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Observations on some symbiont bearing Foraminifera from the shelf and slope sediments of Eastern Arabian Sea

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Original Article

Abstract

The present study records small and large benthic foraminifera with endosymbionts distributed in the shelf sediments of the western continental shelf and continental slope (5-1333 m) of eastern Arabian Sea, with reference to climate change and coral reef monitoring. The larger benthic foraminifera (LBF) include *Alveolinella quoyii, Amphistegina lessonii, Amphistegina gibbosa, Operculina granulosa, Heterostegina depressa* and *Amphisorus hemprichii* which have symbiotic associations with diatoms, dinoflagellates, green algae, red algae and chrysophytes. The symbionts make these very efficient in utilising a wide range of the light spectrum and water depths. The size of species *Alveolinella quoyii* and *Amphistegina lessonii* recorded from water depths of 30 m to 1333 m showed intraspecific variations in size, those collected from deeper waters were larger than those found in shallow waters. It is evident that the presence of endosymbionts probably attributed to the intraspecific variations in size. The species belonging to these genera have evolved strategies like phenotypic plasticity and local adaptation of the concerned photosymbionts which have helped them tolerate thermal variations. The finding that the number of tests of LBFs decreased from shelf to slope areas may be indicative of the relation between oxidative stress, reduced light levels that affect the growth rate of these species. It is confirmed that LBFs have longer lifespan than the smaller forms.

Keywords: *Larger benthic foraminifera, endosymbionts, Amphistegina*

Introduction

Arabian Sea, a biologically productive region at the northern Indian Ocean covers just 1% of the global ocean surface. In spite of its meagre coverage, it contributes 5% to the global marine production. The intensive upwelling during the southwest monsoon along with the reversed circulation and mixed layer deepening during the northeast monsoon has contributed to the enhanced productivity of the sea (Qasim, 1977; 1982). The continental margins are areas which are highly suitable for carrying out faunal exploration to understand the productivity of such regions. The western continental shelf of the eastern Arabian Sea covers an area of about 3,10,000 km^2 which lies between 7°N to 24°N Lat. (Rao and Wagle, 1997). The width of the continental shelf tapers towards south from 345 km off Daman to 120 km off Goa and to 60 km off Kochi. In contrast to the shelf, the continental slope is narrower in north and wider at southern region. The inner shelf is characterised by clayey silt and silty clay sediments having high organic matter and low carbonate content which are gradually replaced by coarse sandy sediments with low organic matter and high carbonates at outer shelves and the continental slope is characterised by clayey silt sediments (Faruque and Ramachandran, 2014).

Marine sediments are of two kinds either of terrestrial origin or of biogenic origin. Biogenic sediments are those which accumulate slowly in deep seas far from the sources of terrigenous sediments, mainly composed of the hard skeletons of planktonic and benthic organisms. The sediments composed of more than 30% microscopic skeletal remains are oozes and they are primarily of two kinds–calcareous and siliceous. Calcareous ooze consists of shells of Foraminifera, Cocolithophores and Pteropods and contribute 48% to the biogenic sediments of the world ocean floor (Rothwell, 2005; Huneke and Mulder, 2011). These sediments are considered as the largest reservoirs of organic carbon on earth and continental margins, are important sites for the accumulation and burial of organic matter (Demaison and Moore, 1980; Cowei, 2005). Studies on the continental margin across the world emphasized the role of benthic fauna in remineralization of organic matter as well as ecosystem processes on regional and global scales. The benthic fauna is subject to sharp gradients in depth, temperature and dissolved oxygen along with considerable heterogeneity in sediment texture and organic matter.

Marine environments such as coral reefs are projected to change at unprecedented rates due to global warming and local disturbances. Close observations on reef organisms could help us in understanding their ability to acclimate to the rapid shifts in environmental conditions (Pandolfi, 2015). Larger benthic foraminifera (LBFs) are a group of single celled protists that build a calcium carbonate test harbouring algal symbionts which provide them with energy for growth and calcification. LBFs respond fast to environmental changes due to their small size and short lifespans which make them ideal indicator organisms to assess the change in their habitats. *Amphistegina* includes species which are sensitive to photic and thermal stress. Therefore, this group has been taken as a corollary to the occurrence of coral bleaching due to exposure to light and heat. The presence of symbionts in species belonging to this group probably relates them to the coral species where exposure to light and heat leads to death and decay of zooxanthellae leading to bleaching.

