorific content. The reaon for this difference probably lies in the inclusion in the analysed material of the chitinous shell of the crustacean.

Discussion

It would be inappropriate here to attempt to compare the composition of the four species from Shertallai and Cochin beaches with that of all the

numerous other invertebrates for which studies of biochemical composition have been made. A recent review of such studies for the mollusca has been given by Giese (1969). However, we may compare these analyses, particularly in the case of the bivalves, with those for closely related species from other areas.

Table 8 compares the data now available in the literature on the composition of species of *Donax* from various areas. The composition of the tropical species *D. cuneatus* shows a broad measure of agreement with the values found for *D. incarnatus* and *D. spiculum,* although the value for carbohydrate for *D. cuneatus* (Rahman, 1966) is rather higher. The determination of the percentage wet tissue weight for *D. faba* (Alagarswami, 1966) is based on formalin-preserved specimens and clearly does not compare with the other determinations.

The northern boreal species, *D. vittatus,* shows regular seasonal changes in composition related to the gonadal cycle and the storage and utilization of reserves (Ansell, 1972). The values for *D. incarnatus* and *D. spiculum* found in this study compare most closely with the values for *D. vittatus* found when the reserves are at a minimum in their annual cycle. Apparently accummulation of large amounts of reserve materials does not occur in the tropical species. This lack may be related to the generally closer balance between the metabolic demands of the animal and the food available from the water throughout the year in tropical species. In contrast, in *D. vittatus,* survival through periods of unfavourable conditions depends on the accumulation of adequate reserves during those periods during the spring and autumn diatom blooms when phytoplankton as food is available in excess of the immediate needs of the animal.

The object of these analyses was to provide information on the extent of fluctuation seasonally in the mean biochemical composition and calorific composition of the more abundant macrofaunal animals on the beaches for use in estimating the magnitude of production by the macrofauna, and the flow of energy through this element of the food chain of a trophical sandy beach. It is clear that for many applications the mean biochemical composition and hence the total carbon and calorific content of the four species examined here may be regarded as more or less constant through the year at one location although the results for *D. incarnatus* suggest that caution must be exercised in applying figures obtained in one area to studies on different beaches. The mean values given in Tables 1-6 may thus be taken as estimates of the mean annual composition of these animals in the macrofauna.

TABLE 1. *The biochemical composition of the tissues of Donax incarnatus collected from Cochin beach during 1968*

Date	% of total weight			% of dry weight						%of wet weight H_2O	K cals/g dry weight
	Shell	Soft tissues wet	Soft tissues Dry	Carbo-hydrate	lipid	Ash	C	N	Nx6.25		
8 Jan.	63.87	21.75	3.94	.....		No Analysis		.....		82.01	—
30 March	62.01	19.14	3.90	3.08	4.59	20.51	38.77	10.45	65.31	79.54	4.25
30 April	63.53	24.36	5.15	2.56	4.69	11.16	42.73	11.44	71.50	78.83	4.59
16 May	62.01	22.65	4.23	8.12	4.31	14.14	41.40	10.74	67.13	80.63	4.53
4 July	61.88	23.54	5.93	.....		No Analysis		.....		74.52	—
4 July	61.27	22.28	4.00	.....		No Analysis		.....		78.36	—
Mean	62.43	22.29	4.52	4.59	4.53	15.27	40.97	10.88	67.98	78.98	4.46
Standard deviation	±1.03	±1.80	±0.83	±3.07	±0.19	±4.78	±2.01	±0.51	±3.18	±2.55	±0.18

TABLE 2. *The biochemical composition of the tissue Donax incarnatus from Shertallai beach during 1968*

Date	% of total weight					% of dry weight				% of wet weight H_2O	K cals/g dry weight
	Shell	Soft tissues Wet	Soft tissues Dry	Carbo-hydrate	lipid	Ash	C	N	Nx6.25		
10 Jan	64.40	23.90	4.87	.....		No Analysis		.....		79.61	—
29 Jan	62.92	21.27	5.27	7.02	8.97	11.62	43.69	10.14	63.38	75.20	4.72
21 Feb	62.92	20.63	4.32	6.58	8.42	13.39	43.79	10.45	65.31	79.08	4.76
13 March	63.25	23.22	5.46	14.12	7.08	12.54	43.20	9.37	58.56	76.53	4.56
1 April	63.56	21.80	5.12	4.17	11.56	13.44	44.72	6.69	60.56	76.45	4.69
10 May	63.11	24.30	6.20	.....		No Analysis		.....		74.92	—
5 June	63.17	23.47	5.91	.....		,,		.....		74.89	—
15 July	63.07	29.17	4.28	.....		,,		.....		85.28	—
31 Aug	64.24	25.99	5.42	2.66	13.16	10.29	46.26	9.81	61.31	78.75	4.82
13 Sept	57.16	24.86	5.49	8.57	7.43	10.00	44.01	10.71	66.94	79.16	4.60
29 Oct	60.25	26.68	8.21	4.43	7.98	10.53	42.87	9.89	61.81	69.29	4.43
30 Nov	61.01	21.97	5.12	.....		No Analysis		.....		76.81	—
Mean	62.42	23.94	5.47	6.79	9.23	11.69	44.08	10.01	62.55	77.16	4.65
Standard deviation	±2.03	±2.47	±1.03	±3.80	±2.27	±1.46	±1.13	±0.46	±2.87	±3.80	±0.13

TABLE 3. *The biochemical compositon of the tissues of Donax spiculum collected from Cochin beach during 1968*

Date	% of total weight			% of dry weight						% of wet weight	K cals/g dry weight
	Shell	Soft tissue		Carbo-hydrate	lipid	Ash	C	N	Nx 6.25	H_2O	
		Wet	Dry								
6 Feb	65.23	20.86	4.04	.....		No Analysis		.....		80.36	—
20 Feb	59.98	19.48	4.96	1.68	5.22	12.19	41.13	11.61	72.56	74.36	4.66
6 March	62.25	22.53	5.61	7.04	5.13	12.39	41.12	10.88	68.00	75.18	4.62
8 May	63.04	22.75	6.18	4.77	5.27	12.82	42.06	11.61	72.56	72.48	4.79
18 May	63.82	25.99	6.56	4.08	4.93	12.80	41.07	11.64	72.75	74.53	4.74
Mean	62.86	22.32	5.47	4.39	5.14	12.55	41.34	11.43	71.47	75.38	4.70
Standard deviation	±1.95	±2.44	±1.00	±2.21	±0.14	±0.31	±0.48	±0.37	±2.31	±2.96	±0.07

TABLE 4. *The biochemical composition of the tissues of Bullia melanoides collected from Shertallai beach, during 1968*

Date	% of total weight			% of dry weight						% of wet weight H_2O	K cals/g dry weight
	Shell	Soft tissues Wet	Soft tissues Dry	Carbo-hydrate	lipid	Ash	C	N	Nx6.25		
29 Jan	59.82	32.44	8.75	1.12	4.95	23.32	40.51	10.39	64.94	73.00	4.18
21 Feb	59.04	31.67	10.18	2.75	4.71	18.29	42.94	11.28	70.50	67.97	4.54
13 March	64.10	28.01	8.60	2.48	4.06	27.09	37.28	9.59	59.94	69.03	3.87
1 April	51.50	24.73	8.63	1.38	3.61	28.77	41.58	10.95	68.44	64.57	4.26
18 May	79 82	19.51	6.92	2.73	4.50	24.08	38.98	9.87	61.69	61.11	4.02
5 June	67.18	25.14	10.23	.....		No Analysis		.....		58.99	—
29 June	62.75	26.67	7.56	.....		,,		.....		71.79	—
5 July	62.09	29.80	9.71	.....		,,		.....		67.09	—
31 Aug	59.71	32.07	9.98	.....		,,		.....		67.97	—
13 Sept	60.03	25.23	8.33	2.13	5.87	17.96	42.38	11.30	70.63	65.99	4.63
21 Oct	52.56	35.24	12.07	1.17	6.23	15.85	41.76	10.81	67.56	65.53	4.45
30 Nov	61.92	18.78	10.33	2.47	6.26	11.74	39.77	10.33	64.56	44.52	4.35
18 Dec	56.46	29.76	8.00			No Analysis				73 55	—
Mean	61.31	27.62	9.18	2.03	5.02	20.89	40.65	10.56	66.03	65.47	4.29
Standard deviation	±7.05	±4.93	±1.39	±0.70	±1.00	±5.87	±1.90	±0.63	±3.94	±7.59	±0.26

TABLE 5. *The biochemical composition of Emerita holthuisi collection from Cochin beach during 1968*

Date	% of total weight	% of dry weight					% of total weight H_2O	K cals/g dry weight
	Dry tissue	Carbo-hydrate	lipid	Ash	C	N	Nx 6.25		
30 April	16.50	1.91	5.20	31.25	35.99	8.17	51.06	83.50	3.45
16 May	34.18	1.85	2.98	33.57	33.91	7.43	46.44	65.82	2.98
4 June	29.30			No Analysis				70.70	—
Mean	26.66	1.88	4.09	32.41	34.95	7.80	48.75	73.34	3.21
Standard deviation	±9.13	±0.03	±1.57	±1.64	±1.47	±0.52	±3.27	±9.13	±0.33

TABLE 6 *The biochemical composition of Emerita holthuisi collected from Shertallai beach during 1968.*

Date	% of total weight Dry tissue	% of dry weight Carbo-hydrate	lipid	Ash	C	N	Nx 6.25	% of total weight H_2O	Kcals/g dry weight	Notes
30 March	35.50	.....	No Analysis		.....			64.50	—	—
15 June	16.10	.....		,,	.....			83.90	—	—
15 July	20.49	1.11	4.10	N.D.	25.71	4.03	25.19	79.51	1.86	—
31 July	17.25	.....	No Analysis		.....			82.75	—	—
23 Aug	N.D.	0.87	6.75	40.08	33.79	5.05	31.56	N.D.	2.46	small
23 Aug	25.50	0.49	8.57	N.D.	37.05	5.54	34.63	74.53	2.79	large
21 Sep	44.59	.....	No Analysis		.....			55.41	—	—
29 Oct	33.25	2.68	7.45	28.93	37.84	7.41	46.31	66.75	3,43	—
Mean	27.52	1.29	6.72	34.50	33.60	5.51	34.42	72.48	2.63	
Standard Deviation	±10.62	±0.96	±1.90	±7.88	±5.54	±1.41	±8.85	±10.62	±0.65	

