# Field and laboratory culturing studies to understand benthic foraminiferal response to dissolved oxygen

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**School of Earth, Ocean and Atmospheric Sciences**
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**DOCTOR OF PHILOSOPHY**

By

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# Declaration

As required under the university ordinance OA.19, I hereby state that the present thesis entitled **“Field and laboratory culturing studies to understand benthic foraminiferal response to dissolved oxygen”** is my original contribution and the same has not been submitted on any pervious occasion. To the best of my knowledge, the present study is the first comprehensive work of its kind from the area mentioned. Literature related to the scientific objectives has been cited. Due acknowledgments have been made wherever facilities and suggestions have been availed of.

**Amrata Kaithwar**

# Certificate

As required under the university ordinance OA.19, I certify that the thesis entitled **"Field and laboratory culturing studies to understand benthic foraminiferal response to dissolved oxygen"** submitted by Ms Amrata Kaithwar for the award of the degree of Doctor of Philosophy in the School of Earth, Ocean, and Atmospheric Sciences, Goa University, Goa is based on original work carried out by her under my supervision. The thesis, partially or completely, has not been previously submitted for any other degree or diploma in any university or institution.

**(Rajeev Saraswat)**
Supervisor

# Preface

The dissolved oxygen concentration in seawater is one of the leading environmental factors modulating the distribution, abundance and diversity of macro- and microorganisms in the oceans. Additionally, the zone in the oceans where dissolved oxygen concentration is <0.5 mL/L, due to excessive use of available oxygen by organisms (for respiration) to feed upon organic matter coupled with restricted supply, resulting from reduced water circulation, are referred as oxygen minimum zones (OMZ). Out of the total global ~1 million square km of the perennial intermediate-depth hypoxic zone, more than half (~59%) is in the northern Indian Ocean. The oxygen-deficient zones are geographically importance because of the formation of organic matter rich sediments under reduced oxidation conditions. OMZ also affects the large-scale biogeochemical re-cycling of elements, and ecosystem functioning by modulating bio-physico-chemical conditions, including bioturbation. Although the detailed processes controlling the formation and intensity of OMZ are hitherto unknown, the spatio-temporal changes in hypoxia are often attributed to anthropogenic activities. Several studies suggest the gradual expansion of dead zones under the warming world. Therefore, many efforts are made to understand the factors that affect hypoxia and its temporal variability, as then remedial measures can be suggested and implemented, if feasible. The reconstruction of the intensity and extent of the oxygen-deficient zones in the past by using proxies, can help to understand the imminent changes in OMZ.

Foraminifera are highly sensitive dominantly marine single celled microorganisms, which have great potential to detect ecological stress at a very early stage. The dissolved oxygen and organic matter are the dominant factors that control benthic foraminiferal distribution, especially in deeper regions. Foraminifera has often been used to reconstruct the intensity and extant of past OMZ, as they are an important factor in organic matter processing in OMZ. At low oxygen concentration (dissolved oxygen <0.11 mL/L), organic matter uptake is dominated by benthic foraminifera. The relative abundance of benthic foraminifera with serially arranged chambers, termed as angular asymmetrical foraminifera, increases in the oxygen deficient zone of the eastern Arabian Sea. A majority of these angular asymmetrical benthic foraminifera are infaunal. However, the riverine influx creates a high energy environment leading to the increased relative abundance of rounded symmetrical foraminifera as compared to the angular asymmetrical foraminifera. Therefore, the change in the relative abundance of angular asymmetrical versus rounded symmetrical foraminifera was suggested as an effective proxy to reconstruct paleomonsoon. Therefore, it is necessary to understand the differences in benthic foraminiferal response to dissolved oxygen and riverine influx induced physico-chemical changes. The laboratory culturing study can help in delineating the differential response of benthic foraminifera to various environmental parameters. Therefore, it was decided to conduct laboratory culturing experiments as well as field studies to understand the response of living benthic foraminifera to dissolved oxygen. The rationale of the doctoral work is given in **Chapter 1**.

Prior to the finalization of the detailed work-plan of the thesis, the laboratory culturing studies done during the last decade to understand the response of benthic foraminifera to different concentration of ambient oxygen and other related factors, were reviewed. The details are given in **Chapter 2**. From the review of laboratory culture studies on benthic foraminifera during the previous decade, it was observed that a growing emphasis during the last decade has been on to understand the effect of ocean acidification on calcification in benthic foraminifera. Additionally, several studies have also been carried out to understand the factors affecting the partitioning of trace elements in benthic foraminiferal tests, especially to develop proxies for quantitative paleoclimatic reconstruction. The response is species-specific, thus necessitating additional efforts to understand the comprehensive response of benthic foraminifera to environmental factors. The studies documenting foraminiferal response to dissolved oxygen under controlled laboratory culture experiments are very limited. In view of the above, I decided to address the following objectives in my doctoral work

- To understand the response of benthic foraminiferal community to different levels of dissolved oxygen under laboratory culture.
- To understand the effect of different amount and frequency of phytodetritus pulse on benthic foraminiferal community.
- To document changes in morphology, especially the test pore density, in selected benthic foraminifera, subjected to different culture conditions.
- To compare the benthic foraminiferal response under controlled laboratory conditions with that in the field.

The work involved both the laboratory culturing of the living benthic foraminifera community collected from the inner shelf region off Goa and study of sediments collected from the Bay of Bengal and the Arabian Sea. The details of both samples and their processing are given in **Chapter 3**. The living benthic foraminifera community was collected by diving in the coastal waters off Goa. Both the surface sediments as well as the seaweeds attached to the rocky patches in coastal regions off Goa were collected to retrieve the living benthic foraminifera. The sediments along with seawater were transferred to glass beakers and covered with paraffin film to avoid evaporation. The material was brought to the laboratory for further experiments. For field studies, a total of 122 sediment samples were used. It includes multi-core samples collected across the oxygen minimum zone of the Gulf of Mannar [onboard RV *Sindhu Sadhana* (SSD004)], Bay of Bengal (11 samples during the ORV *Sagar Kanya* cruise SK308) as well as the Arabian Sea (12 samples during the RV *Sindhu Sadhana* cruise SSD055). The samples were collected by using an Ocean Scientific International Limited Maxi Multi-corer (tube length 600 mm, tube outer diameter 110 mm and tube inner diameter 100 mm), along a coast perpendicular transect covering the region from the inner shelf to the deeper depths. The top five cm section at each station, subsampled at 1 cm, was used for foraminiferal studies. Half of the sediment was stained with rose-Bengal and ethanol solution. The stained sediments were processed following the standard procedure. For the carbon and nitrogen content in the sediments, ~5 g of freeze-dried sediment was finely powdered. Subsequently, a coulometer (CM 5015 CO2) was used to analyze the inorganic carbon whereas an elemental analyzer (FLASH 2000; Thermo Scientific) was used to measure the total carbon. The inorganic carbon percentage was subtracted from the total carbon, to get the organic carbon.

The effect of depleting dissolved oxygen on the marine benthic community is difficult to assess from the field studies, as dissolved oxygen often co-varies with organic matter. The controlled laboratory culture experiments can help to determine the effect of a specific parameter. A majority of the previous culture experiments have used isolated specimens of individual species. Such studies, although helped to understand the response of a species to a particular parameter, have to be scaled up to understand the community level response. **Chapter 4**, includes the details of the laboratory culture experiment to assess the community level response of marginal marine benthic foraminifera to different oxygen concentrations (1.67 mL/L to 5.01 mL/L). Living benthic foraminifera population increased considerably at intermediate oxygen concentration whereas decreased at both the lower and higher concentrations. The decreasing dissolved oxygen caused poor preservation of dead benthic foraminifera due to a drop in pH. The relative abundance trend of the species belonging to the same genus was different, suggesting a species-specific response to the dissolved oxygen. The maximum abundance of benthic foraminifera at 2.91 mL/L dissolved oxygen, as well as the varying response of individual species, clearly suggests a non-linear response of marginal marine benthic foraminifera community to ambient oxygen.

In the tropical oceans, the organic matter and dissolved oxygen are closely coupled. Therefore, it is difficult to assess the relative effect of dissolved oxygen and the organic matter flux on benthic foraminifera, from field studies. Additionally, a few studies demonstrated that the foraminiferal growth, reproduction and thus abundance depend on food as well as the ambient temperature. A few culture experiments have been conducted to understand the effect of various amount of food supply at different temperature, on foraminiferal growth and abundance. **Chapter 5** contains the details of the laboratory experiment to understand the effect of different amount of organic matter under the two warming scenarios, on shallow-water benthic foraminifera. From the relationship between temperature and *Rosalina globularis,* with the simultaneous change in phytodetritus, it is concluded that *Rosalina globularis* prefers a higher temperature range (27ºC-32ºC) for their growth. But in the long term, they prefer a lower temperature range (25ºC-30ºC) as the mortality rate is higher at higher temperatures. Therefore, it is clear that *Rosalina globularis,* a shallow-water benthic species, prefers high productivity regions for their growth. As the mortality increased at the higher temperature, summer monsoon is the perfect season for their optimum growth, as during this time, phytodetritus flux is high and the temperature is also comparatively low. Although *Rosalina globularis* can survive in less phytodetritus flux, long term food scarcity could lead to smaller test size of *Rosalina globularis*.

The studies documenting the modern distribution of living benthic foraminifera are very limited from the Indian margin. Moreover, limited attempts have been made to understand the fraction of benthic foraminifera living at different depths in the sediments of the northern Indian Ocean, barring a few studies from the southern margin of Pakistan, eastern margin of Oman and northeastern margin of India. Therefore, the fraction of total benthic foraminifera living at different depths in the sediments of the Gulf of Mannar and Bay of Bengal was documented and the details are given in **Chapter 6**. Within the low dissolved oxygen zone, a large fraction of the living benthic foraminifera were found in the top 0-1 cm section. The average living depth of benthic foraminifera shoals considerably within the oxygen deficient zone. A large fraction of the living benthic foraminifera, however, are found in deeper sections in the well-oxygenated waters. The living benthic foraminiferal assemblage is dominated by the calcareous foraminifera in both the regions. The agglutinated benthic foraminifera are mainly confined to the middle and lower slope.

The coastal currents carry warmer and more saline water from the Arabian Sea into the Bay of Bengal and colder and fresher water back from the bay into the eastern Arabian Sea. A strong seasonality is observed in the southeastern Arabian Sea, due to this cross-basin exchange of seawater along with very high primary productivity. The details of the effect of this strong seasonal stress on benthic foraminifera living within the oxygen-deficient zone of the southeastern Arabian Sea are given in **Chapter 7**. As the dissolved oxygen varies over a large range, benthic foraminiferal assemblages were delineated to represent different dissolved oxygen concentration in this region. A unique set of living benthic foraminiferal species dominate the depths with varying dissolved oxygen concentration in the southeastern Arabian Sea ODZ. Three species namely, *Eubuliminella exilis, Hopkinsinella glabra* and *Bolivina seminuda,* represent very low dissolved oxygen environment confined to the upper slope region. Another set of three species, namely, *Epistominella exigua, Rotaliatinopsis semiinvoluta* and *Hopkinsinella glabra* also thrive in a similar low oxygen environment but with a comparatively more organic carbon content in the sediments. The chapter includes the details of the change in living benthic foraminiferal population in the ODZ as compared to the well oxygenated regions, as well as the infaunal and epifaunal nature of the abundant living benthic foraminifera in the Gulf of Mannar.