The study involves the ecological observation on the occurrence of six LBFs and 3 smaller benthic foraminifera (SBF) with endosymbionts in the sediments of the Western Continental margin of eastern Arabian Sea.

Material and methods

Thirtysix surface sediment samples analysed for the study were obtained from two cruises 148/15b and 162 conducted on *FORV Sagar Sampada* as well as the cruise 148/6 conducted on *FORV Sagar kanya*, and also from a few surface grab samples collected from various depths along the continental shelf-slope of Arabian Sea (Fig.1). The study was conducted during 2013-2015.

The collected samples were processed using the conventional micro-paleontological technique. 20 gm of sediment sample was soaked in 30% hydrogen peroxide solution overnight and boiled for 2-3 minutes. After cooling, the material was wet sieved over 63 μm and 100 μm screens. Large samples were

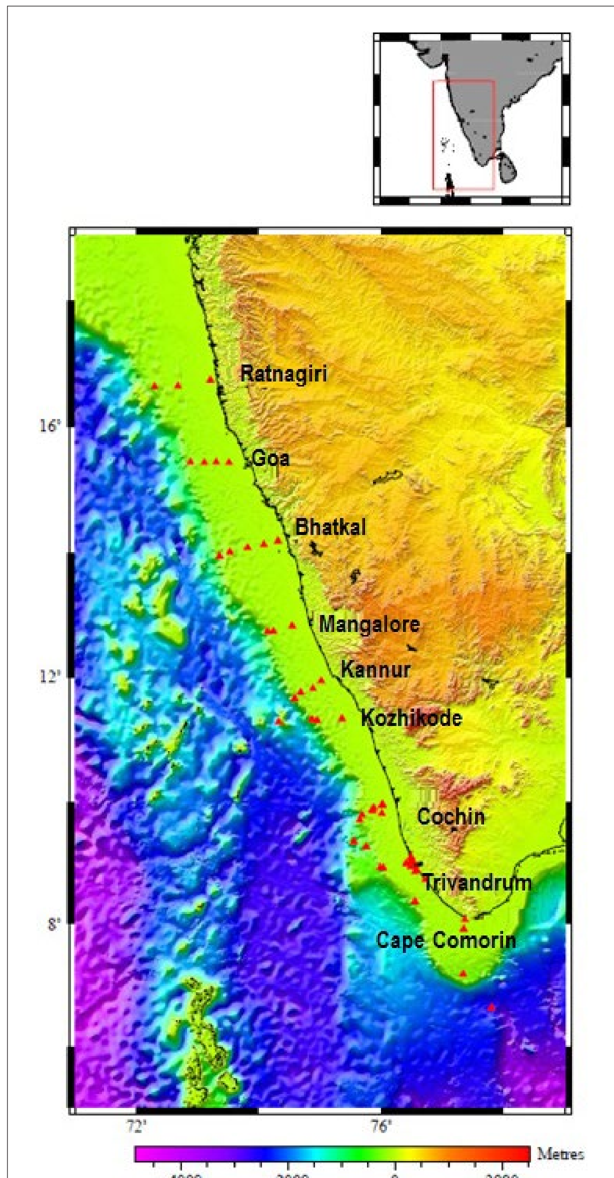

Fig. 1. Map showing the study station

split into suitable aliquots of approximately 250-300 benthic foraminiferal specimens. The residue was dried and kept in plastic tubes for the micro-faunal analysis. The dried samples were sub sampled using a micro otto-splitter in order to obtain representative samples. The sediment samples were analysed under binocular stereo zoom microscopes (WILD MZ 12.5 and MZ8 and the micro-faunal assemblage slides were prepared for the identification of the specimens. For identification of the foraminifera the taxonomic keys of Loeblich and Tappan (1988) and Jones (1994) were used. The identification was confirmed using the Scanning electron micrographs obtained from VEGA3 TESCAN.

Results and discussion

The study involved the recording of 6 large and 3 small benthic foraminifera belonging to 6 families and 7 genera with endosymbionts distributed in the shelf sediments of the western continental shelf and continental slope (15-1333 m) of eastern Arabian Sea (Table 1). These include *Amphistegina lessonii, Amphistegina gibbosa, Heterostegina depressa, Amphisorus hemprichii, Operculina granulosa, Alveolinella quoyii, Elphidium craticulatum, Elphidium crispum* and *Nonion Fabum* of which the first six are LBFs and last three are smaller benthic foraminifera (Fig. 2).