TABLE 7. *The biochemical composition of ash-free tissues of four invertebrates from Cochin and Shertallai beaches during 1968, based on the mean composition in table 1–6*

Species	Area	% of ash-free dry weight Carbo-hydrate	lipid	C	N	Nx 6.25	K cals/g Ash free dry weight
D. incarnatus	Cochin	5.42	5.35	48.35	12.84	80.23	5.26
,,	Shertallai	7.69	10.45	49.92	11.34	70.83	5.27
D. spiculum	Cochin	5.02	5.88	47.27	13.07	81.73	5.37
B. melanoides	Shertallai	2.57	6.35	51.38	13.35	83.47	5.42
E. holthuisi	Cochin	2.78	6.05	51.71	11.54	72.13	4.75
,,	Shertallai	1.97	10.26	51.30	8.41	52.55	4.02

TALE 8. *Comparsion of the biochemical composition of various species of Donax*

Species and location	% of total weight			% of dry tissue weight									% of wet tissue	K cals/g	Authority
	Shell	Soft tissue wet	Soft tissue dry	Carbo-hydrate	lipid	Ash	C	N	Nx 6.25	P_2O_5	CaO	Iron x10^{-8}	H_2O	dry weight	
D. incarnatus Shertallai	62.42	23.94	5.47	6.79	9.23	11.69	44.08	10.01	62.55	—	—	—	77.16	4.65	This paper
D. incarnatus Cochin	62.43	22.29	4.52	4.59	4.53	15.27	40.97	10.88	67.98	—	—	—	78.98	4.46	This paper
D. spiculum Cochin	62.86	22.32	5.47	4.39	5.14	12.55	41.34	11.43	71.47	—	—	—	75.38	4.70	This paper
			(1)		(1)	(1)			(1,2)	(1)	(1)	(1)			
D. cuneatus Pamban	—	25	5.89	—	4.20	19.71	—	—	55.75	1.63	10.79	13.03	76.45	—	Chari & Unny (1946)
								(1)						(1)	
				(1)	(1)	(1)		6.68	(1)						
D. cuneatus Tondi	—	—	—	15.16	8.49	8.33	—	(1,3) 3.64	41.75	—	—	—	75.26	3.78	Rahaman (1965; 1966)
					(1)	(1)							(1)		
D. hanleyana					3.46	12.88							61.03		Velloso, Beck & Wiedem (1951)
D. vittatus-Male	50.9	44.7	10.92	11.94	8.04	9.02	—	10.06	62.87	—	—	—	75.56	4.85	Ansell
(max)-Female	53.6	41.7	9.66	12.41	10.81	9.41	—	9.50	59.37	—	—	—	76.83	4.93	(1972)
D. vittatus (min)	53.6	29.4	4.45	6.25	4.43	17.43	—	10.19	63.69	—	—	—	84.84	4.31	Ansell (1972)
D. faba		(4) 7.25 / 11.98	—	—	—	—	—	—	—	—	—	—	—	—	Alagarswamy (1966)

(1) calculated from the original (2) given as "protein" (3) Non-protein N. (4) based on formalin preserved tissue.

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A KEY FOR THE SEPARATION OF THE INDO-PACIFIC SPECIES OF *UCA* LEACH 1814

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In the present key, the shape and size of the front, the dorsal margin of the merus of the major male chela, the accessory line of granules inside the lower orbital border and the male pleopod 1 receive, as far as they are known, priority as specific characters.

The separation by Bott (1954) of the subgenera *Uca* and *Minuca* based on the shape of the front is supported by other characters. One of them is the different shape of the sternal furrow lodging the telson of the male, another is the difference of size of the species. The species of *Uca* (*Uca*) reach their full development at a size over 25 mm and generally 35 mm for the largest breadth of the carapace; there is one exception for *angustifrons* which hardly reaches 20 mm. The species of *Uca* (*Minuca*) reach their full development at a size of 20 mm and never exceed 25 mm for the largest breadth of their carapace; three species (*triangularis, variabilis, novaeguinae*) hardly reach 18 mm. It is noticeable that several species of *Uca* (*Uca*) have been originally described for specimen not yet fully developed; as in the case of *Uca rosea* for example. The shape of the major chela varies with the size and when using it as a specific character the size of the specimen must be taken into consideration. A similar variation affects the ratio of the frontal breadth to the extra orbital breadth and the ratio of the breadth to the length of the carapace. The median furrow of the front in some species (*dussumieri* for example) could present a slight variation not related to the size of the specimens; but the character keep its specific value as accurate illustration of the front of all the species could demonstrate.

The value of the shape of the male major chela as a specific character being generally considered as somewhat controversial it must be emphasized that in every species of *Uca* s. l. the shape of the major male chela present at least two different forms. The most typical example is that of *Uca vocans*, where three different forms have been originally described as distinct species. In a

paper under printing, I suggest for all species of *Uca* s. 1. to designate under the name of *forma typica,* the specimens having the major chela with elongate palm and a submedian tooth on the edge of the fixed finger and under the name of *forma anodonta,* those having the chela with shorter palm and no submedian tooth on the cutting edge of the fixed finger.

The larger length of the palm separating the form *typica* from the form *anodonata* can be indicated by the ratio of the length of the fingers to the length of the palm; only for some species those data are included in the key. The presence or absence of tooth on the cutting edge of the fingers to separate the form *typica* from the form *anodonta* refers only to the submedian tooth (or other teeth) not including the subdistal one, which is a specific character and as such can exist on the form anodonta. The dactyl as well as the fixed finger generally, but not always, has a submedian tooth on the form *typica* and none on the form anodonta.

The *forma typica* and *forma anodonta* of the species mentioned in the present key are those which I had an opportunity to observe myself or those which other authors have illustrated or described, as in the case of *Uca zamboangana.* For several species the two forms have not yet been described or illustrated, but very probably exist. An accurate illustration of the two forms for all species will clearly demonstrate the specific value of the shape of the chela and that different species never have the same shape of chela. The present confuse situation in the literature results from the insufficiency and inaccuracy of the illustrations. The use of the shape of the chela for the separation of the species must always be taken into consideration the form to which the specimen belongs.

No specimen has been examined for five species (+) *crassipes, mearnsi, forcipata, formosensis, dubia,* included in the key; one of them *mearnsi* is considered as a synonym of crassipes. Their position in the key is only indicative. The nearly certain identity of *signata* (Hess 1865) with *bellator* (White 1848) requests new examination of the type specimens. In the key the information on the colors mainly those of the carapace are only indicative, more accurate observations being necessary.

Some species like *triangularis, variabilis, novaeguinae* have been much less studied compared to others like *annulipes* and *lactea.* The present key mainly intends to provide a guide line for the field observations which could improve our knowledge of the specific characters which are still uncertain like the coloration and establish a more accurate one. It is established for fully developed male, to which the field worker must give prior attention; those specimens are generally difficult to catch; it is significant that they rarely exist in the large collections of *Uca,* which I have the opportunity to examine.

No information on the geographical distribution of the species being given in the key, it is here mentioned that *urvillie* and *inversa* are the only two species with a restricted distribution to the African region (western part) of the Indo-pacific region and that the species of the Pacific coast of the American Continent are not included.

1—Front narrow; frontal breadth always much less than 0.10 of extra-orbital breadth (save nearly 0.10 on *tetragonon*). Sternal furrow lodging male abdomen without hooking rim at level of distal border of segment 6.

.. .. Uca *(Uca)* Leach 1814
.. .. 2

—Front broad; frontal breadth always subequal or more than 0.15 of extraorbital breadth. Sternal furrow lodging male abdomen with hooking rim at level of distal border of segment 6.

.. .. *Uca (Minuca)* Bott 1954
.. .. 18

2(1)—An accessory rim of granules running parallel inside lower orbital border. Carapace broad (extraorbital breadth 1.7 carapace length, save in *mearnsi* 1.5) 13

—No such an accessory rim of granules 9

3(2)—Dactyl of major chela with a reamrkably strong subdistal tooth; anterior border of merus of cheliped (smooth) without marked distal tubercles. Accessory rim inside lower orbital border with 7-11 relatively large granules. Male pleopod in Gordon (1934, fig. 4a-c). Carapace blue grey, major chela with lower half of palm bright red, upper half yellow pale. Size : 15 26.25.

.. *coarctata* (H. Milne Edwards 1852) .. 3a

3a—Palm of major chela elongate with a submedian tooth on cutting edge of fixed finger.

.. .. *coarctata forma typica*

—Palm of major chela shorter without tooth on cutting edge of the two fingers.

.. .. *coarctata forma anodonta*

—Dactyl of major chela without remarkably strong subdistal tooth 4

4(3)—More than 20 (20-22) granules on accessory rim inside lower orbital border. Frontal furrow narrow-triangular with sides concave, tip blunt pointed. Upper orbital border nearly transverse. Major chela with palm and carpus with granules of middle size. Two fingers broad and flat with subdistal teeth and narrow intervening space; dactyl with two longitudinal grooves; fixed finger with one. Male pleopod unknown. Size : 23.4 39.5.

.. .. (+) *zamboangana* Rathbun 1913 .. 4a

4a(4)—Palm of major chela elongate with submedian teeth on two fingers.

.. .. .. *zamboangana forma typica*

—Palm of major chela shorter and fingers without submedian teeth.

.. .. .. *zamboangana forma anodonta*

—Less than 15 granules on accessory rim inside lower orbital border 5

5(4)—Carpus and palm of major chela finely granular nearly smooth. Fixed finger with a broadly triangular elongate tooth beyond middle and a longitudinal furrow close to lower margin; dactyl with a median longitudinal furrow and without marked took on a cutting edge. Anterior border of merus of major cheliped with a distal row of 3-5 acute tubercles 6

—Carpus and palm of major chela coarsely granular. Fixed finger without broadly triangular tooth beyond middle and with subdistal tooth or behind middle or both 7

6(5)—Frontal furrow triangular not reaching middle of front with strongly divergent margins. Accessory rim inside lower orbital border with 8-14 very small granules. Frontal breadth 0.069 (1/13) of extra-orbital breadth. Male pleopod in Gordon (1934, fig. 6). Carapace dark blue with large light blue patches on front along antero-lateral and orbital border and a large median transverse. Major chela with palm light violet. Fingers white. Size : Type of *signata*: 25x30 : (12.5x21 De Man 1891).