The dissolved oxygen affects the morphology, including the pore density and diameter of benthic foraminifera. The pores in benthic foraminifera facilitate gas exchange between the surroundings/environments and organism as well as maintain the oxygen uptake. The higher porosity of dysoxic benthic forms is attributed to the difficulty in secreting calcium carbonate and in providing higher mitochondrial oxygen uptake. The response of benthic foraminifera to dissolved oxygen is species-specific. Therefore, an attempt was made to understand the effect of dissolved oxygen on the pore diameter and density of living benthic foraminifera *Bolivina seminuda* isolated from the surface sediments collected along a depth transect covering the oxygen-deficient zone in the Gulf of Mannar. The details are given in **Chapter 8**. A total 391 Scanning Electron Microscope images were taken to understand the variation in pore size from shallow to deep water depths in the Gulf of Mannar. *Bolivina seminuda* is a typical low dissolved oxygen water infaunal species in the modern ocean.

*Bolivina seminuda* are very small, thin-walled and abundant in oxygen deficient zones of the Gulf of Mannar. The increase in pore size with decreasing oxygen availability is confirmed in the living specimens of *Bolivina seminuda* in the surface sediments of the Gulf of Mannar. The increased pore density at higher dissolved oxygen availability is intriguing. Additionally, the pore density is inversely related to the pore diameter. The pore density and diameter of *B. seminuda* can be used as reliable proxy to reconstruct changes in the intensity and extent of the low dissolved oxygen zones in the past.

The inferences drawn from the doctoral work and future scope are included in **Chapter 9**. This chapter is followed by the references cited in the text.

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**Amrata Kaithwar**

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# Chapter-1: Introduction

The dissolved oxygen concentration in seawater is one of the main environmental factors modulating the distribution, abundance and diversity of macro- as well as micro-organisms in the oceans (Levin et al., 2000; Levin, 2003; Nigam et al., 2007; Woulds et al., 2007; Gooday et al., 2010). Four biofacies are defined according to the dissolved oxygen concentration, viz. (a) Oxic (8.0-2.0 ml/l), (b) Dysoxic (2.0-0.2 ml/l), (c) Suboxic (0.2-0.0 ml/l) and (d) Anoxic (0.0 ml/l) (Tyson and Pearson, 1991). Additionally, the zone in the oceans where dissolved oxygen concentration is <0.5 ml/l, due to excessive use of available oxygen by organisms (for respiration) to feed upon organic matter coupled with restricted supply, resulting from reduced water circulation, are referred as oxygen minimum zones (OMZ) (Wyrtki, 1962; Helly and Levin, 2004). The formation of OMZ, its depth and position in the ocean, mainly depends upon the extent of primary productivity and water circulation (Wyrtki, 1962; McCreary et al., 2013). Out of the total global ~1 million square km of the perennial intermediate depth hypoxic zone, more than half (~59%) is in the northern Indian Ocean (Helly and Levin, 2004) (Figure 1.1). This zone, sometimes also referred as the shadow zone, occurs at the depths of about ~120-1200 m in the northern Indian Ocean (Naqvi et al., 2003). Despite comparable primary productivity, intermediate depth OMZ is deeper in the Arabian Sea as compared to that in the Bay of Bengal (Helly and Levin, 2004).

The oxygen deficient zones have a geographic importance because of the formation of organic rich sediments under reduced oxidation condition (Kennett, 1982; Paropkari et al., 1992). OMZ also affects the large-scale biogeochemical re-cycling of elements, and ecosystem functioning by modulating bio-physico-chemical conditions, including bioturbation (Lohrer et al., 2004; Woulds et al., 2007; Sturdivant et al., 2012). Similar low oxygen zone has also been reported from the western continental shelf of India (Naqvi et al., 2000). The hypoxic zones affect the fish population, which has tremendous economic implications (Stramma et al., 2011). The geographic extent and intensity of hypoxia varies temporally (Sarma et al., 2013). Ocean anoxic events, the times of depleted oxygen concentrations, have been reported from earth's past in all world oceans by using several proxies (Leckie et al., 2002). Albeit the fact that the detailed processes controlling the formation and intensity of OMZ are hitherto unknown (Resplandy et al., 2012), the spatio-temporal changes in hypoxia are often attributed to anthropogenic activities (Platon et al., 2005; Froelicher et al., 2009). Several studies suggest gradual expansion of dead zones under the warming world (Keeling and Garcia, 2002; Diaz and Rosenberg, 2008; Altieri and Gedan, 2015). Therefore, a lot of efforts are made to understand the factors which affect hypoxia and its temporal variability, as then remedial measures can be suggested and implemented, if feasible.

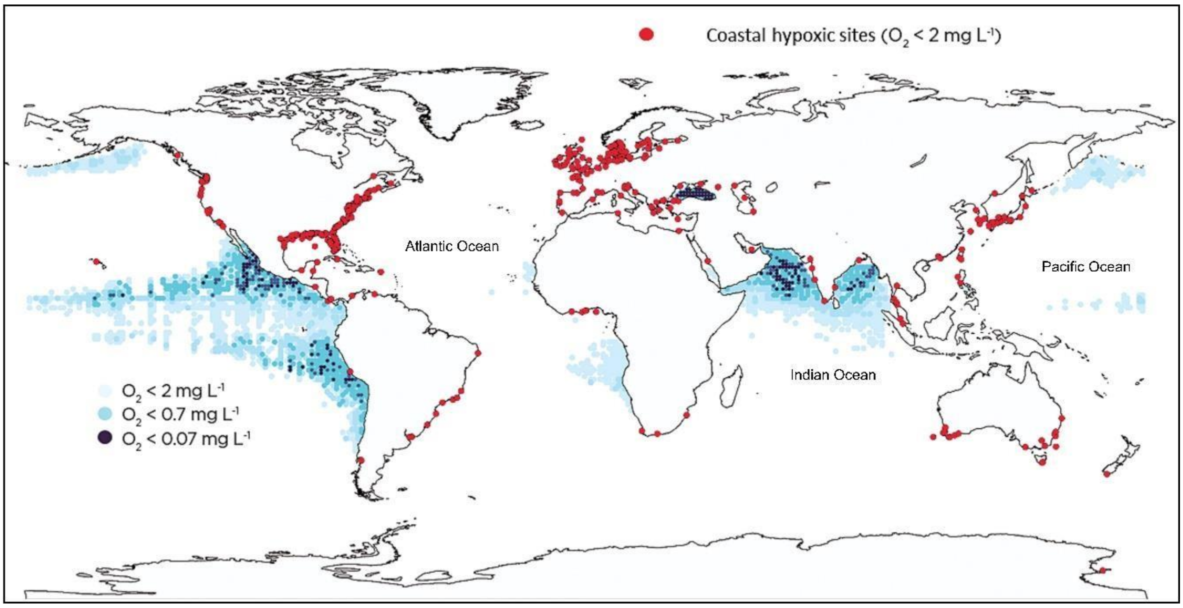

**Figure 1.1: The global distribution of oxygen deficient zones (modified after Grégoire et al., 2019).**

Foraminifera are highly sensitive dominantly marine single celled microorganisms, which have great potential to detect ecological stress at a very early stage. Their abundance may be judged by the fact that about 1000 to 2,500,000 living specimens per square meter may inhabit the marine sediments of the modern times. Foraminifera are influenced by different parameters in marine ecosystem, including dissolved oxygen, food availability, temperature, salinity, depth, sediment texture, and others (Corliss, 1985; Van der Zwaan et al., 1999). The dissolved oxygen and organic matter are, however, dominant factors that control benthic foraminiferal distribution, especially in deeper regions (Jorissen, 1995; 2007). Their presence in a wide spectrum of marine environments may be visualised by their occurrence at varying depths (from the intertidal zone to deeper oceanic levels), in varying salinities (from brackish to hyper saline conditions) and in varying latitudes (from the tropic to poles). Foraminifera has often been used to reconstruct intensity and extant of past OMZ, as they are an important factor in organic matter processing in OMZ. At low oxygen concentration (dissolved oxygen <0.11 ml/l), organic matter uptake is dominated by benthic foraminifera (Woulds et al., 2007). According to their tolerance to different levels of hypoxia (it indicates a degree of oxygen depletion) they have different characteristics. Previous studies suggest increase in infaunal benthic foraminifera in low oxygen environment (Kaiho, 1994; Bernhard and Sen Gupta, 1999). Foraminiferal assemblages have the added advantage of applicability to assess relative amount of oxygen to delineate oxic (>1.5 ml/l $O_2$) and suboxic (0.3-1.5 ml/l $O_2$) facies, which is difficult from organic carbon/sulphur ratio, sulphur isotopes and trace elements (Kaiho, 1994).

Distribution of recent benthic foraminifera in surface sediments along the western continental margin of India, also suggests increase in the relative abundance of angular asymmetrical benthic foraminifera, all of which are infaunal in nature, in low oxygen zones (Nigam et al., 2007). Incidentally, the ratio of angular asymmetrical to rounded symmetrical benthic foraminifera has also been suggested as a proxy to reconstruct past monsoon. The application arises from the fact that the abundance of rounded symmetrical forms increases in turbulent environment in regions where rivers drain into the sea (Nigam et al., 2009a). Therefore, it is necessary to understand the differences in benthic foraminiferal response to dissolved oxygen and riverine influx induced physico-chemical changes. The laboratory culturing study can help in delineating the differential response of benthic foraminifera to various environmental parameters. A few other workers have suggested that foraminifera found in low oxygen environment have high pore density as compared to the low pore density in the test of foraminifera found in high dissolved oxygen environment. Such a technique has however not yet been tested on benthic foraminifera collected from the Arabian Sea and Bay of Bengal OMZ. Due to the close relationship between the organic matter production and dissolved oxygen, it is necessary to differentiate the benthic foraminiferal response to these two critical parameters. Therefore, it was decided to conduct laboratory culturing experiments as well field studies to understand the response of living benthic foraminifera to dissolved oxygen. Prior to the finalization of the detailed work-plan of the thesis, the laboratory culturing studies done during the last decade to understand the effect of dissolved oxygen and other associated parameters, on benthic foraminifera, were reviewed. The details are in the next chapter.

# Chapter-2: Previous Studies

## Introduction

Among protozoan, foraminifera are widely used as a proxy for paleoceanography paleoclimate studies. The sensitivity of foraminifera to the environment and capability to incorporate the ambient signatures in the test, makes it a very efficient tool to study the past climate. The increasing application of foraminiferal proxies in various fields of paleontological research led to an urge to explore the fundamental biological processes of foraminifera. A majority of the foraminiferal proxies were developed based on samples collected from field. Off late, researchers are venturing into the laboratory experiments on foraminifera to validate field based findings. Foraminifera being exclusively marine organism, it is often difficult to recreate the field conditions in laboratory. Even though, only basic laboratory equipment is required to establish and maintain a thriving culture of the benthic foraminifera from a single asexually reproducing specimen (Seears and Wade, 2013), advance techniques are required for complicated experiments. There are several inherent properties that render foraminifera as a group more difficult to handle experimentally than numerous other popular laboratory protozoa. But it didn’t stop the researchers from attempting all possible techniques to reveal whatsoever possible on the biological processes of foraminifera and to align this knowledge to refine many field based results. The outcome was an enormously abundant set of information and knowledge from different corners of the world in the form of books, manuscripts, reports and reviews from time to time. In spite of the limitations, many researchers nationally as well as internationally have ventured in the less travelled road of foraminiferal culture studies. The laboratory culture studies help in understating the response of foraminiferal morphology, diversity, abundance to one or a combination of parameters.