Table 1. Bathymetric details of the sample locations

St. no	Latitude (E)	Longitude (N)	Depth(m)	Station Name
1	77.37	8.07	31	Cape Comorin
2	77.34	7.91	51	Cape Comorin
3	77.33	7.17	208	Cape Comorin
4	76.72	8.72	20	Varkala
5	76.55	8.36	124	Thiruvananthapurm
6	76.45	8.98	15	Neendakara
7	76.03	8.91	101	Kollam
8	75.98	8.91	238	Kollam
9	76.5	10.1	15	Arthunkal
10	76.48	9.08	20	Alapad
11	76.9	9.65	20	Chavara
12	76	9.79	20	Kochi
13	76.01	9.93	30	Kochi
14	76.01	9.94	33	Kochi
15	75.85	9.85	50	Kochi
16	75.88	9.88	51	Kochi
17	75.69	9.76	101	Kochi
18	75.64	9.69	202	Kochi
19	75.55	9.33	890	Kochi
20	75.35	11.33	50	Kozhikode
21	74.95	11.3	102	Kozhikode
22	75.01	11.94	51	Kannur
23	74.88	11.82	67	Kannur
24	74.68	11.75	102	Kannur
25	74.32	11.27	1333	Kannur
26	74.54	12.82	51	Mangalore
27	74.31	14.18	31	Bhatkal
28	74.08	14.12	54	Bhatkal
29	73.81	14.07	68	Bhatkal
30	73.53	14	101	Bhatkal
31	73.11	15.43	51	Goa
32	73.3	15.44	72	Goa
33	73.11	15.43	101	Goa
34	72.88	15.43	206	Goa
35	72.67	16.64	76	Ratnagiri
36	72.29	16.63	101	Ratnagiri

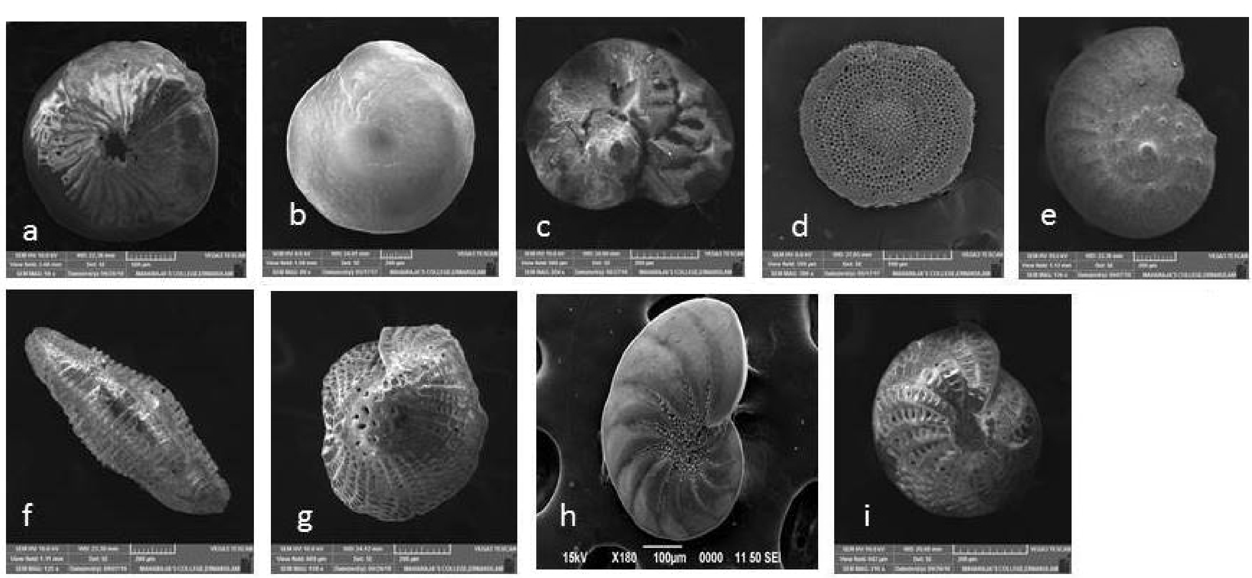

Fig. 2a). *Amphistegina lessonii* b). *Amphistegina gibbosa* c). *Heterostegina depressa* d). *Amphisorus hemprichii* e). *Operculina granulosa* f). *Alveolinella quoyii* g). *Elphidium craticulatum* h). *Nonion fabum* i). *Elphidium crispum*