.. ? *bellator* White 1848 .. *signata* (Hess 1865) 6a

6a—Palm of major chela elongate with a submedian tooth on cutting edge of fixed finger.

.. .. *signata forma typica*

—Palm of major chela shorter without submedian tooth on cutting edge of fixed finger.

.. .. *signata forma anodonta*

—Frontal median furrow narrow reaching beyond middle of front with little divergent margins. Accessory rim inside lower orbital margin with 7-8 small granules. Male pleopod in Gordon (1934, fig. 6b). Size : 10.5 × 18.

.. .. .. *angustifrons* (De Man 1891) .. 6b

6b—Palm of major chela elongate with a submedian tooth on cutting edge of fixed finger.

.. .. *angustifrons forma typica.*

—Palm of major chela shorter without submedian tooth on cutting edge of fixed finger.

.. .. *angustifrons forma anodonta*

7(5)—Pereiopods 2-5 remarkably rough with broad meri; merus of pereiopod 5 as broad as long. Frontal furrow narrow oblong with tip arcuate and margin subparallel. (Accessory rim inside lower orbital border with 7-8 granules, occuping only one-third of its length on *mearnsi*; no information for *crassipes*). Male pleopod unknown. Size : (Type of *mearnsi*, 14.2 21.2).

.. .. (+) *crassipes* (Adams and White 1848)
.. .. (+) *mearnsi* Rathbun 1914 ? = *crassipes*

—Pereiopods 2-5 not remarkably rough and broad.

.. .. 8

8(7)—Dactyl of major chela with two longitudinal furrow; a feable submedian tooth on cutting edge of two fingers. Accessory rim of lower orbital border with 8-9 granules. Male pleopod unknown. Size : 20x24 (in De Man, 1891).

.. .. (+) *forcipata* (Adams and White 1848)

—Dactylus of major chela with only one longitudinal furrow. Accessory rim of lower orbital border with 10-11 granules; strong oblique granular line on inner side of palm. Male pleopod in Crosnier (1965, fig. 195, 196). Carapace blue; major chela orange red; ambulatory legs violet grey) Size : (Type : 10.3x18.6), 13.7x24.5 (in De Man 1891).

.. *urvillei* (H. Milne Edwards 1852) .. 8a

8a(8)—Palm of major chela elongate with submedian tooth on cutting edge of fixed finger (see Barnard 1950, fig. 18d-e).

.. .. *urvillei forma typica*

—Palm of major chela shorter without submedian tooth on cutting edge of fixed finger (see H. Milne Edwards 1852, pl. 3, fig. 10,).

.. .. *urvillei forma anodonta*

9(a)—Dorsal margin of merus of major chela without subdistal acute triangular tooth. Carapace narrow (extraorbital breadth = 1.5 carapace length). Lateral border of dorsum of carapace few converging backward ..10

—Dorsal margin of merus of major chela without subdistal acute triangular tooth. Carapace broader (extraorbital breadth..1.6 carapace length). Lateral border of dorsum of carapase more converging backward 11

10(9)—Frontal breadth 0.11 (1/8.5) of extraorbital breadth; front as broad as long. Frontal furrow widely open with inner lateral marging diverging backward. Carpus of male cheliped finely granular nearly smooth; outer face of palm nearly smooth. Inner surface of palm with feable lower granular crest. Fixed finger with feable and short proximal longitudinal groove. Male pleopod in Crosnier (1965, fig. 197, 198). Carapace blue dark with patches of yellow irregularly speckled with red; a white patch at antero lateral angle; ambulatory legs red; chela yellow with brick red patch at base of fixed finger. Size : 18.4 × 27.9.

.. .. .. *tetragonon* (Herbst 1799) .. 10a

10a(10)—Palm of major chela elongate with a submedian tooth on cutting edge of fixed finger.

.. .. .. *tetragonon forma typica*

—Palm of major chela shorter without submedian tooth on cutting edge of fixed finger.

.. .. .. *tetragonon form anodonta*

—Frontal breadth 0.05 (1/20) of extraorbital breadth. Front longer than broad; frontal furrow narrow with inner lateral margins diverging backward. Carpus and outer surface of palm of major cheliped coarsely granular. Inner surface of palm with strongly salient lower granular crest. Male pleopod in Crosnier (1965, fig. 194). Carapace blue grey with small white spot. Major chela with lower half of palm and fixed finger red orange upper half yellow, dactylus white milky. Size : 18.5 × 26.5.

.. .. *vocans* (Linne 1758) .. 10b

10b(10)—Palm of major chela short, its upper border less than 1/3 of length of dactylus. Cutting edge of the two fingers without teets; subdistal tooth of fixed finger obsolete.

.. .. [*marionis* (Desmarest 1823)]

.. .. *vocans forma vocans* (Linne 1758)

—Palm of major chela elongate with subdistal tooth of fixed finger strongly marked 10c

10c(10b)—Fixed finger without submedian tooth, sometimes indicated as a feable undulation.

.. *vocans forma cultrimana* (Adams and White 1848)

—Fixed finger with strong submedian tooth separated from subdistal by broad deep concavity.

.. .. .. [*nitida* (Dana 1851)]

.. *vocans forma excisa* (Nobili 1906)

11(9)—No median frontal furrow. Upper orbital border markedly arcuate but nearly transverse. External orbital angle projected almost anteriorly. Carpus and palm of major chela finely granular; finger much compressed, straight without subdistal tooth and accuminate only at tip; one feable longitudinal furrow. Male pleopod unknown. Size : 19.6 31.5 (in Sakai 1939).

.. .. .. (+) *formosensis* Rathbun 1921

—Median frontal furrow short or long, narrow or broad but always marked 12

12(11)—Dactyl of major chela with only one longitudinal furrow. Carapace around 1.60 as broad as long. 13

—Dactyl of large chela with two longitudinal furrows. Carapace around 1.70 as broad a long 16

13(12)—Two fingers of major chela without subdistal tooth 14

—Two fingers of major chela with subdistal tooth 15

14(13)—Carapace remarkably narrowed backward. Upper orbital border nearly transverse; external orbital angle sharply spine tipped; sharp lateral rim of dorsum strongly convergent and extending far backward. Frontal median furrow long, narrow, nearly linear with sides parallel. Frontal breadth 0.55 (1/18) of extraorbital breadth. Dorsal margin of merus of major chela with distal marked acute granule. Meri of

pereiopods 2-5 broad, around twice as long as broad. Male pleopod unknown. Size : 21 × 34.
.. .. .. *rubripes* Lucas and Jacquinot 1852

—Frontal median furrow short subtriangular with sides few divergent backward (like in vocans, fide Stimpson, 1858); upper orbital border strongly oblique. Dorsal margin of merus of major chela "spinuloso" (Stimpson). Meri of pereiopods 2-5 broad. Male peopod unknown. Size (Type specimen) 13.25 × 20.80.
.. .. + *dubia* (Stimpson 1858)

15(13)—Frontal median furrow narrow with inner margin proximally divergent. Lateral rim of dorsum straight strongly convergent backward; lateral border of carapace remarkably concave. Dorsal margin of merus of major chela smooth. Two fingers of major chela remarkably convex with large gap between them when close. Carapace with reticulation of vandyke red. Male pleopod unknown. Size: (Type specimen) 22.5 × 36.4.
.. .. .. *arcuata* (De Haan 1835) .. 15a

15a(15)—Palm of major chela elongate with submedian tooth on cutting edge of fixed finger (De Man 1891, fig. 7b).
.. .. .. *arcuata forma typica*

—Palm of major chela shorter without submedian tooth on fixed fingers (Maccagno, 1928, fig. 6b).
.. .. .. *arcuata forma anodonta*

—Median frontal furrow narrow but open with lateral border parellel; frontal breadth 0.066 (1/15) of the extraorbital breadth. Upper orbital border and lateral margin of dorsum finely denticulate. Margin of dorsum slightly sinuous and not remarkably convergent backward; lateral border of carapace not remarkably concave, nearly straight. Outer surface of palm of major chela with large granules. Male pleopod in Tweedie (1937, fig. 2b). Carapace and legs black; anterior half of carapace with subsymmetrical pattern of yellow spots; sharp delimitation between spotted and unspotted parts; major chela brown on upper third, lower two-third dark purple, fingers white. Size : 19.5 × 30, (14 × 25 in De Man, 1888).
.. .. *mani* Rathbun 1909 .. 15b

15b(15)—Palm of major chela elongate with submedian tooth on cutting edge of fixed finger. (De Man 1888, pl. 8, fig. 1, 2,

4 as *acutus*).

.. .. .. *mani forma typica*

—Palm of major chela short without submedian tooth on fixed finger (De Man, 1888, pl. 8, fig. 3 as *acutus*).

.. .. .. *mani forma anodonta*

16(12)—Median furrow of front generally close, and linear (sometimes a little open) with lateral border parallel. Frontal breadth 0.050 (1/20) of extraorbital breadth. Supraorbital border and margin of dorsum nearly smooth; margins of dorsum short not remarkably converging backward. Outer surface of palm of major chela with granules less strong than on *mani* and extending on the fingers. Male pleopod in Gordon (1934, fig. 5). Carapace sepia blue with dark green irregular marking. Major chela with lower half of palm light brown or brown red; upper part pale grey. Fixed finger brown, dactyl pale yellow; tips of two fingers white. Ambulatory legs dark like carapace with dactyli yellow gold. Size : 19x33 (in De Man, 1888).

.. *dussumieri* (H. Milne Edwards 1852) .. 16a

16a(16)—Palm of major chela elongate with submedian tooth on cutting edge of fixed finger (De Man, 1888, pl. 7, fig. 4, 5, 7).

.. .. .. *dussumieri forma typica*

—Palm of major chela shorter without submedian tooth on cutting edge of fixed finger (De Man, 1888, pl. 7, fig. 6).

.. .. .. *dussumieri forma anodonta*

—Median frontal furrow widely open. Margin of dorsum long, remarkably converging backward; supraorbital border and margin of dorsum finely denticulate or granular; granules of palm not extending on the fingers. 17

17(16)—Median frontal furrow distally rounded with lateral border parallel. Frontal breadth 0.090 (1/11) of extraorbital breadth. Male pleopod in Tweedie (1937, fig. 1). Carapace light grey with antero lateral part pink; major chela with lower half of palm red orange; upper half light pink; two fingers white pink.
Size : (Type: 15x25.6); 18.5x31.