Linshy et al. (2007) compiled the laboratory studies carried out on benthic foraminifera from the year 1935 to 2007. Based on the thorough review, it was suggested that the proper understanding of parameters affecting the morphology as well as the exact mechanism that causes deformities in benthic foraminifera, is still lacking. They further observed that the factors affecting the isotopic composition of benthic foraminifera were not explored fully as well as the calibration equations to reconstruct quantitative paleoclimatic information from benthic foraminifera, have to be developed. A comprehensive review on the morphology based biodiversity and trophic diversity of deep sea benthic foraminifera was provided by Gooday et al. (2008). Later, Martinez-Colon et al. (2009), du Châtelet and Debenay (2010) and Frontalini and Coccioni (2011) compiled the studies covering the application of benthic foraminifera as pollution bio-indicators. Subsequently, Kontakiotis et al. (2016) compiled the studies to assess the reliability of foraminiferal Mg/Ca thermometry by comparing field-samples and culture experiments. This review is a continuation of the laboratory culture studies on foraminifera, from 2007 to present. With the advancement of technology, laboratory culture studies have increased profusely. The international (Table 1.1) and national studies (Table 1.2) are discussed separately to compare the gaps effectively.

## Effect of phytodetritus pulse on benthic foraminifera

Food is one of the essential factors for growth and other activities of all living organisms. Foraminifera mostly feed upon organic matter, including small organisms, mainly diatoms, bacteria, coccolithophores, dinoflagellates, and parts of other plants and animals. It is believed that the type and amount of phytodetritus can alter foraminiferal population. The effect of *Thalassiosira pseudonana* (species of marine centric diatom) on benthic foraminifera was studied by Koho et al. (2008) and it was found that, several foraminiferal taxa, namely *Melonis barleeanum, Bigenerina cylindrica, Chilostomella oolina*, responded to the diatom bloom and its abundance increased. The vertical distribution of these infaunal species was, however not significantly influenced by the additional food. The abundance of only two infaunal species, viz. *Pullenia sp*. and *Trochammina sp*., increased in surface sediments. Foraminifera have diverse food preferences. Based on long-term laboratory monitoring of benthic foraminifera under different phytodetritus regimes, benthic foraminifera can be grouped into three categories. The Category 1 included taxa dependent on seasonal supply of fresh phytodetritus to maintain their population. As compared to the fresh phytodetritus dependent taxa, Category 2 included taxa that do not require regular supply of fresh organic material and instead utilize organic material and degradation products. Surprisingly, Category 3 included taxa that were able to maintain their population for two years without any supply of fresh organic material (Alve, 2010). Benthic foraminifera immensely control the fate of various lipid biomarkers derived from primary producers and subsequent carbon cycling at the deep-sea floor (Nomaki et al., 2009). The grazing of intertidal calcareous benthic foraminifera (*Haynesina germanica* and *Ammonia beccarii,* and the single-chambered agglutinated species *Psammophaga sp*.,) on bacteria (*Halomonas sp*.), was observed by $^{3}$H and $^{14}$C labelling technique (Mojtahid et al., 2011). Both *Ammonia tepida* and *Bolivina variabilis*, showed fast and strong ingestion of the added food after 2 days, followed by a decreasing isotopic signal in the biomass with time (Linshy et al., 2014). The work suggested radioisotope labelling technique as a promising tool to study foraminifera prey interactions and to understand the trophic pathways in foraminifera and the fate of ingested carbon under laboratory condition.

## Calcification and Reproduction

A majority of benthic foraminifera are calcareous in nature. The secretion of calcareous test under a diverse set of conditions is a complicated phenomenon. The ocean acidification is expected to adversely affect calcification. Therefore, several attempts have been made to understand the calcification process. The relation between seawater up take and calcification in juvenile specimens of *Ammonia tepida* was observed under controlled laboratory condition and it was found that endocytosis of seawater is a part of the calcification process (de Nooijer et al., 2009a). Benthic foraminiferal abundance depends on reproduction efficiency and frequency under different ambient conditions. Benthic foraminiferal propagules (numerous small juveniles) can survive transport, remain "dormant" for two years, and then start growing and reproducing once conditions are favourable (Alve and Goldstein, 2010). Additionally, the propagule banks provide a tool for documenting changes in coastal assemblages that potentially result from warming or cooling climates (Goldstein and Alve, 2011).

## Effect of ocean acidification on benthic foraminifera

The ambient pH is very critical for all calcifying organisms, including foraminifera. The open ocean pH varies from 7.9 to 8.3. As the concentration of $CO_2$ is increasing in the atmosphere, in near future, it is expected that the pH of the ocean, which is said to be one of the biggest sinks for this atmospheric $CO_2$, will decrease. A decrease in pH will adversely affect calcifying organisms. The effect of ocean acidification may vary from organism to organism. Realizing the need of the hour, many researchers are trying to understand the effect of decrease in pH, due to increase in $CO_2$ in atmosphere, on calcifying organisms. Proper experimental design is required for carrying out ocean acidification experiments, especially the contamination free media, as benthic foraminifera may not survive due to ciliate infestation (Diz et al., 2015). The laboratory culture studies suggest that, ongoing ocean acidification can result in decrease of calcite production by foraminifera (de Nooijer et al., 2009b). The results are further supported by another study wherein it was observed that ≥929 µatm $CO_2$, caused reduced growth and shell dissolution in *Ammonia aomoriensis* (Haynert et al., 2011). In an interesting study, it was suggested that benthic foraminifera can't survive and thus likely to be extinct in the near future under $pCO_2$ exceeding 700 µatm, (Uthicke and Fabricus, 2012). The findings were later contested by several studies. No lethal effect on the fitness and survival of *Amphistegina gibbosa* was observed under elevated $pCO_2$ or the associated decrease in pH as well as the calcite saturation state of the seawater (McIntyre-Wressnig et al., 2013). The growth and mortality of living *Ammonia aomoriensis* were not affected by elevated $pCO_2$ levels, but ~30% of empty tests of *A. aomoriensis* were subjected to dissolution at high $pCO_2$ of 3247 µatm and $\Omega_{calc}$ undersaturation. The tests of subdominant species *Elphidium incertum*, however remained intact (Haynert et al., 2014). No significant effect of elevated $pCO_2$ on benthic foraminifera *Amphistegina radiata* and *Heterostegina depressa* net production and dark respiration was observed after long and short term exposures (Vogel and Uthicke, 2012). The shell weight of *Marginopora kudakajimensis* was most closely dependent upon pH, suggesting that fossil shell weight can be more useful for reconstruction of paleo-pH changes (Kuroyanagi et al., 2009). Yet in another study, Dissard et al. (2010b), reported that *Ammonia tepida* shell weight decreases with decreasing $[CO_3^{2-}]$, and also with increasing temperature. Increase in size normalized weight and growth rate of *Ammonia* sp. was found under high $[CO_3^{2-}]$, which confirmed that size normalized weight can be used as a proxy for $[CO_3^{2-}]$ (Keul et al., 2013). The growth in *Amphisorus* and *Calcarina* sp. showed opposite response to the carbonate species (carbonate ion and $CO_2$) which may be because of the different symbiotic algae (Hikami et al., 2011). The main factor influencing the response to changes in pH levels in *Amphistegina lessonii and Marginopora vertebralis* is the difference in biochemical pathways of calcification (Prazeres et al., 2015). These species are also capable to regulate biochemical functions to cope with short-term increase in acidity. Growing emphasis is on conducting community level experiments to understand differential interaction between groups. The elevated $CO_2$ concentration may result in increased nanobenthos density (Ishida et al., 2013). The calcification during chamber formation of *Ammonia sp.* strongly influences the extracellular pH of the microenvironment (Glas et al., 2012). The laboratory culture studies suggest a very large pH tolerance range of benthic foraminifera and a clear species specific response to ocean acidification.

## Factors affecting stable isotopic composition of benthic foraminifera

The stable isotopic ratio (Oxygen and Carbon) of calcareous foraminifera are extensively used to reconstruct past hydrographic changes. Therefore, continuous efforts have been made to understand the effect of various ambient parameters on stable isotopic fractionation in foraminifera. Laboratory culture studies showed that the carbonate ion composition of seawater, growth rate, developmental stage, light levels affect the stable oxygen and carbon isotopic composition of benthic foraminifera. The $\delta^{18}O$ in *Amphistegina lobifera* decreases with increasing pH and a change of 0.2‰ was observed with every °C change in temperature, in line with the response of planktic foraminifera (Rollion-Bard et al., 2008). A similar ($-0.22‰°C^{-1}$) difference in $\delta^{18}O$ of *Bulimina marginata* cultured over a wide range of temperature (4 to 19°C) was also observed confirming that the temperature dependency of foraminiferal $\delta^{18}O$ was parallel to the thermodynamically determined changes observed in inorganically precipitated calcite and thus further validating the use of $\delta^{18}O$ in paleoceanographic studies (Barras et al., 2010). A comparison of $\delta^{18}O$ and $\delta^{13}C$ of cultured benthic foraminifera with water chemistry and field specimens suggests differences due to species-dependent vital effects, ontogenetic variations in shell chemistry; and the aqueous carbonate chemistry ([$CO_3^{2}$] or pH) of the experimental system (McCorkle et al., 2008). In another study, it was confirmed that the combination of $\delta^{18}O$ and Mg/Ca of *Ammonia beccarii* can be applied to reconstruct $\delta^{18}O_{seawater}$ as well as the salinity (Toyofuku et al., 2011). The effect of ontogenetic variations on $\delta^{18}O$ was also observed in *Bulimina aculeata* and *Bulimina marginata*, thus suggesting a consistency with patterns observed in earlier culture studies (Filipsson et al., 2010). As compared to oxygen, limited attempts have been made to understand the factors affecting carbon isotopic fractionation in benthic foraminifera. The persistent methane emanation also impacts the carbon isotopic composition of deep-sea benthic foraminifera (Wollenburg et al., 2015). In addition to O and C, a few other stable isotopes have also been measured to develop potential new proxies. Recently, it was reported that Li and its isotopes may serve as a new complementary proxy for the past ocean carbonate chemistry (Vigier et al., 2015).