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A. lessonii belonging to Amphesteginids, the most studied symbiont bearing foraminiferan families was collected off Cape Comorin to off Ratnagiri and the maximum abundance of 49.12% and 40% was noted at stations 1 and 2 respectively. This species having a test with umbiliconvex form flourished in abundance in sandy sediments probably enabling free locomotion (Hoheneger, 1994; Murray, 2006). Generation time of 3-6 months at depths < 30m has been recorded (Hallock, 1981a, c). If it is assumed that the growth of benthic foraminifera recorded here, mainly depend on symbionts, the availability of light certainly would influence the ultimate size attained by the individual. The findings of the present study show that the same symbiont bearing species, which lived in the shelf area with high light availability, were larger than those recorded from the slope with the diameter of their test's measuring 2.3 mm and 1.8 mm respectively. Actual role of feeding and photosynthesis can differ substantially from theoretical predictions and may vary in different species. *A. lessonii* appears to behave most closely to model predictions and physiological studies indicate ingested food provides most nutrients while respiratory energy is obtained primarily from photosynthesis (ter Kuile *et al.,* 1987). *A. lessonii* actively feeds on primary producers like diatoms implying that the energy supplied by the symbiont is a supplementary source of energy. It is theorized that the symbionts aid in enhancement of calcification in the host since the ATP released from the photosynthesis provide energy for the removal of ions such as NH_4^+, PO_4^{3-} and Mg^{2+} which inhibit calcification (ter Kuile, 1991). Thus the host species uses sunlight instead of food resources, as a source of energy for ATP, which account for the significant enhancement of calcification. This species has an exceptionally high tolerance to survive low temperatures and the presence of this species at a depth of 1333 m clearly indicates that this eurythermal and eurybathic protozoan is capable of tolerating temperature range of 28ºC to10.2ºC (temperatures of the stations). The morphological integrity of the animal is not affected in the case of specimens collected from 20 and 1333 m.

A. gibbosa, the sibling species of *A. lessonii* was recorded only from shallow waters. Highly tolerant to variations in light, *A. gibbosa* is not symbiont specific since ten species of diatoms have been recorded from this species by Lee *et al.* (1995). Lee (1998) indicated that it does not require a particular species of symbiont, but rather a suite of acceptable symbionts. Flexibility in the symbiotic relationship is of advantage to the host which is dependent on the process of symbiosis rather than a particular symbiont since the symbiotic relationship is not species specific. Biological trimorphism has been reported in *A. gibbosa* (Harney *et al.,* 1998). The foram zygote is in need of symbionts following zygosis and capability of selecting any of the ten diatom species increases the survival rate of sexually produced individuals. The presence of this species only from the shallow waters of Kochi probably indicates distribution contributed by ballast water discharge by ships frequenting Cochin Port from European waters.

A. quoyi, a dominant species of the Indo-Pacific has been recorded only from shallow water depths. Contrary to this, in the study *A. quoyii* are recorded from the continental slope at a depth of 1333 m. This species, a common occupant of the coral reefs can live in greater depths indicated by live materials collected from such a depth. The examination of grab sample which contain specimen of this species had numerous live specimens indicated by yellow pigments, probably derivations from the green pigments. The possibility of reviving these symbionts to an active phase is possible when these specimens are brought to the euphotic zone by upwelling. The surface samples collected off Cape Comorin contained both dead and symbiont bearing *A. quoyii*. There are reports of faecal pellets of copepods recorded from greater depths containing chlorophyll bearing algae (Bathmann *et al.,* 1987). The corals have been recorded from this area (Pillai, 2010). In this connection, the observation of Hallock *et al.* (1995) and Langer *et al.* (2003) that the species belonging to the genera *Alveolinella, Amphistegina* and *Operculina* co-exist and can be considered as the index fauna of coral reefs is of interest. Holzmann *et al.* (2001) pointed out that algae found in the chamberlets of *A. quoyii* has molecular structure indicating a phylogenetic relation with members of the symbiont bearing family Soritidae. The comparable size of symbiotic algae bearing forams at greater depth indicate the presence of attenuated light since light is a limiting factor controlling the wall structures of forams. In the shallow shelf sediments (5-100 m), on hard substrates like the crevices of coral rubbles, the species is found to have an epifaunal mode of living, which probably favours its existence at these depths.