.. .. *rosea* (Tweedie 1937) .. 17a

17a(17)—Palm of major chela with submedian tooth on cutting edge of fixed finger.

.. .. .. *rosea forma typica*

—Palm of major chela without submedian tooth on cutting edge of fixed finger.

.. .. *rosea forma anodonta*

—Median furrow of front oblong triangular distally rounded with lateral border divergent; frontal breadth 0.071 (1/14) of extraorbital breadth. Male pleopod in Tweedie (1950, fig. 7a). Carapace black in posterior third; yellowish anteriorly with black subsymmetrical reticulate pattern; major chela with palm light brown, finger white.
Size : (Type : 10x17.5).
.. .. *rhizophorae* Tweedie 1950 .. 17b

17b(17)—Palm of major chela with submedian tooth on cutting edge of fixed finger and teeth all along cutting edge of dactyl (Tweedie, 1950, fig. 7a).
.. .. .. *rhizophorae forma typica*

—Palm of major chela without submedian tooth on cutting edge of fixed finger and cutting edge of dactylus devoid of teeth on more than proximal half.
.. .. .. *rhizophorae forma anodonta*

18(1)—Lower oblique crest on inner surface of palm of major chela quite absent; dactyl with subdistal tooth forming bifurcate truncate tip; no subdistal tooth on fixed finger. Male pleopod without subdistal lobe (see Crosnier, 1965, fig. 210, 211). Size: 10.7x17.7.
.. .. .. *inversa* (Hoffmann 1874)

—Lower oblique crest on inner surface of palm of major chela distinct but more or less developed; dactyl with accuminate tip. .. 19

19(18)—Major chela without (pilose) depression on outside surface of palm near origin of fixed finger. 20

—Major chela with a small (pilose) depression on outside surface of palm near origin of fixed finger. On inner surface of palm, oblique lower proximal granular row regularly convex (not triangular); one feeble distal obliquely subvertical granular row continued on cutting edge of fixed finger; at some distance behind the distal and running parallely a short feable vertical row of granules. 24

20(19)—Lateral border of carapace few converging backward. Fixed finger of major chela with subtruncate tip well marked or at least indicated. Inner surface of palm with two obliquely subvertical granular row near articulation of fingers; the proximal (subdistal) continued on cutting edge of fixed finger; the distal short. 21

—Lateral border of carapace strongly convergent backward; lateral border of dorsum finely granular. Fixed finger of major chela with acu-

minate tip. Inner surface of palm of major chela with a single distal obliquely subvertical granular row near articulation of fingers but not extending on fixed finger. 22

21(20)—Eyebrow extending far over middle of upper orbital border. Lateral rim of dorsum posteriorly strongly curved towards longitudinal median axis of carapace and widely separate from postero-lateral transverse rim. On major chela subdistal tooth of fixed finger always marked, but less on form *anodonta;* outer surface of palm with groove running parallel and close to inferior margin; inner surface with lower oblique granular crest strongly salient and angular and two obliquely subvertical granular subdistal crest well marked; subdistal with 10 granules, distal with 7. Ambulatory legs with meri relatively broad with convex borders; on pereiopod 4, merus 2.70 as long as broad. Male pleopod with long and narrow subdistal lobe situated relatively far from distal chitinous process, which is somewhat long and nearly tubiform. Palm of major chela white pink. Size: 11x18.5 (Type).
.. *annulipes* (H. Milne Edwards 1852) 21a

21a(21)—Major chela with short palm and without submedian tooth on two fingers; dactyl 1.80 as long as palm length (see De Man, 1888, pl. 8, fig. 7).
.. .. .. *annulipes forma anodonta*

—Major chela with submedian tooth on two fingers 21b

21b(21a)—Palm elongate: dactyl 1.45 as long as palm length (see H. Milne Edwards, 1852, pl. 4, fig. 15b).
.. .. .. *annulipes forma typica*

—Palm shorter; dactyl 1.55 as long as palm length (see Nobili, 1901, fig. A).
.. .. .. *annulipes forma intermedia*

—Eyebrow not extending over middle of upper orbital border. Lateral rim of dorsum less convergent and longer (than on *annulipes*) posteriorly not remarkably curved and nearly reaching the postero-lateral rim, which is much less transverse (than on *annulipes*). On major chela subdistal tooth of fixed finger absent or faintly indicated; outer surface of palm with faintly indicated or absent groove running parallel to inferior margin; inner surface with proximal lower oblique granular crest less salient and only convex (not angular); two subdistal subvertical granular crest less marked with respectively 7 and 5 granules each. Ambulatory legs with meri narrower with nearly straight borders; on pereiopods 4 merus 2.96 as long as broad. Male pleopod

with short and broad subdistal lobe, situated close to distal chitinous process, which is short and widely open like a lamellar unguis. Palm of major chela whitish yellow. Size: 10x16.5.

.. .. *lactea* (De Haan 1835) .. 21c

21c(21)—Major chela with elongate palm and submedian tooth on fixed finger; dactyl 1.55 as long as palm length (see H. Milne Edwards 1852, pl. 4, fig. 16).

.. .. .. *lactea forma typica*

—Major chela with short palm and no submedian tooth on fixed finger; dactyl 2.06 as long as palm length (see Rathbun 1910, pl. 1, fig. 1 as *perplexa*).

.. .. .. *lactea forma anodonta*

22(20)—No accessory row of granules inside lower orbital border. Major chela with outer surface of palm smooth and without longitudinal furrow parallel and close to lower border. Outer surface of dactyl with longitudinal groove. Merus of pereiopods 2-5 a few slender than on *annulipes*. Male pleopod unknown. Palm of major chela orange yellow. Size : 8x15 (Type specimen).

.. .. *triangularis* (A. Milne Edwards 1873)

—An accessory row of 15-20 granules inside lower orbital border .. 23

23(22)—Major chela with carpus and palm without pigmented spots. Outer surface of palm smooth and without longitudinal furrow parallel to lower border. Merus of pereiopods 2-5 more slender than on *triangularis*. Male pleopod unknown. Size : 7x12.

.. .. .. *variabilis* (De Man 1891)

—Major chela with carpus and palm dotted with brown dark pigmented spots. Lateral sides of carapace less convergent than on *variabilis* and front less truncate. Front breadth less than 1/5 of extraorbital breadth. Size : 9x15 (Type specimen).

.. .. *novaeguinae* Rathbun 1913

24(19)—Major chela with fingers at least 1.5 as long as palm length, (on small specimen as long as palm). Ambulatory legs with anterior border of merus few convex; on pereiopod 4, merus (2.50) more than twice and half as long as broad. Male pleopod with tubiform chitinous apex and on inner ventral side a subdistal short lobe (see Crosnier 1965, p. 214, 215). Size : 14x22.

.. .. *gaimardi* (A. Milne Edwards 1853) .. 24a

24a(24)—Major chela with elongate palm and differentiated teeth on fingers; dactyl 1.56 as long as palm length (see Forest and

Guinot 1961, fig. 140).
.. .. .. *gaimardi forma typica*

—Major chela with short palm and without differenciated teeth on fingers; dactyl 1.96 as long as palm length (see Forest and Guinot 1961, fig. 140).
.. .. .. *gaimardi forma anodonta*

—Major chela with fingers always clearly less than 1.5 as long as palm length (on small specimen much shorter). Ambulatory legs with anterior border of merus strongly convex; merus (2.40) less than twice and half as long as broad. Male pleopod with tubiform chitinous apex and with a very small lobe on inner ventral sides only indicated as a hump. (see Forest and Guinot 1961, fig. 157a, b).
Size : 13.5x21.
.. .. *chlorophthalmus* (H. Milne Edwards 1853) 24b

24b(24)—Major chela with elongate palm long and differentiated teeth on fingers; dactyl 1.30 as long as palm length.
.. .. .. *chlorophthalmus forma typica*

—Major chela with short palm and without differenciated teeth on fingers; dactyl 1.45 as long as palm length.
.. .. .. *chlorophthalmus forma anodonta*

Singapore, 8/3/1973

SALINITY REQUIREMENTS IN THE LARVAL LIFE HISTORY OF FRESHWATER PRAWN, *MACROBRACHIUM MALCOLMSONII* (H. MILNE EDWARDS)

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ABSTRACT

The preliminary laboratory studies on the larval life history of *M. malcolmsonii*, considered as a freshwater prawn, have indicated the necessity of salinity requirements for successful rearing of larval stages subsequent to first zoea.

Prawn, as a fishery commodity, has attained such a magnitude of commercial importance all the world over, that the methods to increase its production are being given the emphasis in the fisheries development. Fishing effort for prawns is fast spreading to exploit all possible aquatic resources to the extent that natural stocks can sustain. Prawn cultivation is being improved upon by changing from merely trapping the juveniles of mixed species to selecting juveniles of desirable species from the incoming tides for stocking in the impoundments for further growth. The method, which is gaining rapid interest, is farming of prawns of suitable species, by raising all the developmental stages up to marketable size, in captivity. It has been known that the environmental requirements of larvae in several species of prawns are known to be invariably different from those of juveniles and adults. As such, farming of suitable species necessitates pre-requisite considerations of physico-chemical and biological requirements, which mainly fall into components, one catering for the larval stages and the other concerning the needs of the post-larval stages. In pre-farming investigations, the salinity requirements for different stages in the life history of a prawn, constitutes one of the most important environmental factors. It is in this context that the extensive studies on the osmotic physiology of prawns have been stressed (Panikkar, 1968).

Amongst the prawns, the genus *Macrobrachium* includes some species which grow to large size, commercially called 'jumbo' variety. Such species are, therefore, important from the viewpoint of prawn-farming. For farming *M. rosenburgii,* the salinity requirements for rearing the larval stages in captivity to raise the necessary 'seed prawn', have been worked out by Ling (1962, 1969a, 1969b). Rajyalakshmi (1968) considers that *M. malcolmsonii* constitutes another important species for prawn-farming. This prawn abounds mainly in the complex of the river Godavari. Since it is found in the entire 1400 km stretch of this river, right from its mouth to the uppermost reaches, it is considered as a freshwater prawn, as against *M. rosenburgii* which is found in freshwaters only up to about 200 km from the coast. Although considerable information is available on the fishery biology and population characteristics of *M. malcolmsonii* in the river Godavari (Ibrahim, 1962; Rajyalakshmi *et al.,* 1969), the information on its larval life history is lacking. Ibrahim (1962b) described merely the embryonic development up to gastrulation and Rajyalakshmi (1960) gave only an account of the embryonic development and 1st stage larva, hatched out on the 14th day, by rearing in captivity the berried specimens caught from the river Hooghly. The breeding migration of this species has also not been known (Panikkar *loc. cit.*).