## Factors affecting elemental composition of benthic foraminifera

Elemental composition of foraminiferal test is also used for paleoceanographic and paleoclimatic interpretations. Trace elements get incorporated into the test from the seawater during the test secretion. Laboratory culture studies have helped evaluate the factors affecting elemental composition of several benthic foraminiferal species. A majority of culture studies have been conducted on benthic foraminifera to understand the effect of ambient conditions on Mg/Ca and Sr/Ca (Dissard et al., 2009; 2010a; 2010b; Duenas- Bohorquez et al., 2011; de Nooijer et al., 2014). A precise evaluation of the effect of ambient conditions on trace element ratio requires to delineate the earlier formed calcite from that secreted under controlled laboratory conditions. A fluorescent dye calcein was suggested as potential technique to track newly formed calcite. The effect of fluorescent dye calcein on benthic foraminifera *Ammonia tepida* was investigated and it was found that the presence of calcein does not impact Mg and Sr incorporation into biologically and inorganically precipitated calcium carbonate (Dissard et al., 2009). The impact of salinity on Mg/Ca and Sr/Ca ratio was evaluated from the change in partition coefficients ($D_{Me}$=(Me/Ca calcite)/(Me/Ca seawater); where (Me: i.e. Sr and Mg)). $D_{Mg}$ per unit salinity is 2.8% at 10°C and 3.3% at 15°C, for the salinity interval 20-40 psu. It implies that a salinity increase of 2 psu results in enhanced Mg incorporation equivalent to 1°C increase in temperature. As compared to $D_{Mg}$, $D_{Sr}$ increase per unit salinity was 0.8% at 10°C and 1.3% at 15°C, for the salinity interval 20–40 psu (Dissard et al., 2010a). It should however be noted that the partition coefficient of trace elements is species specific. Allison et al., 2010 also suggested that a correlation between ambient water $\Delta$ [$CO_2^{2-}$] and test Mg/Ca is not ubiquitous in all calcareous foraminiferal species. *Heterostegina depressa* and *Ammonia tepida* species responded differently to the seawater chemistry (Raitzsch et al., 2010). They observed that, the partition coefficient of Mg ($D_{Mg}$) in *A. tepida* significantly decreases with increasing [$Ca^{2+}$] and, therefore calcite saturation state (Ω), while $D_{Sr}$ in the same benthic species does not vary. On the other hand, $D_{Mg}$ of *H. depressa* shows only a minor decrease with increasing [$Ca^{2+}$] and thus (Ω), while $D_{Sr}$ increases considerably with [$Ca^{2+}$] and also (Ω). Interestingly, changes in [$CO_3^{2-}$] or dissolved inorganic carbon, does not significantly affect Mg distribution coefficient. Contrary to that, Sr incorporation increases with increasing [$CO_3^{2-}$] (Dissard et al., 2010b). The effect of seawater carbonate ion concentration ([$CO_3^{2-}$]), and thereby calcite saturation state (Ω), on Mg and Sr incorporation into calcite of *Ammonia tepida* and *Heterostegina depressa* and has also been observed. It was found that the ions involved in biomineralization (i.e. $Ca^{2+}$ and dissolved inorganic carbon (DIC) are processed by separate cellular transport mechanisms. Further based on similar response of Mg and Sr incorporation, it was proposed that differences in the $Ca^{2+}$ transport mechanism only affect divalent cation partitioning (Raitzsch et al., 2010) *Ammonia tepida* was cultured under constant conditions while determining its growth rates, size-normalized weights and single-chamber Mg/Ca and Sr/Ca (de Nooijer et al., 2014). No detectable ontogenetic control on the incorporation of these elements in the species was observed. Difference between the groups was similar to the intra-clone group variability in elemental composition, suggesting that any genetic differences between the studied clone groups do not affect trace element partitioning. As benthic foraminiferal species abundance varies regionally, continuous efforts are made to explore trace element partitioning coefficients in multiple species. *Bulimina marginata* was found to have a low sensitivity for trace element incorporation, and thus is not ideal for reconstructing paleotemperature due to associated large uncertainties and large sample size needed for an accurate temperature reconstruction (Wit et al., 2012). No significant correlation was observed between Mg/Ca and Sr/Ca, either within single tests or between tests cultured at the same pH, thus suggesting additional control on incorporation of these elements in foraminiferal tests (Allison et al., 2011). Laboratory culturing of benthic foraminifer *Ammonia* sp. at a range of carbonate chemistry manipulation treatments suggests a strong potential of foraminiferal U/Ca as a $[CO_3^{2-}]$ proxy (Keul et al., 2013a). Recently, it was suggested that foraminiferal Zn/Ca might be useful when combined with other $[CO_3^{2-}]$ proxies to reconstruct past nutrient profiles (van Dijk et al., 2017a). Additionally, combining foraminiferal Zn/Ca with other independent carbonate system proxy (for pH), enables reconstruction of the complete carbon system and thereby, past atmospheric $CO_2$. In another experiment, van Dijk et al. (2017b) observed a higher incorporation of Zn and Ba when $pCO_2$ increases from 350 to 1200 ppm. They also observed a contrasting trend in element incorporation in both hyaline and porcelaneous foraminifers whereas, a similar trend was observed in element incorporation as a function of sea- water carbonate chemistry. Similar studies with metals like Ni, Cu and Mn were also carried out on benthic foraminifera *Ammonia tepida* and partition coefficients for Cu and Ni (0.14±0.02 and 1.0±0.5, respectively) were calculated. These coefficients can thus be used in environmental and paleoclimatic studies to more accurately determine the Cu/Ca and Ni/Ca ratio of sea water (Munsel et al., 2010). The culture studies are thus exploring novel elemental proxies for better paleoclimatic reconstruction.

**Table 1.1: Laboratory culture studies on benthic foraminifera in the last decade.**

| **Authors and Year of Publication** | **Study Details** |
|---|---|
| Koho et al., 2008 | Reported the response of benthic foraminifera to phytodetritus, either directly or indirectly due to enhanced bacterial activity; the response can be measured as an increase in total standing stalk of foraminifera. |
| McCorkle et al., 2008 | Difference in the offset of $\delta^{13}C$ and $\delta^{18}O$ was noticed between the cultured specimens and the water in which the specimens were growing. |
| Rollion-Bard et al., 2008 | Studied influence of seawater carbonate chemistry and temperature on the intra-shell oxygen isotope ratio in *Amphistegina* |
| Dissard et al., 2009 | Effect of the fluorescence indicator calcein on Mg and Sr incorporation into foraminiferal calcite |
| Kuroyanagi et al., 2009 | Growth rate, shell weight and the number of chambers, generally decreased with decreasing pH, after 10 weeks of culture in asexually produced individually of *Marginopora kudakajimensis*. |
| Nomaki et al., 2009 | In situ feeding experiment using $^{13}C$-labelled unicellular algae, showed microbial degradation of $^{13}C$ labelled algal material and the production of bacterial biomass within 2 days. The biomass produced was gradually turned over by respiration or predation within 6 days. |
| de Nooijer et al., 2009a | Physiological controls on seawater uptake and calcification in the benthic foraminifer *Ammonia tepida*. |
| de Nooijer et al., 2009b | Foraminifera promote calcification by elevating their intracellular pH. |
| Pucci et al., 2009 | Experimental results show that all dominant foraminiferal taxa from the sixteen short sediment cores from a 35  m deep site in the |

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| | Adriatic Sea survive strong hypoxic conditions. |
| Sabean et al., 2009 | Monitoring of oil spill using marsh foraminifera as indicators. |
| Alve, 2010 | Studied the response of benthic foraminiferal taxa to food for two years under laboratory conditions. |
| Allison et al., 2010 | Evaluated the effect of pH, $\Delta[CO_3^{2-}]$ on Mg/Ca in *Elphidium williamsoni*. |
| Alve and Goldstein, 2010 | Propagules of certain species are sufficiently resilient to survive transport, remain dormant for two years, and then start growing and reproducing once conditions are favourable. |
| Barras et al., 2010 | Studied the calibration of $\delta^{18}O$ of cultured benthic foraminiferal calcite as a function of temperature. |
| Dissard et al., 2010a | Studies the impact of salinity on Mg/Ca and Sr/Ca ratio in *Ammonia tepida*. |
| Dissard et al., 2010b | Impact of seawater $pCO_2$ on calcification and Mg/Ca and Sr/Ca ratio in *Ammonia tepida*. |
| Filipsson et al., 2010 | Calibrated paleotemperature proxies from $\delta^{18}O$ and Mg/Ca. |
| Munsel et al., 2010 | Studies the effect of heavy metal Ni, Cu and Mn in *Ammonia tepida*. |
| Raitzsch et al., 2010 | Investigated the effect of calcite saturation state on Mg and Sr incorporation into benthic foraminifera *Heterostegina depressa* (high Mg calcite, symbiont-bearing) and *Ammonia tepida* (low Mg calcite, symbiont-barren). |
| Allison et al., 2011 | Effect of seawater pH and calcification rate on test Mg/Ca and Sr/Ca in *Elphidium williamsoni.* |
| Duenas-Bohorquez et al., 2011 | Studied the impact of carbonate ion concentration on Mg and Sr incorporation in *Ammonia tepida* and *Heterostegina depressa*. |
| Enge et al., 2011 | Studied the response of individual benthic foraminifera to a simulated phytodetritus pulse. |
| Goldstein and Alve, 2011 | Studied viability of foraminiferal communities from coastal propagule banks. |
| Haynert et al., 2011 | Effect of high $pCO_2$ concentration on benthic foraminifera |

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| | *Ammonia aomoriensis*. |
| Hikami et al., 2011 | Studied the response of two reef foraminifera harboring different algal symbionts to ocean acidification. |
| Mojtahid et al., 2011 | Studied grazing of intertidal benthic foraminifera on bacteria by using pulse-chase radio-tracing. |
| Prazeres et al., 2011 | Studied the effect of zinc (Zn) on symbiont-bearing foraminifer *Amphistegina lessonii*. |
| Toyofuku et al., 2011 | Evaluated the effect of different salinity and temperature on Mg/Ca and $\delta^{18}O$. |
| Denoyelle et al., 2012 | Evaluated the application of benthic foraminifera as potential bio-indicator. |
| Frontalini and Coccioni, 2012 | Studied the response of benthic foraminiferal assemblages to Copper. |
| Glas et al., 2012 | pH within extracellular microenvironment decreases during calcification in symbiont-free benthic foraminifera *Ammonia sp*. |
| Prazeres et al., 2012 | Observed the impact of metal exposure in symbiont-bearing foraminifer *Amphistegina lessonii.* |
| Uthicke and Fabricus, 2012 | Studied productivity, respiration, and abundance of symbiont bearing foraminifer *Marginopora vertebralis* near natural $CO_2$ seeps, as well as under artificially enhanced $pCO_2$. |
| Vogel and Uthicke, 2012 | Investigated the impact of ocean acidification on calcification rates of large benthic foraminifera (*Amphistegina radiata* and *Heterostegina depressa* and dinoflagellate-bearing *Marginopora vertebralis*). |
| Wit et al., 2012 | Assessed the effect of vital processes on Mg/Ca in benthic foraminifer *Bulimina marginata*. |
| Hess et al., 2013 | Effect of burial by water-based drill cuttings and natural test sediment were investigated in a mesocosm experiment. |
| Ishida et al., 2013 | Observed the effects of $CO_2$ on benthic biota. |
| Keul, et al., 2013 | Confirms the strong potential of *Ammonia* sp. foraminiferal size-normalized weights (SNW) as a [CO $^{2-}$] proxy. |