O. granulosa was collected from off Varkala to Ratnagiri (15 -890 m), the abundance of the species in stations (7, 19 and 28) having sandy, silty clay and sandy silt sediments shows that this species can survive in sediments with varied sediment characteristics. Although this species is common in sandy, low energy and medium light conditions, they can also exist in eutrophic and hypersaline situations in shelf and lagoon areas. The eurybathy of the species belonging to genus *Operculina* is clearly indicated by the occurrence of this species in abundance at 890 m. The members of this genus *Operculina* is capable of existing in varying ecological conditions.

H. depressa, collected from off Kochi to Ratnagiri (20-102 m), had a very rare occurrence in all stations (7, 12, 21 & 36). Epifaunal on hard substrates and in rock pools of reef crests it seeks shade. *H. depressa* usually prefers a depth range of 0-100 m, having a behavioral pattern which protects it from overexposure to light. This species also has an ability to repair the damaged tests in order to survive the mechanical damage ever since the Paleozoic time period (Rottger, 1978; Rottger and Hallock, 1982). It is also evident that porous test of the foraminifera functions as a greenhouse for the diatom symbiont which probably require less light and do possess highly production efficient chlorophyll *a*. This is necessary since the foram in majority of times depends exclusively on the symbiont as a source of food which implicates continuous binary fission of the symbiont inside the foraminifera. But in few rare cases as Azam and Smith (1991) had explained the presence of carbohydrate rich sheaths on the test of this species attracts certain bacteria and provides a substrate for the bacterial farming. The foraminifera could then either feed on those bacteria or uptake the nutrient wastes of the bacteria and the microplankton that come to feed on these bacteria (Bernhard and Bowser, 1992). One possible explanation for this apparent enigma is that in natural environments free living algae should be far superior competitors for dissolved nutrients than are symbionts that are enclosed within the host test, so additional feeding of bacteria by host could improve the survival rate of these endosymbionts as host would depend partly on the bacteria for energy supplement. Biological trimorphism has also been documented in *H. depressa* by Rottger *et al.* *(*1990). This helps in the vertical transfer of the symbiont by asexual reproduction.

A. hemprichii was collected from off Kochi to Goa (50-101 m depths) from stations 16, 17 and 31. A typical species of the Indo-Pacific which is epiphytic on sea grasses and also rarely on algae and seen in high light habitats on the upper slope and fore reef crest. It reduces the overexposure to light by hiding in these marine plants and gathering plant fragments and detritus which provide shade. It is eurythermal (temperature range of 14- 38ºC) like *A. lessonii* and *A. hemprichii* is stenohaline surviving in the salinity range of 35-42 ppt (Murray, 2006). In the study it was found only at 3 stations where the salinity was within this range. It avoids high energy habitats. *A. hemprichii* mostly house dinoflagellate symbionts unlike most other LBF's which have algal symbionts. Presence of these symbionts helps the species to survive in oligotrophic environments (Hallock, 1999). In 1980, Lee had opined that this species can survive only in the presence of light and the pseudopores seen on its test are a structural adaptation to facilitate obligate symbiosis. He had also documented that individuals of *A. hemprichii* normally have feeding territories and if accidentally the pseudopodia of two individuals touch each other they take avoidance reaction. They pick up organic and inorganic detritus to cover the test and reticulopodia or to form bolus around the aperture. Consumption is directly proportional to the concentration of food near the pseudopodial web. The acid phosphatase activity in these symbiont bearers indicate that the digestion occurs in food clumps around the individuals and in the final chambers (Faber and Lee, 1991).