Considering that *M. malcolmsonii* was a freshwater prawn, it would be reasonable to expect that it would complete its life history in freshwater, particularly when berried females could be obtained from the uppermost reaches of the river. Further expectation would be that the larvae carried alongwith the flood waters during the monsoon, would grow in the outpockets of the rivers and connected ponds, to constitute at least a small fishery in these captive resources. After the receding of floods, a detailed survey, undertaken in such resources along the river complex traversing the State of Maharashtra, revealed no such fishery in any of the captive resources. Failure of the larvae to thrive in these resources was possibly the reason, and this could be due to the necessity of salinity requirements, as one of the factors. Keeping this in view, the plankton collections made from the tributaries of the river revealed the presence of only Zoeae I. These considerations promoted to undertake investigations on finding out the necessity of salinity requirements in the larval life history of *M. malcolmsonii.*

The experiments on rearing the larvae were conducted at the Taraporevala Marine Biological Research Station, Bombay, where the live specimens of mature males, females and berried females, airshipped from Nagpur, were maintained in aquarium tanks and plastic pools. The water temperature in the rearing containers, glass bowls and troughs, varied from 28° to 32°C, during the entire period

of the experiment. Amongst the prepared foods given to the larvae, such as shredded prawn, fish flesh, fish roe and boiled egg, and amongst live foods, such as copepods, daphnids and *Artemia* nauplii. The larvae showed preference to fish roe and *Artemia* nauplii.

The mature males and females bred in captivity. Each berried female was maintained separately in an aquarium tank, provided with aeration. The larvae, Zoea I, which hatched out after the incubation period of about 15 days, did not moult for 13 days. Starving them for this period indicated that they were active for first 10 days, thereafter sinking to the bottom of the containers, eventually dying by the 15th day. It was also observed that these larvae could withstand considerable turbulence of water, mechanically brought about in the containers. Very few Zoeae I moulted in freshwater to Zoeae II, but all these also died. The Zoeae I were, therefore, subjected to different dilutions of seawater, 10%, 20% . . . up to pure seawater (100%), both by transfer directly from freshwater and also by process of gradual acclimation. It was interesting to observe that the larvae could tolerate all the dilutions and pure seawater. Of the larvae transferred directly from freshwater to seawater, some even survived for as many as 15 days. The dilutions below and above 40% were found to adversely affect both the metamorphosis and the survival percentage. The experiments on the salinity requirements of the larval stages subsequent to Zoea I, indicated that these stages needed a gradual rise from 40% to 70% seawater. Rearing of the Zoeae I for further metamorphosis was, therefore, undertaken in the medium, wherein the concentration was increased by 5% once a week to 70%; this resulted in successful metamorphosis, moulting occurring, on an average, every third day. By following this procedure, Zoea I passed through 15 moults in about 45 days. At the end of this period, the larva, which on hatching was about 2 mm in length, reached the length of about 7.5 mm in the XVI larval stage, which appeared to be the last larval stage. The detailed morphology of all the larval stages has been separately described (Kewalramani *et al.*, 1971).

Conclusions

This preliminary study has indicated the necessity of salinity requirements for completion of the larval life history, in captivity, of *M. malcolmsonii*, in principle and methods similar to the requirements in the larval life histories of *M. rosenburgii* (Ling *loc. cit.*) and *M. carcinus* (Lewis *et al.*, 1965). It seems probable that Zoeae I, which hatch out in freshwater in the river complex of Godavari, but may not metamorphose, have to undergo downstream migration to encounter brackishwater habitat. The upstream migration of juveniles in

the Godavari, particularly observable over the first anicut at Dowleishwaram (Ibrahim, 1962a), seems to lend further evidence in the migratory trends in the larval life history of *M. malcolmsonii*.

For prawn farming, the species which complete their larval development within a few moults seem to be better suited than those which hatch as small larvae and pass through many moults (Willismson, 1968). In this consideration, *M. malcolmsonii* has an elaborate larval life history, but the size attraction of the adult prawn constitutes sufficient justification to advance knowledge on this species for prawn farming as has been done in the case of *M. rosenburgii*.

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A CONTRIBUTION TO THE THREE-DIMENSIONAL COMPUTATION OF OCEAN CURRENTS IN PRESENCE OF BOTH VERTICAL AND HORIZONTAL MIXING

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ABSTRACT

The mathematical treatment of three dimensional computation of Ocean Currents have been discussed in the presence of both vertical and horizontal mixing. The depth to the bottom is assumed to be sufficiently large. A solution for the sufface slopes is obtained in terms of known density distribution and the surface wind stress components.

INTRODUCTION

Hidaka (1970), published a method to compute the ocean currents in presence of both vertical and horizontal mixing when they can be regarded as zonal, or the flow has little variation in an E-W direction. This has been an attempt to make the matter simpler, reducing the independent variables to two--or meridional and vertical coordinates only. Such a treatment can be often applicable to a certain case of approximately zonal flow in tropical waters around the equator. The mathematical procedure was by no means simple, though not impossible. Some numerical result was worked out for the wind-driven currents produced by a wind stress pattern approximately similar to actual distribution of average annual wind stress in the tropical waters.

Extension of the theory to three dimensions were not considered at that time, because of very complicated mathematical nature of the two-dimensional theory. However, the author recently

considers that three dimensional theory is possible to formulate, although not easy. It is not difficult at least to evaluate the part coming from wind stress.

For this reason, the complete theoretical treatment will be left to brilliant hydrodynamicians, because the author considers that it will not be difficult to get the numerical solution of this problem by an electronic computor.

The Problem.

Suppose a spherical surface representing a rotating earth. Take a point on the equator for the origin of the coordinate system and take x-axis positive eastward, the y-axis northward and z-axis vertically downward from an undisturbed level surface. Then the steady-state equations of motion are, if we neglect the non-linear terms arising from the field accelerations, as follows:

$$\left.\begin{aligned} A_x\frac{\partial^2 u}{\partial x^2}+A_y\frac{\partial^2 u}{\partial y^2}+A_z\frac{\partial^2 u}{\partial z^2}+2\omega\sin\phi\,\rho\cdot v &= \frac{\partial p}{\partial x}\ ;\\ A_x\frac{\partial^2 v}{\partial x^2}+A_y\frac{\partial^2 v}{\partial y^2}+A_z\frac{\partial^2 v}{\partial z^2}-2\omega\sin\phi\,\rho\cdot u &= \frac{\partial p}{\partial y}\ ;\\ g\rho &= \frac{\partial p}{\partial z} \end{aligned}\right\} \qquad (1)$$

where u and v are the x- and y- components of velocity, p is the pressure, ρ the density of sea water. A_x, A_y and A_z are the coefficients of horizontal and vertical mixing respectively, both supposed constant but not necessarily equal, ω the angular velocity of the Earth's rotation and ϕ the latitude connected with y by a relation $y=R\phi$ where R is the average radius of the Earth. The conditions to be satisfied at the sea surface are

$$z = 0 : \quad -A_z \frac{\partial u}{\partial z} = \tau_x \; ; \quad -A_z \frac{\partial v}{\partial z} = \tau_y \tag{2}$$

where τ_x and τ_y are the components of wind stress and generally functions of x and y. Further let us use the bottom conditions:

$$z = h : \quad \frac{\partial u}{\partial z} = \frac{\partial v}{\partial z} = 0 \tag{3}$$

which mean that there is no shearing stress at the bottom $z = h$, where h is supposed constant.

The equation of continuity is

$$\frac{\partial}{\partial x}(\rho u) + \frac{\partial}{\partial y}(\rho v) + \frac{\partial}{\partial z}(\rho w) = 0 \tag{4}$$

or

$$\rho\left(\frac{\partial u}{\partial x} + \frac{\partial v}{\partial y} + \frac{\partial w}{\partial z}\right) + u\frac{\partial \rho}{\partial x} + v\frac{\partial \rho}{\partial y} + w\frac{\partial \rho}{\partial z} = 0$$

In the density distribution in an ordinary ocean, the terms

$$u\frac{\partial \rho}{\partial x} + v\frac{\partial \rho}{\partial y} + w\frac{\partial \rho}{\partial z} \tag{5}$$

is small compared with the terms $\rho\left(\frac{\partial u}{\partial x} + \frac{\partial v}{\partial y} + \frac{\partial w}{\partial z}\right)$, so that (4) reduces to

$$\frac{\partial u}{\partial x} + \frac{\partial v}{\partial y} + \frac{\partial w}{\partial z} = 0 \tag{6}$$

without a perceptible error. For this reason the expression (6) will be used as the equation of continuity throughout the later discussion.

If we combine two equations in (1) using a complex form:

$$u + iv = U \ , \tag{7}$$

it will follow from (1)

$$A_x \frac{\partial^2 U}{\partial x^2} + A_y \frac{\partial^2 U}{\partial y^2} + A_z \frac{\partial^2 U}{\partial z^2} - i \cdot 2\omega\rho \sin\varphi U = +\left(\frac{\partial p}{\partial x} + i\frac{\partial p}{\partial y}\right) \tag{8}$$

3. Boundary Conditions.

For the calculation of the horizontal velocity components, the equation (8), where U stands for $u+iv$ must be solved for a number of boundary conditions, or the surface conditions (2) and bottom conditions (3).

In order to solve the equation (8) subject to the boundary conditions (2) and (3), or

$$z = 0 \ : \ -A_z \frac{\partial U}{\partial z} = \tau_x + i\tau_y \tag{9}$$

and

$$z = h \ : \ \frac{\partial U}{\partial z} = 0 \ , \tag{10}$$

suppose that the stations are distributed in grid points formed by intersections of meridians and latitude circles including the equator, all spaced at an equal interval Δy on the meridians and at an equal longitude interval $d\lambda$ on the latitude circles.