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| Keul, et al., 2013a | Confirms the strong potential of foraminiferal U/Ca as a [$CO_3^{2-}$] proxy. |
| Langlet et al., 2013 | Observed the effect of experimentally induced anoxia in insitu experiment on benthic foraminifera. |
| McIntyre-Wressnig et al., 2013 | Effect of ocean acidification on the growth and survival of symbiont-bearing benthic foraminifer *Amphistegina gibbosa*. |
| Seears and Wade, 2013 | A note on the laboratory culture of benthic foraminifer *Cornuloculina balkwilli.* |
| Enge et al., 2014 | Role of benthic foraminifera in uptake of phytodetritus in the core regions of the Indian margin OMZ. |
| Geslin et al.,2014 | The survival rate, growth and reproduction capacities of *Ammonia tepida*, *Melonis barleeanus* and *Bulimina marginata* were studied under strongly oxygen depleted conditions. |
| Haynert et al., 2014 | Culture experiment was conducted on benthic foraminifera to observe its response to ocean acidification in its natural sediment environment. |
| de Nooijer et al., 2014 | Studied Mg/Ca and Sr/Ca variability in clones of benthic foraminifera *Ammonia tepida*. |
| Nardelli et al., 2014 | Reported that benthic foraminifera not only survive, but also calcify under anoxic conditions. |
| Diz et al., 2015 | Described an experimental set up to carry out ocean acidification experiments with non-symbiotic benthic foraminifera (*Miliolinella* spp.). |
| Frontalini et al., 2015 | The response of *Ammonia parkinsoniana* to different concentrations of Pb was evaluated at the cytological level. |
| Prazeres et al., 2015 | Assessed the biochemical and morphological impact of different pH on *Amphistegina lessonii* and *Marginopora vertebralis*. |
| Vigier et al., 2015 | Suggested lithium isotope of foraminifera as a novel proxy for ocean dissolved inorganic carbon (DIC). |
| Brouwer, et al., 2016 | Reported diet shift and population dynamics of estuarine foraminifera under experimentally induced hypoxia. |
| Cesbron et al., 2016 | Reported the uptake of oxygen in intertidal sediments which is |

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| | almost five times more than the maximum recorded by other authors. |
| Enge et al., 2016 | Foraminifera dominate the short-term processing of phytodetritus in the OMZ core but are less important in the lower OMZ boundary region of the Indian margin. |
| Frontalini et al., 2016 | Examined the response of *Ammonia parkinsoniana*, to different concentration of Hg. |
| Yu et al., 2016 | Observed the potential application of *Ammonia aomoriensis* mean proloculus size as a salinity index. |
| van Dijk et al., 2017a | Impact of pH and [CO $^{2-}$] on Zn incorporation. |
| van Dijk et al., 2017b | Observed the element incorporation in hyaline and porcelaneous foraminifera as a function of pCO$_2$.. |

## Effects of specific pollutants on foraminifera

Anthropogenic activities severely affect the marginal marine regions. Being abundant, benthic foraminifera have been often used to understand the effect of pollutants on marine ecosystem. Laboratory culture studies help in understanding specific effect of particular pollutant on benthic foraminifera. Sabean et al. (2009) observed the effect of residual oil on benthic foraminifera *Miliammina fusca* and reported that the percentage of deformed tests in foraminifera can be an excellent indicator of oil pollution. Lead contamination can cause numerical increase in lipid droplets, proliferation of residual bodies, thickening of the organic lining, mitochondrial degeneration, autophagosome proliferation and the development of inorganic aggregates in *Ammonia parkinsoniana* (Frontalini et al., 2015). The presence of Hg at the basal part of pores, in the organic linings of the foramen/septa, and as cytoplasmic accumulations in the foraminiferal test of *Ammonia parkinsoniana,* was observed in response to different concentrations of Hg (Frontalini et al., 2016). Prazeres et al. (2011) observed the effect of zinc on benthic foraminifera *Amphistegina lessonii* and suggested that that an activation of some components of the antioxidant system occurred in this species to counteract the oxidative stress induced by Zn exposure, and therefore, a possible complete loss of the symbiont was prevented. In another study, the Ca$^{2+}$-ATPase activity was evaluated in adult holobionts of *Amphistegina lessonii* and the results indicate that holobiont Ca$^{2+}$-ATPase activity is a good biomarker of metal exposure, allowing the detection of local stressors and implementation of management directives for coral reef preservation (Prazeres et al., 2012). Denoyelle et al. (2012) observed the effect of different concentrations of cadmium, Fuel Oil no. 2 and two types of drilling muds (non-aqueous based mud (NABM) and water based mud (WBM) and reported that, the foraminifera show a strong physiological response to 30 day incubation with high concentrations of all tested pollutant. It appears that NABM has a higher toxicity than WBM. Increased concentrations of Cu (normally higher than 120 µg/l) lead to a lowering of foraminiferal density and diversity and an increased occurrence of abnormalities (Frontalini and Coccioni, 2012). Hess et al. (2013), studied the foraminiferal response to sediments covered with drill cuttings as compared to the sediment covered with defaunated natural test sediments and reported reduction in abundance and species richness in water based drill cutting as compared to natural test sediment. Water-based drill cuttings affect reproduction in surviving populations of *B. marginata* and *Nonionellina labradorica*.

## Effect of temperature and salinity on benthic foraminifera

Seawater temperature and salinity are important ecological parameter for all marine organisms. Individual species has a narrow range of optimum temperature and salinity for growth as well as reproduction. It is also seen that the growth rate changes if the species are subjected to temperature or salinity other than optimum. Zhoufei et al. (2016) observed that salinity could be one of the prime factors responsible for the dimorphic behavior of *Ammonia momoriensis* wherein, megalospheric forms will be dominant under optimum conditions and in unstable conditions trimorphism will be observed.

## Effect of oxygen on benthic foraminifera

Oxygen is another important parameter that defines the microhabitat of benthic foraminifera. Depending upon the climate change and eutrophication, the concentration of oxygen may vary. The response of benthic foraminifers to different oxygen concentration varies from species to species. *Nouria polymorphinoides* and *Nonionella turgida* show a clear tendency to move to the oxygen deficient sediment surface in the nitrogen-bubbled cores, whereas, *Bulimina* spp. and *Eggerella scabra* did not show such a migrational response (Pucci et al., 2009). The differential response was attributed to the nutrition concentration at the sediment water interface. Observation of oxygen respiration rates and fluxes for seventeen species of benthic foraminifera by using microelectrodes suggest that foraminifera contribute more to anaerobic organic matter mineralization than to aerobic organic matter mineralization (Geslin et al., 2011). The relative foraminiferal contribution to aerobic and anaerobic carbon remineralization, however varies from location to location. Aerobic carbon remineralization attain 7% of diffusional oxygen uptake in intertidal sediments, and is almost five times more than the maximum reported by Geslin et al. (2011) (Cesbron et al., 2016). Due to the differential response to oxygen availability, both the calcareous as well as agglutinated benthic foraminifera can survive up to 10 months of anoxia with co-occurring hydrogen sulfides (Langlet et al., 2013). Foraminiferal standing stocks however, decreases with sampling time in an irregular manner. *Ammonia tepida* and *Melonis barleeanus* showed a very high survival and growth rate under strongly oxygen-depleted conditions alternating with short periods of anoxia in all experimental conditions (Geslin et al., 2014). The survival rate of *Bulimina marginata* was comparatively much lower. In another study, however, both *Ammonia tepida* and *Bulimina marginata* as well as *Cassidulina laevigata* not only survived but were also able to calcify at different depths, under anoxic conditions with or without nitrates (Nardelli et al., 2014). The benthic foraminiferal population density was more at sediment surface and decreased gradually with depth, thus confirming field results (Enge et al., 2011). Due to the capability to thrive under oxygen depleted condition, foraminifera may play an important role in short-term carbon cycling in the oxygen minima zone (OMZ) core region on the Indian margin as observed from the uptake of large amounts of organic matter by a few species (Enge et al., 2014). It should however be noted that even though the foraminifera dominate the short-term processing of phytodetritus in the core region of the oxygen minimum zone but are less important in the lower oxygen minimum zone boundary region of the Indian margin as biological interactions and species distribution of foraminifera change with depth and oxygen levels (Enge et al., 2016). The differential effect of diet and induced winter hypoxia on the population structure of benthic foraminifera was further confirmed and it was found that benthic foraminifera generally responded inversely to progressive stages of ecosystem recovery (Brouwer et al., 2016).

## Experimental studies on benthic Foraminifera: National Scenario

The literature review on laboratory culture studies on benthic foraminifera, indicates that, experimental studies on benthic foraminifera are popular in many countries over the world.

Such studies are yet to attain proper attention in India. The laboratory culture studies on benthic foraminifera in India are only carried out at the National Institute of Oceanography, Goa. The response of benthic foraminifera collected from eastern Arabian Sea, to various ecological conditions under controlled laboratory culturing conditions has been studied by several workers (Nigam et al., 2006; 2008; Kurtarkar et al., 2011; Saraswat et al., 2011; 2015). The optimum temperature, salinity conditions vary from species to species. Even though the salinity as well as temperature tolerance range of benthic foraminifera is large, the reproduction is restricted to a very narrow set of temperature-salinity combination (Saraswat et al., 2011). Benthic foraminifera can overcome short-term ecological stress, although the signatures of stress are evident in increased abnormality (Kurtarkar et al., 2011). Fresh water influx induced decrease in ambient seawater pH, also reduces the growth, resulting in stunted specimens. Additionally, the drop not only reduces the frequency of reproduction, but also the number of juveniles produced when a specimen reproduces under low pH (Saraswat et al., 2015).

During the last decade, the effect of ecological parameters (salinity, temperature, pH) and heavy metal pollution (Mercury, cadmium) on benthic foraminifera has been studied in this lab. From the culturing of benthic foraminifera *Rosalina leei* at a range of salinity (25 psu, 30 psu and 35 psu) and temperature (25°C, 30°C and 35°C), it was found that 25°C temperature and 35 psu salinity is the most suitable for the growth (Nigam et al., 2008). Further, since the specimens did not reproduce under the experimental conditions, it was inferred that it requires a narrow range of temperature and salinity for reproduction. In another study, it was observed that the optimum growth of *Rosalina globularis* took place at 30 °C temperature and the highest percentage of reproduction took place in the specimens subjected to 27°C temperature (Saraswat et al., 2011). The fresh water influx induced drop in pH adversely affects calcification and reproduction in *Rosalina globularis* (Saraswat et al., 2015). The dissolution of calcareous foraminifera below 20 psu salinity, suggests that salinity induced changes control the carbonate inventory in the coastal regions subjected to seasonal fresh water influx. The dissolution of test under hyposaline condition suggests adverse effect of low salinity on benthic foraminifera. The specimens however, recovered from a short term exposure to hyposaline conditions and regenerated its test (Kurtarkar et al., 2011). Experiments under controlled conditions suggest that the changes in $\delta^{18}$O of *Pararotalia nipponica* can be effectively used to infer past seawater temperature changes (Linshy et al., 2013). A sudden addition of heavy metal mercury (25 to 300 ng/l at 25 ng/l intervals) into the media under laboratory culture experiments adversely affected the growth rate in *Rosalina leei* (Nigam et al., 2009). Increased concentration of heavy metal cadmium also affected normal growth, caused morphological abnormalities and a peculiar change in coiling direction in *Pararotalia nipponica* (Linshy et al., 2013). Kurtarkar et al. (2015) proposed that that short-term exposure to low calcein concentration can be used as an effective technique to distinguish newly formed chambers in laboratory experiments with foraminifera. However, long-term (5–6 weeks or more) exposure, even to low calcein has an adverse effect on benthic foraminifera.