Although true symbiosis is a more frequently reported phenomenon in benthic foraminifera, chloroplast sequestration has also been noted especially in habitats with high nutrient concentrations. In the study the occurrence of three smaller benthic foraminifera *E. crispum, E. craticulatum and N. fabum* have been recorded from off Cape Comorin to Ratnagiri (15 to 238 m water depths). These forams unlike the LBFs, retain the chloroplast of the ingested algal symbionts and utilise them for energy gain. The kleptoplastic forams were found to be abundant in stations off Kochi (13 &15) where the organic matter concentration was high. In nutrient rich waters, symbiosis is less advantageous to both the symbiont and the host than in oligotrophic stations (Hallock, 1985). Species with the potential of chloroplast sequestration respond to phytodetritus input from blooms and dominate in the inner shelves where the coastal blooms occur more frequently (Lopez, 1979; Lee *et al.*, 1988; Cedhagen, 1991). As the chloroplast within their cells are not subject to temperature control, these forams with husbanded chloroplast live down to maximum depths of light penetration where they aid in assimilation of inorganic nitrogen (Hollaus and Hottinger, 1997; Grymski, 2002). Closer observations on these species help us in understanding their ecological adaptations which allow them to survive the changing ecosystems. Even though the LBFs are recorded from the stations studied, their numerical abundance was less compared to the SBFs. The fact that large number of dead tests of LBFs was present in the core sample accompanied with reduced live ones from stations which recorded high organic matter probably supports smaller foraminifera. The enrichment of the coastal waters with nutrients due to both natural and anthropogenic causes probably research in the building up copious quantities of organic carbon in the bottom waters of sediments conceivably resulting in the structure of benthic community which might include opportunistic taxa also. The phenotypic plasticity has allowed the LBFs to adjust their physiology and morphology according to local conditions. Populations of the same species existing in different environmental conditions could lead to development of groups with different phenotypic characteristics and genetic structure. This could be the reason that controls the existence of such species in a broad range of habitat.

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References

Azam, F. and D. C. Smith. 1991. Bacterial influence on the variability in the oceans biogeochemical state: A mechanistic view, in Particle Analysis in Oceanography, (ed S. Demers), *Springer-Verlag*, Berlin, NATO ASI Series., 27:213-46.

Bathmann U. V, T. T. Noji, M. Voss and R. Peinert. 1987. Copepod fecal pellets: abundance, sedimentation and content at a permanent station in the Norwegian Sea in May/June 1986. *Mar. Ecol. Prog. Ser.,* 38:45-51.

Berhard, J. and S. Bowser. 1992. Bacterial biofilms as a trophic resource for certain benthic foraminifera. *Mar. Ecol. Prog. Ser.,* 83: 263-272.

Cedhagen, T. 1991.Retention of chloroplasts and bathymetric distribution in the sublittoral foraminiferan *Nonionellina labradorica. Ophelia*., 33: 17-30.

Cowie, G. L. 2005.The biogeochemistry of Arabian Sea surficial sediments: a review of recent studies. *Prog. Oceanogr.,* 65:260–289.

Demaison, G. J. and G. T. Moore. 1980. Anoxic environments and oil source bed genesis. *Org. Geochem.,* 2:9-31.

Faber, W. W. and J. J. Lee. 1991. Histochemical evidence for digestion in Heterostegina depressa and *Operculina ammonoides* (Foraminifera). *Endocytobiosis Cell Res.*, 8:53-9.

Faruque, B. M. and K. V. Ramachandran. 2014. The Western continental shelf of India. In: Chiocci, F. L.& Chivas, A. R.(eds.) *Continental shelves of the World: Their evolution during the last glacio- eustatic cycle*. Geological society, London, Memoirs, 41:211-220.

Grzymski, J., O. M. Schofield, P. G. Falkowski and J. M. Bernhard. 2002. The function of plastids in the deep sea benthic foraminifer *Nonionella stella. Limnol. Oceanogr.*, 47:1569-1580.

Hallock, P.1981a. Algal symbiosis: a mathematical analysis. *Mar. Biol*., 62:249-55.

Hallock, P. 1981c. Light dependence in *Amphistegina. J. Foraminiferal Res*., 11:40-6.

Hallock, P. 1985. Why are large foraminifera large? *Paleobiology*, 11:195-208.

Hallock, P., H. K. Talge, E. M. Cockey and R. G. Muller. 1995. A new disease in reef-dwelling foraminifera: implications for coastal sedimentation. *J. foraminiferal Res*., 25: 280-286.

Hallock, P. 1999. In Modern Foraminifera (Ed. Sen Gupta, B. K.) p.123-149 (Kluwer, 1999).