If $z=-\zeta$ is the equation of the height of the sea surface above a level surface, it follows

$$p = \int_{-\zeta}^{z} g\rho\, dz$$
$$= g\rho_0\zeta + \int_0^z g\rho\, dz \ ,$$

where ρ_0 is the value of ρ at the sea surface, and the pressure gradients becomes

$$\frac{\partial p}{\partial x} = g\rho_0\frac{\partial \zeta}{\partial x} + \int_0^z g\frac{\partial \rho}{\partial x}\, dz$$

and

$$\frac{\partial p}{\partial y} = g\rho_0\frac{\partial \zeta}{\partial y} + \int_0^z g\frac{\partial \rho}{\partial y}\, dz \ ,$$

so that (8) becomes

$$A_x\frac{\partial^2 U}{\partial x^2} + A_y\frac{\partial^2 U}{\partial y^2} + A_z\frac{\partial^2 U}{\partial z^2} - i\cdot 2\omega\rho\sin\varphi U$$
$$= g\rho_0\left(\frac{\partial \zeta}{\partial x} + i\frac{\partial \zeta}{\partial y}\right) + \int_0^z g\left(\frac{\partial \rho}{\partial x} + i\frac{\partial \rho}{\partial y}\right) dz \tag{11}$$

Elimination of the Variable y.

Now replace in (8) the second derivative $\frac{\partial^2 U}{\partial y^2}$ by a finite difference, or

$$\frac{\partial^2 U}{\partial y^2} = \frac{U_{k-1} - 2U_k + U_{k+1}}{(\Delta y)^2}$$

where U_k and $\partial^2 U_k/\partial y^2$ represent U and its second derivative at a particular station (kth station) on the meridian under consideration, and U_{k-1} and U_{k+1} refer to the $k-1$ th and $k+1$ th stations which are located at a spacing Δy to the south and north of the k th station respectively. Then the equation (8) reduces to the following set of m simultaneous equations:

$$\left.\begin{aligned}
&A_x\frac{\partial^2 U_1}{\partial x^2} + A_z\frac{\partial^2 U_1}{\partial z^2} + A_y\frac{U_S - 2U_1 + U_2}{(\Delta y)^2} - i\cdot 2\omega\sin\varphi_1\,\rho_1 U_1 \\
&\quad = g\rho_{0,1}\left(\frac{\partial \zeta_1}{\partial x} + i\frac{\partial \zeta_1}{\partial y}\right) + g\int_0^z \left(\frac{\partial \rho_1}{\partial x} + i\frac{\partial \rho_1}{\partial y}\right) dz, \\
&A_x\frac{\partial^2 U_2}{\partial x^2} + A_z\frac{\partial^2 U_2}{\partial z^2} + A_y\frac{U_1 - 2U_2 + U_3}{(\Delta y)^2} - i\cdot 2\omega\sin\varphi_2\,\rho_2 U_2 \\
&\quad = g\rho_{0,2}\left(\frac{\partial \zeta_2}{\partial x} + i\frac{\partial \zeta_2}{\partial y}\right) + g\int_0^z \left(\frac{\partial \rho_2}{\partial x} + i\frac{\partial \rho_2}{\partial y}\right) dz, \\
&A_x\frac{\partial^2 U_3}{\partial x^2} + A_z\frac{\partial^2 U_3}{\partial z^2} + A_y\frac{U_2 - 2U_3 + U_4}{(\Delta y)^2} - i\cdot 2\omega\sin\varphi_3\,\rho_3 U_3 \\
&\quad = g\rho_{0,3}\left(\frac{\partial \zeta_3}{\partial x} + i\frac{\partial \zeta_3}{\partial y}\right) + g\int_0^z \left(\frac{\partial \rho_3}{\partial x} + i\frac{\partial \rho_3}{\partial y}\right) dz, \\
&\qquad\qquad \cdots\cdots \\
&A_x\frac{\partial^2 U_m}{\partial x^2} + A_z\frac{\partial^2 U_m}{\partial z^2} + A_y\frac{U_{m-1} - 2U_m + U_N}{(\Delta y)^2} - i\cdot 2\omega\sin\varphi_m\,\rho_m U_m \\
&\quad = g\rho_{0,m}\left(\frac{\partial \zeta_m}{\partial x} + i\frac{\partial \zeta_m}{\partial y}\right) + g\int_0^z \left(\frac{\partial \rho_m}{\partial x} + i\frac{\partial \rho_m}{\partial y}\right) dz,
\end{aligned}\right\} \quad (12)$$

where ρ_0 is the surface value of ρ and U_S and U_N are the values of U at the southern and northern boundaries on a particular meridian, and

$$g\rho_{01}\left(\frac{\partial\zeta_1}{\partial x}+i\frac{\partial\zeta_1}{\partial y}\right)+g\int_0^h\left(\frac{\partial\rho_1}{\partial x}+i\frac{\partial\rho_1}{\partial y}\right)dz,\ g\rho_{02}\left(\frac{\partial\zeta_2}{\partial x}+i\frac{\partial\zeta_2}{\partial y}\right)+g\int_0^h\left(\frac{\partial\rho_2}{\partial x}+i\frac{\partial\rho_2}{\partial y}\right)dz,$$

... are the values of $g\rho_0\left(\frac{\partial\zeta}{\partial x}+i\frac{\partial\zeta}{\partial y}\right)+g\int_0^h\left(\frac{\partial\rho}{\partial x}+i\frac{\partial\rho}{\partial y}\right)dz$

at stations located in between.

Multiply both sides of (12) by a set of m undetermined multipliers $l_1, il_2, i^2l_3, \cdots, i^{k-1}l_k, \cdots, i^{m-1}l_m$ respectively, neglecting small variation in ρ in some terms, and add together; then we shall have

$$\begin{aligned}
&\left(A_z\frac{\partial^2}{\partial z^2}+A_x\frac{\partial^2}{\partial x^2}\right)\left(l_1U_1+il_2U_2+i^2l_3U_3+\cdots+i^{m-1}l_mU_m\right)\\
&\quad+\frac{A_y}{(\Delta y)^2}\Big[\Big\{-\left(2+i\cdot2\omega\sin\varphi_1\frac{(\Delta y)^2}{A_\ell}\rho_1\right)l_1+il_2\Big\}U_1\\
&\qquad+\Big\{l_1-\left(2+i\cdot2\omega\sin\varphi_2\frac{(\Delta y)^2}{A_\ell}\rho_2\right)il_2+i^2l_3\Big\}U_2\\
&\qquad+\Big\{il_2-\left(2+i\cdot2\omega\sin\varphi_3\frac{(\Delta y)^2}{A_\ell}\rho_3\right)i^2l_3+i^3l_4\Big\}U_3\\
&\qquad+\cdots\cdots\\
&\qquad+\Big\{i^{m-2}l_{m-1}-\left(2+i\cdot2\omega\sin\varphi_m\frac{(\Delta y)^2}{A_\ell}\rho_m\right)i^{m-1}l_m\Big\}U_m\\
&=-\frac{A_y}{(\Delta y)^2}\left(l_1U_S+i^{m-1}l_mU_N\right)\qquad(13)\\
&\qquad+\left\{g\rho_{0,1}\left(\frac{\partial\zeta_1}{\partial x}+i\frac{\partial\zeta_1}{\partial y}\right)+g\int_0^h\left(\frac{\partial\rho_1}{\partial x}+i\frac{\partial\rho_1}{\partial y}\right)dz\right\}l_1\\
&\qquad+\left\{g\rho_{0,2}\left(\frac{\partial\zeta_2}{\partial x}+i\frac{\partial\zeta_2}{\partial y}\right)+g\int_0^h\left(\frac{\partial\rho_2}{\partial x}+i\frac{\partial\rho_2}{\partial y}\right)dz\right\}il_2
\end{aligned}$$

$$+\left\{g\rho_{0,3}\left(\frac{\partial\zeta_3}{\partial x}+i\frac{\partial\zeta_3}{\partial y}\right)+g\int_0^h\left(\frac{\partial\rho_3}{\partial x}+i\frac{\partial\rho_3}{\partial y}\right)dz\right\}i^2l_3$$

$$+\ \cdots\cdots$$

$$+\left\{g\rho_{0,m}\left(\frac{\partial\zeta_m}{\partial x}+i\frac{\partial\zeta_m}{\partial y}\right)+g\int_0^h\left(\frac{\partial\rho_m}{\partial x}+i\frac{\partial\rho_m}{\partial y}\right)dz\right\}i^{m-1}l_m$$

where $\rho_1, \rho_2, \rho_3, \cdots, \rho_h, \cdots, \rho_m$ are density of sea water at the hth station considered dependent on z.

Here we introduce an unknown ξ which satisfies the following equations:

$$\begin{aligned}
-\left(2+i\cdot 2\omega\sin\varphi_1\frac{(\Delta y)^2}{A_y}\rho_1\right)l_1+il_2 &= -(2+i\xi)l_1,\\
l_1-\left(2+i\cdot 2\omega\sin\varphi_2\frac{(\Delta y)^2}{A_y}\rho_2\right)il_2+i^2l_3 &= -(2+i\xi)il_2,\\
il_2-\left(2+i\cdot 2\omega\sin\varphi_3\frac{(\Delta y)^2}{A_y}\rho_3\right)i^2l_3+i^3l_4 &= -(2+i\xi)i^2l_3,\\
&\cdots\cdots\\
i^{m-2}l_{m-1}-\left(2+i\cdot 2\omega\sin\varphi_m\frac{(\Delta y)^2}{A_y}\rho_m\right)i^{m-1}l_m &= -(2+i\xi)i^{m-1}l_m
\end{aligned}$$

or

$$\left.\begin{aligned}
\left\{\xi-2\omega\sin\varphi_1\ \frac{(\Delta y)^2}{A_y}\rho_1\right\}l_1+l_2 &= 0,\\
-l_1+\left\{\xi-2\omega\sin\varphi_2\ \frac{(\Delta y)^2}{A_y}\rho_2\right\}l_2+l_3 &= 0,\\
-l_2+\left\{\xi-2\omega\sin\varphi_3\ \frac{(\Delta y)^2}{A_y}\rho_3\right\}l_3+l_4 &= 0,\\
&\cdots\cdots\\
-l_{m-2}+\left\{\xi-2\omega\sin\varphi_{m-1}\frac{(\Delta y)^2}{A_y}\rho_m\right\}l_{m-1}+l_m &= 0,\\
-l_{m-1}+\left\{\xi-2\omega\sin\varphi_m\ \frac{(\Delta y)^2}{A_y}\rho\right\} &= 0
\end{aligned}\right\}\quad(14)$$