**Table 1.2 - Laboratory culture studies on benthic foraminifera in India during the last decade.**

| **Authors and Year of Publication** | **Study Details** |
|---|---|
| Nigam et al., 2008 | Response of *Rosalina leei* to different salinity and temperature. |
| Nigam et al., 2009 | Effect of sudden stress due to heavy metal mercury on benthic foraminifer *Rosalina leei*. |
| Saraswat et al., 2011 | Reported that the optimum temperature for growth and reproduction of *Rosalina globularis* are different. |
| Kurtarkar et al., 2011 | *Rosalina leei* can recover from adverse effect of short-term salinity changes. |
| Kurtarkar et al., 2015 | Effect of temperature and salinity on stable isotopic composition of shallow water benthic foraminifera *Rosalina sp*. and *Pararotalia nipponica* |
| Linshy et al., 2013 | Observed the effect of heavy metal cadmium on benthic foraminifera *Pararotalia nipponica*. |
| Linshy et al., 2014 | Specimens of *Ammonia tepida* and *Bolivina variabilis* were subjected to the marked green algae *Dunaliella tertiolecta* for 2, 7, 21 and 42 days and were analysed for carbon signals. |
| Saraswat et al., 2015 | Reported that salinity induced pH changes affect calcification as well as reproduction in benthic foraminifera *Rosalina globularis*. |
| Kurtarkar et al., 2015 | Assessed the effect of calcein incorporation on physiological processes of benthic foraminifera. |

## Foraminiferal response to dissolved oxygen: Previous Studies

Recent benthic foraminifera have been documented from the Arabian Sea OMZ (Hermelin and Shimmield, 1990; Gooday et al., 2000; Erbacher and Nelskamp, 2006; Nigam et al., 2007; Schumacher et al., 2007a; Mazumder and Nigam, 2014). Majority of these studies were carried out from the northeastern or western Arabian Sea. Benthic foraminiferal assemblages of eastern Arabian Sea OMZ are, however different than other world oceans. *Bulimina marginata* suggested as an indicator of OMZ in several parts of the world oceans constitutes only 2% of the total benthic foraminiferal assemblage in the eastern Arabian Sea OMZ. Similarly, another species *Bulimina costata*, which is rarely present in other world ocean OMZs, is dominant in the eastern Arabian Sea OMZ (Mazumder et al., 2003; Mazumder and Nigam, 2014). The above findings suggest that benthic foraminifera of the eastern Arabian Sea OMZ are different than other world oceans. Increased abundance of rectilinear benthic foraminifera was reported from the eastern Arabian Sea OMZ (Nigam et al., 2007a). Based on the relative abundance of oxic and dysoxic specimens, a benthic foraminifera oxygen index (BFOI) has also been proposed.

Benthic Foraminifera Oxygen Index (BFOI) = [(oxic/(oxic + dysoxic)]*100

BFOI, however varies from ocean to ocean (Kaiho, 1994). So far, no attempt has been made to test the applicability of BFOI in the northern Indian Ocean OMZ.

Benthic foraminifera inhabiting dysoxic environments are thin walled (Kaiho, 1994) and small (spiral forms with diameter <200 µm while serial forms with length <500 µm) (Phleger and Soutar, 1973; Perez-Cruz and Machain-Castillo, 1990). Additionally, low oxygen indicators (e.g. *Bolivina*, *Bulimina*, *Cassidulina*) are usually, flat elongated tapered forms, mostly infaunal with highly porous test, as compared to oxic condition indicators (e.g. *Cibicides*, *Cibicidoides*), which are epifaunal planoconvex, biconvex, rounded trochospiral, and spherical in shape (Gary et al., 1989; Kaiho, 1994). The higher porosity of dysoxic benthic forms is attributed to the difficulty in secreting calcium carbonate and in providing higher mitochondrial oxygen uptake (SenGupta and Machain-Castillo, 1993). A comparison of pore density in living (rose-Bengal stained) specimens of shallow infaunal *Bolivina pacifica*, and deep-infaunal species *Fursenkoina mexicana*, and *Chilostomella oolina* isolated from surface sediment samples collected from OMZ off Namibia and Pakistan, suggests that pore density depends on dissolved oxygen, as well as nitrate concentration and temperature (Kuhnt et al., 2013). Further, the response of benthic foraminifera to dissolved oxygen is species specific.

So far, only a few laboratory culture experiments were conducted to understand the effect of dissolved oxygen on foraminifera. The experiments on planktic foraminifera suggest that *Orbulina universa* and *Globigerina bulloides* can survive under dysoxic conditions (Kuroyanagi et al., 2013). The shell weight increased with increasing dissolved oxygen, suggesting that shell weight can be used as a proxy for dissolved oxygen conditions. The pore diameter and density also varied with dissolved oxygen concentration. The experiment however was conducted on planktic foraminifera and their tolerance was also attributed to their evolution from benthic foraminifera. Culture experiments on both the deeper and shelf benthic foraminiferal assemblages suggest that dissolved oxygen concentration controls the vertical migration and density of benthic foraminifera on short time scale as the long term changes in community structure and population are controlled by food availability (Gross, 2000; Duijnstee et al., 2003; Ernst and Van der Zwaan, 2004; Geslin et al., 2004; Ernst et al., 2005). In a few taxa, however, temperature also had a pronounced effect of vertical migration speed of foraminifera (Gross, 2000). The overall population increased when additional food was supplied (Heinz et al., 2002) and decreased with decreasing dissolved oxygen levels (Ernst et al., 2005). Interestingly, in the northern Adriatic Sea, the response of a few of the previously suggested dysoxic and anoxic species (*Bolivina* spp., *Eggerella* spp., *Bulimina marginata*), to the induced environmental changes, was not clear (Ernst et al., 2005). The presence and absence of tests as well as its composition is crucial in determining benthic foraminiferal response to oxygen, as soft-shelled foraminifera preferred the oxic zone suggesting their less tolerance to anoxic conditions as compared to hard-shelled foraminifera (Moodley et al., 1998).

Foraminifera have also been used to trace the long term changes in the extent and intensity of both coastal and intermediate water hypoxic zones in the Arabian Sea (Sen Gupta et al., 1996; Reichart et al., 1998; 2004; Bernhard et al., 1999; von Rad et al., 1999a; 1999b; den Dulk et al., 2000; Agnihotri et al., 2003; Platon et al., 2005; Nigam et al., 2009). The extent and intensity of OMZ is largely controlled by processes associated with monsoon. Changes in the relative abundance of rectilinear benthic foraminifera have been used as a proxy to reconstruct past OMZ of eastern Arabian Sea (Nigam et al., 2009). Changes in stable isotopic ratio of benthic foraminifera have also been used to reconstruct past oxygenation off the Pakistan shelf (Schmiedl and Mackensen, 2006). Even though changes in seawater chemistry over the last few decades indicate variation in OMZ intensity and extent in the eastern Bay of Bengal (Sarma et al., 2013), geological reconstruction of OMZ from the northern Indian Ocean has very coarse resolution to assess the effect of anthropogenic activities.

From the review of laboratory culture studies on benthic foraminifera during the last decade, it is observed that a growing emphasis during the last decade has been on to understand the effect of ocean acidification on calcification in benthic foraminifera. Additionally, several studies have also been carried out to understand the factors affecting partitioning of trace elements in benthic foraminiferal tests, especially to develop proxies for quantitative paleoclimatic reconstruction. The response is species specific, thus necessitating additional efforts to understand comprehensive response of benthic foraminifera to environmental factors. The studies documenting foraminiferal response to dissolved oxygen under controlled laboratory culture experiments are very limited.

## Objectives

In view of the above, I've decided to address the following objectives in my doctoral work

- To understand the response of benthic foraminiferal community to different levels of dissolved oxygen under laboratory culture.
- To understand the effect of different amount and frequency of phytodetritus pulse on benthic foraminiferal community.
- To document changes in morphology, especially the test pore density, in selected benthic foraminifera, subjected to different culture conditions.
- To compare the benthic foraminiferal response under controlled laboratory conditions with that in the field.

# Chapter-3: Materials and Methodology

The doctoral work involved both the laboratory culturing of the living benthic foraminifera community collected from the inner shelf region off Goa and study of sediments collected from the Bay of Bengal and the Arabian Sea. The details of both samples are given below.

## Laboratory Culturing

### Collection of living benthic foraminiferal community

Monthly sampling was carried out in the coastal areas of western coast off Goa, India, during low tides, to collect living benthic foraminifera from the surface sediments and sea grass attached to the rocks. The living benthic foraminifera community was collected by diving in the coastal waters off Goa. Both the surface sediments as well as the seaweeds attached to the rocky patches in coastal regions off Goa were collected to retrieve the living benthic foraminifera. The top half centimeter of the sediments was carefully scrapped by using sterile spatula, to avoid contamination. The sediments along with seawater were transferred to glass beakers and covered with paraffin film to avoid evaporation. The seaweeds attached to the rocks were gently removed and stirred vigorously in a bucket to detach living benthic foraminifera. The material was then sieved by using 63 µm and 1000 µm sieves to concentrate living benthic foraminifera. The >63 µm and <1000 µm fraction was transferred to glass beakers partially filled with the seawater. The beakers were covered with paraffin film to avoid excessive evaporation while maintaining the gas exchange. The material with living benthic foraminifera was carefully collected in clean glass beakers and brought to the laboratory along with ambient sea water. Along with the living foraminifera community and sediments, seawater was also collected in 20 L jerry cans. The material brought from the field was incubated at 27°C temperature for two weeks.

### Maintaining living benthic foraminiferal community in the laboratory

The beakers containing living benthic foraminifera were covered with cling film to avoid excessive evaporation. The samples were allowed to stabilize for two weeks by changing the overlying water at a regular interval, usually several times a day to maintain the salinity and pH level of sea water. The material brought from the field was left to stabilize for two weeks by changing the overlying water at a regular interval, usually several times a day, initially. The process helped in restricting the damage to the benthic foraminiferal community, by the rapid decay of seagrass fragments in the material. The water was aerated continuously to maintain dissolved oxygen levels. When the overlying water becomes clear, the material brought from the field was divided into aliquots by using Falsom Splitter. A fraction of the stabilized material was freeze-dried while another fraction was stained with rose-Bengal to understand initial benthic foraminiferal population and diversity, prior to the experiment. The split aliquots were subjected to different experiments.