Harney, J. N., P. Hallock and H. K. Talge. 1998. Observations of a trimorphic life cycle in *Amphistegina gibbosa* populations from the Florida Keys. *J. Foraminiferal Res*., 28:141-7.

Hohenegger, J. 1994. Distribution of living larger foramnifera NW of Sesoko-Jima, Okinawa, Japan*, Mar. Ecol*., 15: 291-334.

Hollaus, S. S. and L. Hottinger. 1997. Temperature dependence of endosymbiotic relationships? Evidence from the depth range of Mediterranean *Amphistegina lessonii* (foraminifera) truncated by the thermocline, *Ecologae Geologicae Helvetiae,* 90:591-597.

Holzmann, M., J. Hohenegger and P. Hallock. 2001. Molecular Phylogeny of large miliolid Foraminifera (Soritacea Ehrenberg 1839). *Mar. Micropaleontol*, 43(1-2):57-74.

Huneke H and T. Mulder. 2011 Deep-sea sediments. London: Elsevier Press. p. 46–54.

Jones, R. W. 1994. The Challenger Foraminifera. Oxford University Press, Oxford, 1-149.

Langer, M., R. Lipps and H. Jere. 2003. Foraminiferal distribution and diversity, Madang Reef and Lagoon, Papua New Guinea. *Coral Reefs,* 22: 143-154.

Lee, J. J., E. Lanners and B. ter Kuile.1988. Retention of chloroplasts by the foraminifer *Elphidium crispum. Symbiosis*, 5:45-60.

Lee, J. J. 1998.Living sands: Larger foraminifera and their endosymbiotic algae. *Symbiosis*, 25:71-100.

Lee, J. J., C. G. Wray, and C. Lawrence. 1995. Could foraminiferal zooxanthellae be derived from environmental pools contributed to by different coelenterate hosts? *Acta Protozoologica,* 34:75-85.

Loeblich Jr., A. R. and H. Tappan .1988. Foraminiferal Genera and Their Classification: Van Nostrand Reinhold Company, New York, 2: 970.

Lopez, R. 1979. Algal chloroplasts in the protoplasm of three species of benthic foraminifera: Taxonomic affinity, viability and persistence. *Mar. Biol.,* 53:201-11.

Murray, J. W. 2006. *Ecology and Applications of Benthic Foraminifera*. Cambridge University Press. Cambridge, 426 pp.

Pandolfi, J. M. 2015.Incorporating uncertainity in predicting the response of coral reefs to climate change. *Ann. Rev. Ecol. Evol. Syst.,* 46: 281-303.

Pillai,C. S. G. 2010. A review of the states of corals and coral reefs of India. *Indian J Anim Sci.,* 80(4):53-56.

Qasim, S. Z. 1977. Biological productivity of the Indian Ocean. *Indian J. Mar. Sci*., 6:122-137.

Qasim, S. Z. 1982. Oceanography of the northern Arabian Sea. *Deep Sea Res*., 29:1041-1068.

Rao, V. P. and B. G. Wagle. 1997. Geomorphology and surficial geology of Western Continental shelf and slope of India: a review. *Curr. Sci*., 73: 330-350.

Rothwell, R. G. 2005. Deep Ocean Pelagic Oozes, Volume 5 of Selley RC, McCocks LR, Plimer IR, Encyclopedia of Geology, Elsevier Ltd., Oxford.

Rottger, R. and P. Hallock. 1982. Shape trends in *Heterostegina depressa* (Protozoa, Foraminiferida). *J. Foraminiferal Res*., 12: 197-204.

Rottger, R., R. Kruger and S. De Rijk. 1990. Trimorphism in foraminifera (Protozoa): Verification of an old hypothesis. *Eur. J. Protistol.,* 25: 226-8.

Rottger, R. 1978. Unusual multiple fission in the gamont of the Larger Foraminiferan *Heterostegina depressa* (Rhizopoda). *J. Protozool.,* 25:41-4.

ter Kuile, B., J. Erez and J. J. Lee. 1987. The role of feeding in the metabolism of larger, symbiotic foraminifera. *Symbiosis*, 4: 335-50.

ter Kuile, B. 1991. Mechanisms for calcification and carbon cycling in algal symbiont-bearing foraminifera. *In Biology of Foraminifera*, (Eds. J. J. Lee and O. R. Anderson), Academic Press, New York, p.73-89.