From the system of equations (14), we shall have an algebraic equations of mth order in ξ. This equation will have m roots, ξ_1, ξ_2, ξ_3, ---, ξ_m all real. For each of these roots, or ξ_j (j = 1, 2, 3, ---, m), we have a set of multipliers l_{1j}, l_{2j}, l_{3j}, ---- , l_{mj} (j = 1, 2, 3, ---, m) or l_{kj}. Then the equation (13) will take the following form:

$$\frac{\partial^2 V_j}{\partial z^2} - \frac{A_x}{A_z}\frac{\partial^2 V_j}{\partial x^2} - \frac{A_y}{A_z}\cdot\frac{2+i\xi_j}{(\Delta y)^2}V_j = F_j(x,z) \tag{15}$$

where

$$\begin{aligned} V_j &= l_{1j}U_1 + i l_{2j}U_2 + i^2 l_{3j}U_3 + \cdots + i^{m-1}l_{mj}U_m \\ &= \sum_{k=1}^{m} i^{k-1} l_{kj} U_k \end{aligned} \tag{16}$$

and

$$\begin{aligned} F_j(x,z) = &-\frac{A_y}{A_z}\cdot\frac{l_{1j}U_S + i^{m-1}l_{mj}U_N}{(\Delta y)^2} \\ &+ \frac{1}{A_z}\sum_{k=1}^{m} i^{k-1} l_{kj}\cdot\left\{g\rho_0\left(\frac{\partial\zeta}{\partial x}+i\frac{\partial\zeta}{\partial y}\right)+g\int_0^z\left(\frac{\partial\rho}{\partial x}+i\frac{\partial\rho}{\partial y}\right)dz\right\}_k \end{aligned} \tag{17}$$

The conditions to be satisfied by V_j can easily be derived as

$$z = 0 : \frac{d}{dz}V_j = -\frac{\bar{\tau}_j}{A_z} \tag{18}$$

where

$$\bar{\tau}_j = \sum_{k=1}^{m} i^{k-1} l_{kj}(\tau_x + i\tau_y)_k \tag{19}$$

and

$$z - h : \frac{d}{dz}V_j = 0 \tag{20}$$

According to the result of numerical solution of the equations (13), the quantities l_{kj} have largest values along the diagonal ($k=j$) of the

matrix $|l_{kj}|$ and decrease rapidly as we go away from the latter, or the larger the value of $|k-j|$, the smaller becomes l_{kj}. This means that the term:

$$-\frac{A_2}{A_1}\cdot\frac{l_{ij}U_S + i^{m-1}l_{mj}U_N}{(\Delta y)^2}$$

in (17) has very little influence on the result except at a few stations closest to the southern and northern boundaries of the meridional section. For this reason, we may put $U_S = U_N = 0$ in (17) and use a simpler expression of $F_j(x,z)$, or

$$F_j(x,z) = \frac{1}{A_1}\sum_{k=1}^{m} i^{k-1} l_{kj}\left\{g\rho_0\left(\frac{\partial\zeta}{\partial x} + i\frac{\partial\zeta}{\partial y}\right) + g\int_0^{\bar{z}}\left(\frac{\partial\rho}{\partial x} + i\frac{\partial\rho}{\partial y}\right)dz\right\}_k \tag{21}$$

provided that we avoid to apply the result to a few stations closest to the southern and northern boundaries.

Application of Fourier Integrals.

Now it follows by the theorem of Fourier integrals

$$\begin{aligned} V_j(x,z) &= \frac{1}{\pi}\int_0^{\infty}\alpha\,d\alpha\int_{-\infty}^{\infty} V_j(\lambda,z)\cos\alpha(\lambda-x)\,d\lambda \\ &= \frac{1}{\pi}\int_0^{\infty}\left\{V_j^{(1)}(\alpha,z)\cos\alpha x + V_j^{(2)}(\alpha,z)\sin\alpha x\right\}d\alpha \end{aligned} \tag{22}$$

and

$$\frac{\partial^2 V_j}{\partial x^2} = -\frac{1}{\pi}\int_0^{\infty}\left\{\alpha^2 V_j^{(1)}(\alpha,z)\cos\alpha x + \alpha^2 V_j^{(2)}(\alpha,z)\sin\alpha x\right\}d\alpha \tag{23}$$

where

$$\left.\begin{aligned} V_j^{(1)}(\alpha,z) &= \int_{-\infty}^{\infty} V_j(\lambda,z)\cos\alpha\lambda\,d\lambda, \\ V_j^{(2)}(\alpha,z) &= \int_{-\infty}^{\infty} V_j(\lambda,z)\sin\alpha\lambda\,d\lambda \end{aligned}\right\} \tag{24}$$

In a similar manner

$$F_j(x,z)=\frac{1}{\pi}\int_0^\infty\{F_j^{(1)}(\alpha,z)\cos\alpha x+F_j^{(2)}(\alpha,z)\sin\alpha x\}\,d\alpha \tag{25}$$

where

$$\left.\begin{aligned}F_j^{(1)}(\alpha,z)&=\int_{-\infty}^{\infty}F(\lambda,z)\cos\alpha\lambda\,d\lambda,\\ F_j^{(2)}(\alpha,z)&=\int_{-\infty}^{\infty}F(\lambda,z)\sin\alpha\lambda\,d\lambda.\end{aligned}\right\} \tag{26}$$

Further

$$\frac{\partial^2 V_j}{\partial z^2}=\frac{1}{\pi}\int_0^\infty\left\{\frac{\partial^2 V_j^{(1)}(\alpha,z)}{\partial z^2}\cos\alpha x+\frac{\partial^2 V_j^{(2)}(\alpha,z)}{\partial z^2}\sin\alpha x\right\}d\alpha \tag{27}$$

where

$$\left.\begin{aligned}\frac{\partial^2 V_j^{(1)}(\alpha,z)}{\partial z^2}&=\int_{-\infty}^{\infty}\frac{\partial^2 V_j(\lambda,z)}{\partial z^2}\cos\alpha\lambda\,d\lambda,\\ \frac{\partial^2 V_j^{(2)}(\alpha,z)}{\partial z^2}&=\int_{-\infty}^{\infty}\frac{\partial^2 V_j(\lambda,z)}{\partial z^2}\sin\alpha\lambda\,d\lambda.\end{aligned}\right\} \tag{28}$$

Let

$$\left.\begin{aligned}\tau(x,y)&=\tau_k(x)\\ &=\{\tau_x(x)+i\,\tau_y(x)\}_k\end{aligned}\right\} \tag{29}$$

be the complex representation of the wind stresses in zonal and meridional directions at the k th station. Further let

$$\left.\begin{aligned}\bar{\tau}_j(x)&=\sum_{k=1}^{m}i^{k-1}\,l_{kj}\,\tau_k(x)\\ &=\sum_{k=1}^{m}i^{k-1}l_{kj}\{\tau_x(x)+i\,\tau_y(x)\}_k.\end{aligned}\right\} \tag{30}$$

The boundary conditions to be satisfied at the sea surface are

$$-A_z\left.\frac{\partial V_k(x,z)}{\partial z}\right|_{z=0}=\{\tau_x(x)+i\,\tau_y(x)\}_k. \tag{31}$$

Multiply $i^{k-1}l_{kj}$ on both sides of the expression (31), again

multiply $\cos\lambda x d\lambda$ and $\sin\lambda x d\lambda$ respectively, integrate from $\lambda=-\infty$ to $\lambda=+\infty$, and sum up with respect to k, from $k=1$ to $k=n$; then follow the boundary conditions to be satisfied at the sea surface.

$$\left.\begin{aligned} -A_z\frac{\partial V_j^{(1)}(\alpha,z)}{\partial z}\Big|_{z=0} &= \int_{-\infty}^{\infty}\{\tau_x(\lambda)+i\tau_y(\lambda)\}_j\cos\alpha\lambda\,d\lambda, \\ \text{and}\quad -A_z\frac{\partial V_j^{(2)}(\alpha,z)}{\partial z}\Big|_{z=0} &= \int_{-\infty}^{\infty}\{\tau_x(\lambda)+i\tau_y(\lambda)\}_j\sin\alpha\lambda\,d\lambda, \end{aligned}\right\} \tag{32}$$

while the conditions to be satisfied at the ocean floor ($z=h$) are

$$-A_z\frac{d}{dz}V_j^{(1)}(\alpha,z)\Big|_{z=h} = -A_z\frac{d}{dz}V_j^{(2)}(\alpha,z)\Big|_{z=h}=0 \tag{33}$$

Substituting (22) —, (32) into (15) and assuming $A_x=A_y=A_e$ for the sake of simplicity, the following equations can be derived

$$\left.\begin{aligned} \frac{d^2V_j^{(1)}}{dz^2}-\frac{A_e}{A_z}\left(\lambda^2+\frac{2+i\xi_j}{(\Delta y)^2}\right)V_j^{(1)} &= F_j^{(1)}(\lambda,z) \\ \frac{d^2V_j^{(2)}}{dz^2}-\frac{A_e}{A_z}\left(\lambda^2+\frac{2+i\xi_j}{(\Delta y)^2}\right)V_j^{(2)} &= F_j^{(2)}(\lambda,z) \end{aligned}\right\} \tag{34}$$

where $V_j^{(1)}$ and $V_j^{(2)}$ are functions of α and z.

If $+\sqrt{\frac{A_e}{A_z}}\left(\lambda^2+\frac{2+i\xi_j}{(\Delta y)^2}\right)^{\frac{1}{2}}$ be denoted by q_j, it follows for $V_j^{(1)}$ from (34)

$$\frac{d^2V_j^{(1)}}{dz^2}-q_j^2V_j^{(1)} = F_j^{(1)}(\lambda,z). \tag{35}$$

$$q=+\sqrt{\frac{A_e}{A_z}}\left(\lambda^2+\frac{2+i\xi_j}{(\Delta y)^2}\right)^{\frac{1}{2}} \tag{36}$$

The boundary conditions to be satisfied on the sea surface and the bottom are given by (32) and (33).