### Methodology for dissolved oxygen experiment

Several preliminary experiments were conducted to understand changes in the dissolved oxygen concentration in seawater at different atmospheric oxygen concentration. Desired dissolved oxygen values have to be obtained to understand benthic foraminiferal response to dissolved oxygen. According to the dissolved oxygen concentration, four biofacies are defined, viz. (a) Oxic (8.0-2.0 mL/L), (b) Dysoxic (2.0-0.2 mL/L), (c) Suboxic (0.2-0.0 mL/L) and (d) Anoxic (0.0 mL/L) (Tyson and Pearson, 1991). Two preliminary experiments were conducted to create oxic and dysoxic conditions in the filtered sea water, under controlled laboratory conditions, with the help of Sanyo $O_2/CO_2$ gas incubators. The oxygen concentration was modulated by purging the air high quality nitrogen. The carbon-di-oxide was maintained at ambient level. The seawater was filtered by using Millipore filter paper (0.22 µm). Subsequently, the filtered seawater was transferred to incubators with 5% and 20% oxygen concentration. The Masterflex L/S digital dispensing pump were used to circulate oxygen, homogenously in the sea water for 30 and 19 days, respectively. Key parameters (temperature, salinity and DO) were continuously measured throughout the experiment. At 20% atmospheric oxygen concentration, average dissolved oxygen was 7.45 mg/L and at 5% concentration, the average dissolved oxygen was 2.86 mg/L. But the dissolved oxygen dropped down to <2.0 mg/L, after a week.

The filtered seawater (0.4 µm) was used for the detailed experiment. The filtered seawater was transferred to five, pre-leached, washed and oven dried, wide mouth 2000 mL glass reagent bottles. The bottles were rinsed three to four times with filtered seawater. After rinsing, filtered seawater was filled in each glass stock bottle. The bottles with seawater were placed in multi-gas incubators (Sanyo MCO 19M) with different concentrations of $O_2$ (1%, 5%, 10%, and 15%). One bottle was kept in cooling incubator (MIR 154) as the control set (ambient oxygen, ~20%). The average dissolved oxygen concentration at these air oxygen concentration was 1.67 mL/L, 2.04 mL/L, 2.91 mL/L, 4.35 mL/L, and 5.01 mL/L, respectively. The material brought from the field was homogenized and split in 12 aliquots by using a Folsom splitter. One aliquot was stained with rose-Bengal ethanol solution (2 g rose-Bengal in 1 L ethanol) to determine the living foraminifera at the time of the start of the experiment. Rest, 10 aliquots were transferred to 500 ml conical flasks with side arm. The conical flasks were sealed with corks wrapped in cling film. The water in the conical flask was continuously pumped from the 2000 mL glass stock bottle, by inserting a tube through the cork. The water overflowing through the side arm drained back to the stock bottle, thus creating a re-circulating system. The water in the 2000 mL stock bottle was continuously aerated, to equilibrate the dissolved oxygen with the ambient air in the incubator. All the incubators were maintained at 27°C temperature. The seawater salinity (35.0±0.5 psu) was also maintained throughout the experiment. The seawater salinity, pH, and dissolved oxygen (DO) was measured after transferring the sediment samples to the flasks. These parameters were also measured every fourth week. The freeze dried diatom, *Navicula* was fed to the foraminifera. The experiment was conducted for 35 weeks.

### Methodology for food and warming experiment

The laboratory experiment was conducted on shallow water benthic foraminifera *Rosalina globularis*. The living specimens were collected from the Dias Beach, off Goa. The specimens collected from the field were maintained in the laboratory till they reproduced. The juveniles were subjected to the experiment. A total of 400 juvenile specimens were subjected to a combination of food and ambient temperature for 10 weeks to study ecological and morphological changes in shallow water benthic foraminifera with response of seasonal phytodetritus pulses. Five food concentrations were selected on the basis of seasonal diatom fluxes in the study area. The selected diatom concentrations were, 1. Control set (no feed), 2. 25 cells/mL, 3. 50 cells/mL (post-monsoonal flux), 4. 100 cells/mL (pre-monsoonal flux) and 5. 200 cells/mL (SW monsoon flux). The freeze dried *Navicula* (diatoms) was added to the media weekly as food for the foraminifera. The concentration of cells in the diatom stock culture, was counted by using Sedgewick rafter (for cells count per ml). Subsequently, a known volume of *Navicula* stock culture, containing the desired number of cells, was transferred to centrifuge vials to prepare the food. The tubes containing the diatom stock culture were centrifuged to settle the cells. The supernatant was siphoned off and replaced with distilled water. The process was repeated several times to remove the salt. After final centrifugation, the supernatant was siphoned off and the remaining material was freeze dried. The freeze dried organic matter was thus fed to the culture specimens.

To simulate the warming scenarios, the experiment was conducted at two different temperatures. All the previous experiments have maintained the culture at one set temperature. As the temperature varies during the different times of the day in the field, especially shallow water regions, for the first time, we subjected the specimens to a diurnal range of temperature (27°C to 32°C and b. 25°C to 30°C), very closely mimicking the condition in the field. The experiment was conducted in replicate.

### Processing and picking of samples

At the end of the experiment, the sediments were split into two parts. One part of the sediments was stained with rose-Bengal ethanol solution and the other part was stored for the grain-size analysis. The wet sediments from each experimental set were poured over 63 μm mesh and washed with very low water pressure. The coarse fraction (>63 μm) retained on the mesh was transferred into pre weighed beakers and dried. The dried coarse fraction was weighed and stored into neatly labelled plastic vials. A representative coarse fraction was weighed and used for picking. A minimum of 300 specimens (including both the dead as well as rose-Bengal stained living benthic foraminifera) were picked from each sample. The similar procedure was followed to pick rose-Bengal stained specimens, after storing the sediments for three to four weeks. Thus, benthic foraminifera were picked from a total of 22 samples. The total number of foraminifera (TFN) was standardized to 1 g dry sediment, to facilitate the comparison between different samples. T–test for independent variables was performed in order to test the significant difference between the control and the experimental sets (p values <0.05 were considered to be significant).

## Sample collection from the field

### Study area and physiographic setting

The surface sediments were collected from the Gulf of Mannar, west-central Bay of Bengal and north-eastern Arabian Sea.

A. Gulf of Mannar (the south-eastern Arabian Sea), is at the intersection of the eastern Arabian Sea and western Bay of Bengal. The area is influenced by the Indian monsoon and seasonally reversing winds (Vinayachandran and Yamagata, 1998). The seasonal winds strongly modulate the coastal currents. During the southwest monsoon, west Indian coastal current brings higher salinity water from the Arabian Sea into the bay. The low salinity water from the Bay of Bengal is transported to the eastern Arabian Sea by the equatorward east India coastal current, during the northeast monsoon season (Shankar et al., 2002). The strong monsoon wind causes upwelling/vertical mixing, resulting into higher primary productivity throughout the year (Jyothibabu et al., 2014). The marine primary productivity, however, remains higher during the southwest monsoon because of much stronger wind strength, in comparison to the northeast monsoon winds. Thus, plenty of food is available for planktic as well as benthic fauna.

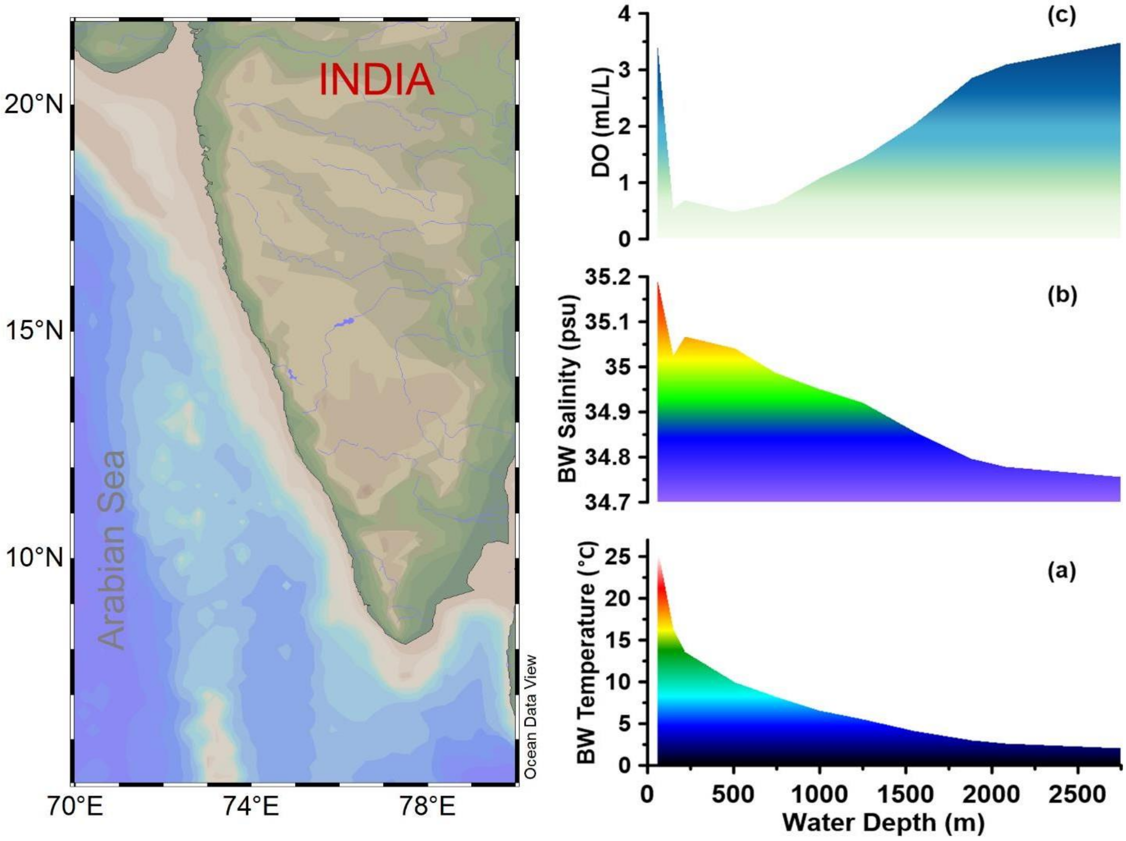

**Figure 3.1: The eastern Arabian Sea (left panel) and the bottom water a) temperature (°C), b) salinity (psu) and c) dissolved oxygen (mL/L) along the Gulf of Mannar transect (right panel).**

The higher primary productivity also generates secondary biological mass (Jagadeesan et al., 2013). The organisms feeding on the settling organic matter consume oxygen from the water column. This creates perennial ODZ in the intermediated depths. The bottom water dissolved oxygen varied between 0.48-3.48 mL/L (21-155 µM) (Figure 3.1) with the lowest value at 510 m. These seasonally reversing winds are also responsible for the changes in the physico-chemical properties of ambient seawater. Due to the upwelling of cold water (<26°C), the ocean surface temperature decreases to its lowest value during the south-west monsoon. Whereas, during the pre-monsoon, the warmest SST is ~29.0°C, due to the Indo-Pacific Warm Pool (IPWP) effect (Boyer et al., 2013). Bottom water temperature varies between 2.06 to 25.96°C with lower value towards deeper depth (Figure 3.1). The movement of both the high and low salinity water through the region imparts a distinct seasonality, with higher sea surface salinity (~35 psu) during summer and lower values during winter (~33 psu). Bottom water salinity also varies seasonally, although the amplitude of variation was much reduced (34.75 to 35.19 psu; Figure 3.1) and increased with depth.