The solution of (35) subject to the conditions (32) and (33)

$$V_j^{(1)}(\alpha,z) = -\frac{\cosh q_j(h-z)}{A_z q_j \sinh q_j h}\cdot\int_{-\infty}^{\infty}\left\{\tau_x(z_1)+i\tau_y(z_1)\right\}_j \cos\alpha z_1\, dz_1 - \int_0^h F_j^{(1)}(z_1,\alpha)K_j(z,z_1)\,dz_1 \tag{37}$$

where $K(z,z_1)$ is

$$\left.\begin{aligned} K_j(z,z_1) &= \frac{\cosh q_j(h-z-z_1)+\cosh q_j(h-z+z_1)}{2q_j\sinh q_j h} \quad (z>z_1>0)\\ &= \frac{\cosh q_j(h-z-z_1)+\cosh q_j(h+z-z_1)}{2q_j\sinh q_j h} \quad (h>z_1>z)\end{aligned}\right\} \tag{38}$$

In a similar way

$$V_j^{(2)}(\alpha,z) = -\frac{\cosh q_j(h-z)}{A_z q_j \sinh q_j h}\cdot\int_{-\infty}^{\infty}\left\{\tau_x(z_1)+i\tau_y(z_1)\right\}_j \sin\alpha z_1\, dz_1 - \int_0^h F_j^{(2)}(z_1,\alpha)K_j(z,z_1)\,dz_1 \tag{39}$$

Substituting (37) and (39) in (22) and inversing the series (16), u_k+iv_k becomes as follows

$$u_k + iv_k = \sum_{j=1}^{m}\bar{l}_{jk}V_j(z) \tag{40}$$

where

$$u_k + iv_k = U_k = \sum \bar{l}_{jk}V_j \tag{41}$$

and $\bar{l}_{jk}$'s are another set of multipliers obtained by inversing this series.

The final expression for u_k+iv_k, or the E- and N- components of velocity at k th station will be

$$\begin{aligned} u_k+iv_k = \sum_{j=1}^{m}\frac{\bar{l}_{jk}}{i^{k-1}}\int_z^h\Bigg[\frac{1}{\pi}\int_0^{\infty}\Bigg\{&+\frac{\bar{\tau}_j^{(1)}(\lambda)}{A_z}\cdot\frac{\sinh\lambda_j(h-z_1)}{\sinh\lambda_j h}\\ &+\int_0^h F_j^{(1)}(\lambda,z_1)K_j(z,z_1)\,dz_1\Bigg\}\cos\lambda x\,d\lambda\\ &+\frac{1}{\pi}\int_0^{\infty}\Bigg\{+\frac{\bar{\tau}_j^{(2)}(\lambda)}{A_z}\cdot\frac{\sinh\lambda_j(h-z_1)}{\sinh\lambda_j h}\\ &+\int_0^h F_j^{(2)}(\lambda,z_1)K_j(z,z_1)\,dz_1\Bigg\}\sin\lambda x\,d\lambda\Bigg]\end{aligned} \tag{42}$$

Wind-Driven Circulation.

It will be noticed that the solutions both for the horizontal and vertical components consist of two parts, that is to say, the terms involving τ_x and τ_y while the other those depending upon $\frac{\partial \rho}{\partial x} + i \frac{\partial \rho}{\partial y}$. From the construction of the formulae, the former terms, representing wind-generated circulation is more easy to further transform the expressions into definite forms. On the other hand, those terms depending upon $\frac{\partial \rho}{\partial x} + i \frac{\partial \rho}{\partial y}$ are not easy to numerically compute because they involve Green's functions or symmetric kernels.

For this reason, only the purely wind-produced circulation will be transformed into a more definite mathematical forms.

The part of the expression for u_k and v_k arising from the wind stresses will be from equation (42).

$$u_k + i v_k = \sum_{j=1}^{m} \frac{\bar{l}_{jk}}{i^{k-1}} \int_0^k \left[\frac{1}{\pi} \int_0^\infty \left\{ \frac{\bar{\tau}_j^{(1)}(\lambda)}{A_z} \cdot \frac{\sinh \lambda_j (h-z)}{\sinh \lambda_j h} \right\} \cos \lambda x \, d\lambda \right.$$
$$\left. + \frac{1}{\pi} \int_0^\infty \left\{ \frac{\bar{\tau}_j^{(2)}(\lambda)}{A_z} \cdot \frac{\sinh \lambda_j (h-z)}{\sinh \lambda_j h} \right\} \sin \lambda x \, d\lambda \right. \tag{43}$$

Since we have very closely

$$\frac{\sinh \lambda_j (h-z)}{\sinh \lambda_j h} = e^{-\lambda_j z} , \tag{44}$$

provided the depth to the bottom is sufficiently large.

Thus we have

$$u_k + i v_k = \sum_{j=1}^{m} \frac{\bar{l}_{jk}}{i^{k-1}} \left\{ \frac{1}{\pi} \int_0^\infty \frac{\tau_j^{(1)}(\lambda)}{A_z} \cdot \frac{e^{-\lambda_j z}}{\lambda_j} \cos \lambda x \, d\lambda \right.$$
$$\left. + \frac{1}{\pi} \int_0^\infty \frac{\tau_j^{(2)}(\lambda)}{A_z} \cdot \frac{e^{\lambda_j z}}{\lambda_j} \sin \lambda x \, d\lambda \right\} \tag{45}$$

Now on the meridian under consideration, we shall have

$$u_k + i v_k = \sum_{j=1}^{m} \frac{\bar{l}_{jk}}{i^{k-1}} \cdot \frac{1}{\pi A_z} \cdot \int_0^\infty \tau_j^{(1)}(\lambda) \frac{e^{-i\delta}}{\lambda_j} d\lambda \tag{46}$$

which can easily be integrated numerically because $\tau_j^{(1)}(\lambda)$ is known.

Particularly when $\tau_j^{(1)}(\lambda)$ and $\tau_j^{(2)}(\lambda)$ are constants as pointed out by Stommel (1948) Munk (1950) (46) will be reduced to

$$u_k + i v_k = \sum_{j=1}^{m} \frac{\bar{l}_{jk}}{i^{k-1}} \cdot \left[\frac{\tau_j^{(1)}}{\pi \sqrt{A_l A_z}} \cdot \int_0^\infty \frac{\exp\left\{ \frac{z}{\Delta y} \left(\frac{A_l}{A_z} \right)^{\frac{1}{2}} \sqrt{2 + i\xi_j + (\Delta y \lambda)^2} \right\}}{\sqrt{2 + i\xi_j + (\Delta y \lambda)^2}} d(\Delta y \lambda) \right] \tag{47}$$

This expression can be transformed further as

$$u_k + i v_k = \sum_{j=1}^{m} \frac{\bar{l}_{jk}}{i^{k-1}} \left\{ \frac{\tau_j^{(1)}}{\pi \sqrt{A_l A_z}} K_0 \left(\frac{z}{\Delta y} \sqrt{\frac{A_l}{A_z}} \cdot \sqrt{2 + i\xi_j} \right) \right\} \tag{48}$$

where $K_0(x)$ is the modified Bessel function of zero order.

This function can be evaluated, if x is small, as

$$K_0(x) = -I_0(x)\left(\log \frac{x}{2} + \gamma\right) + \left(\frac{1}{2}x\right)^2 + \left(1 + \frac{1}{2}\right) \cdot \frac{\left(\frac{1}{2}x\right)^4}{1^2 \cdot 2^2} + \left(1 + \frac{1}{2} + \frac{1}{3}\right) \cdot \frac{\left(\frac{1}{2}x\right)^6}{1^2 \cdot 2^2 \cdot 3^2} + \cdots \tag{49}$$

where γ is Euler's constant

$$\gamma = 0.5772157$$

and

$$I_0(x) = 1 + \frac{\left(\frac{1}{2}x\right)^2}{1^2} + \frac{\left(\frac{1}{2}x\right)^4}{1^2 \cdot 2^2} + \frac{\left(\frac{1}{2}x\right)^6}{1^2 \cdot 2^2 \cdot 3^2} + \cdots \tag{50}$$

For large values of χ , the following asymptotic series may be employed

$$K_0(\chi) \approx \left(\frac{\pi}{2\chi}\right)^{\frac{1}{2}} e^{-\chi} \left\{ 1 - \frac{1^2}{1 \cdot 8\chi} + \frac{1^2 \cdot 3^2}{2!\,(8\chi)^2} - \frac{1^2 \cdot 2^2 \cdot 3^2}{3\,(8\chi)^3} + \cdots \right\} \tag{51}$$

Sea Surface Slopes and Vertical Flows.

The equation of continuity is

$$\frac{\partial}{\partial x}(\rho u) + \frac{\partial}{\partial y}(\rho v) + \frac{\partial}{\partial z}(\rho w) = 0 \tag{52}$$

Assuming that w vanishes on the sea floor which is supposed horizontal or sufficiently deep so that there is no horizontal motion, it follows, by integrating (52) from $z = z$ to $z = h$,

$$-\rho w(h) + \rho w(z) = \int_z^h \left\{ \frac{\partial}{\partial x}(\rho u) + \frac{\partial}{\partial y}(\rho v) \right\} dz . \tag{53}$$

Since $w(h) = 0$ by assumption, the above equation becomes

$$w(z) = \frac{1}{\rho} \int_z^h \left\{ \frac{\partial}{\partial x}(\rho u) + \frac{\partial}{\partial y}(\rho v) \right\} dz \tag{54}$$

or

$$w(z) = \int_z^h \left(\frac{\partial u}{\partial x} + \frac{\partial v}{\partial y} \right) dz \tag{55}$$

very closely.

If further it is assumed that the vertical component $w(z)$ vanishes on the sea surface $z = 0$, it follows from (54)

$$\int_0^h \left\{ \frac{\partial}{\partial x}(\rho u) + \frac{\partial}{\partial y}(\rho v) \right\} dz = 0 \tag{56}$$

or

$$\frac{\partial M_x}{\partial x} + \frac{\partial M_y}{\partial y} = 0 \tag{57}$$

where M_x and M_y are the components of the mass transport such that

$$M_x = \int_0^h \rho u \, dz \quad ; \quad M_y = \int_0^h \rho v \, dz .$$

Substituting U_k and V_k derived as (42) into (56), it will follow an expression involving $\frac{\partial \zeta}{\partial x}$ and $\frac{\partial \zeta}{\partial y}$, $\frac{\partial \rho}{\partial x}$ and $\frac{\partial \rho}{\partial y}$ and τ_x and τ_y for the kth station. This expression will enable us to determine the surface slopes $\frac{\partial \zeta}{\partial x}$ and $\frac{\partial \zeta}{\partial y}$ in terms of the known density distribution $\frac{\partial \rho}{\partial x}$, $\frac{\partial \rho}{\partial y}$ and the surface wind stress components τ_x and τ_y at each stations $k = 1, 2, \ldots$.

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