B. The west-central Bay of Bengal is strongly influenced by the riverine influx. Some of the world’s largest rivers drain into the western Bay of Bengal with the average runoff being, Ganga- 11892 $m^3s^{-1}$, Brahmaputra- 16186 $m^3s^{-1}$, Godavari- 3180$m^3s^{-1}$, Krishna- 1730 $m^3s^{-1}$, Pennar- 95 $m^3s^{-1}$ and Cauveri- 664 $m^3s^{-1}$. The contribution of lithogenic components is ~39% in the northern bay and ~12.6% in the southern bay (Unger et al., 2003). The riverine influx depends on monsoon intensity. Monsoon-driven winds are also responsible for the stratification (Gomes et al., 2000) and surface circulation in the Bay of Bengal, resulting in ocean currents. The surface circulation (East India Coastal Current) reverses seasonally along the western boundary of the bay, flowing southwards during the winter season and northward during the summer season (Shankar et al., 2002). The precipitation resulting from the seasonal reversal of winds in the Bay of Bengal, is maximum during the summer monsoon (318 mm/month) as compared to the winter monsoon (88 mm/month) (Ramesh Kumar and Prasad, 1997). The direct precipitation causes strong spatial variation in the ambient physico-chemical parameters in the bay.

Additionally, as all the major rivers including Ganga, Brahmaputra, Mahanadi, Krishna, Godavari, Pennar, Cauveri, drain freshwater into the bay, it creates a unique hydrography. The northern Bay of Bengal receives immense freshwater runoff (183 x $10^{11}$ $m^3$) and sediments (1350 million tons/yr) (Varkey et al., 1996, Prasanna Kumar et al., 2002). The sea surface salinity varies from 29.1 psu to 33.7 psu with the lowest salinity water being confined to the shallower inner shelf. The warmer water input from the rivers is evident by the relatively higher sea surface temperature (29ºC - 30ºC) in the vicinity of the river mouths. The dissolved oxygen is deficient at intermediate depths (~100 m to ~1000 m), with concentration being as low as 5 µM (Wyrtki, 1971; Rao et al., 1994; Sardessai et al., 2007; Bristow et al., 2017). The shallower inner shelf water in the vicinity of the rivers have higher dissolved oxygen. The chlorophyll-a concentration varies from ~0.3 mg/$m^3$ to 2.0 mg/$m^3$ in the western Bay of Bengal with higher concentration closer to the river mouth. A strong wind induced upwelling spread over ~40 km wide band, all along the eastern margin of India, is observed in the western Bay of Bengal, during the summer season. As a consequence of this upwelling, salinity increases coastward (Shetye et al., 1991).

C. The north-eastern Arabian Sea is also influenced by both the winter and summer monsoon seasons. The region has the strongest perennial oxygen deficient zone at intermediate depths, as well as the seasonal hypoxic zone on the continental shelf. Narmada and Tapti are the two major rivers draining in the area with the fresh water influx being very low as compared to the northern Bay of Bengal.

### Sample collection

A total of 122 sediment samples were used. During the 4th cruise of RV *Sindhu Sadhana* (SSD004), eleven undisturbed surface samples were collected along a longitudinal transect (between 8.92°N, 78.75°E to 7.22°N, 79.02°E) in the Gulf of Mannar, covering the oxygen minimum zone (water depth varying from 58 m to 2750 m). Similarly, samples were also collected from the west-central Bay of Bengal (11 multi-core samples during the ORV *Sagar Kanya* cruise SK308) as well as the north-eastern Arabian Sea (12 multi-core samples during the RV *Sindhu Sadhana* cruise SSD055) (Figure 3.2). The samples were collected along a coast perpendicular transect covering the region from the inner shelf to the deeper depths. The samples were collected by using an Ocean Scientific International Limited Maxi Multi-corer with 600 mm long core tubes of 110 mm outer diameter and 100 mm internal diameter. The multi-core samples were sub-sampled at 1 cm interval, and half of each sub-sample was stored in 100 mL wide mouth plastic vial. Ethanol and rose-Bengal stain (2 g rose-Bengal dissolved in 1 L ethanol) was added into the vial and shaken gently to mix well with the sediments, to stain and preserve living benthic foraminifera. The top five sections of each multi-core were stained to study the vertical distribution of living benthic foraminifera. The stained samples were stored at 4°C for three weeks, to completely stain living foraminifera.

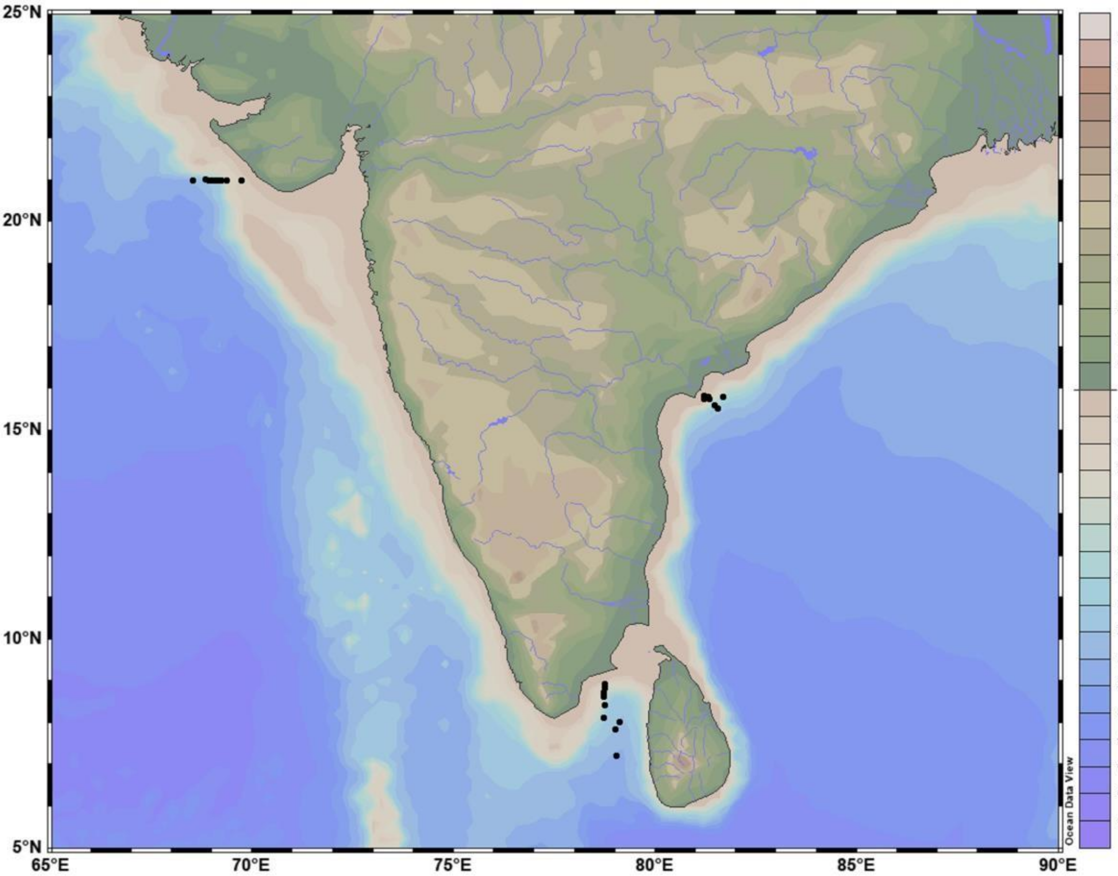

**Figure 3.2: The multi-core sample locations in the Gulf of Mannar (the south-eastern Arabian Sea), west-central Bay of Bengal and north-eastern Arabian Sea. The coloured contours represent bathymetry.**

### Processing of sediments

The stained sediments were processed following a procedure slightly modified after the Jorissen et al. (1992) (Manasa et al., 2016). After three weeks, the overlying ethanol and Rose-Bengal solution was removed from the storage vials. A 63 µm muslin cloth was fixed at the tip of the pipette to prevent the loss of foraminifera. The sediment samples were soaked overnight, to remove excess ethanol. The total removal of ethanol was necessary for the complete freezing of sediments. Subsequently, the sediments were transferred into pre-weighed and labelled glass petri dishes. The sediments were deep-frozen at -30°C overnight and subsequently dried in a freeze-drier. The dried samples were weighed, transferred to l000 ml glass beaker and soaked in distilled water. After 24 hr, the overlying water was decanted without disturbing the sediment. Often, in case of organic matter rich sediments, the overlying water contained colloidal material. The colloidal material obstructed complete sieving of the sediments. The soaking and decanting helped in removal of colloidal material. Once the overlying water was clear, the sediment was sieved by using a 63 µm sieve with a very slow shower and low water pressure to prevent foraminiferal test breakage. The coarse fraction (>63 µm) retained on the sieve, was transferred to a pre-weighed beaker for drying.

### Foraminifera picking

A representative aliquot of the dried coarse fraction was taken after coning and quartering, weighed and uniformly spread in a tray to pick living (rose-Bengal stained) and dead benthic foraminifera and planktic foraminifera from each sample, by using a stereo zoom microscope (Olympus SZX 12). A minimum of 300 specimens of benthic foraminifera were picked, provided that a sufficient number of specimens were available. In the case of less abundance of stained benthic foraminifera, a maximum of 0.5 g of coarse fraction was used to pick living benthic foraminifera. The limit of the maximum coarse fraction weight to be used to pick living benthic foraminifera was set, depending on the availability of coarse fraction and time involved in picking. The absolute abundance of living benthic foraminifera was calculated in 1 g dry sediment by using the following equation

Absolute abundance = [(number of living benthic foraminifera/ weight of coarse fraction taken for picking)*(weight of total coarse fraction/weight of dry sediment)]

A total 38161 specimens (including 8196 living benthic, 27450 dead benthic and 2515 planktic foraminifera) were picked. Average living depth (ALD) was calculated at every station by following the Jorissen et al. (1995) equation, to understand the vertical living preference of fauna. The specimens were grouped into epifaunal and infaunal forms. We followed benthic morpho-group classification suggested by Severin (1983), Corliss and

Chen (1988) and Nigam et al. (1992) to segregate benthic foraminifera into morpho-groups. As per this scheme of classification, the entire benthic foraminiferal population can be grouped into angular asymmetrical and rounded symmetrical morpho-groups. The angular asymmetrical foraminifera are mainly infaunal and rounded symmetrical forms are epifaunal. The abundance of both the calcareous and agglutinated foraminifera was also counted. The abundance of individual species was not counted. The principal component analysis (PCA) was performed to identify patterns between ecological parameters and foraminiferal abundance. In the PCA plot, the length of the arrow is proportional to its importance in determining foraminiferal abundance while its direction indicates the nature (positive or negative) of that relationship.

All the picked specimens were identified up to the species level. The species were identified by comparing the morphology (shell material; number, shape and arrangement of chambers; ornamentation; type and position of aperture; sutures; periphery; and others) of the specimens found in the south-eastern Arabian Sea with the previously published plates. The identification was further confirmed by checking the type-specimen description in the Ellis and Messina Catalogue of Foraminifera (Ellis and Messina, 1940-2015).

## Pore density and diameter measurement

The surface sediment samples collected along a coast perpendicular transect covering the continental shelf to abyssal region of the south-eastern Arabian Sea, by using the multicorer, were used. The samples ranged from shallow to deep water depth (50-2750 m) covering the intermediate oxygen-depleted zone. The top 5 cm of the sediment was sub-sampled at 1 cm interval and immediately preserved in ethanol rose-Bengal solution. All the living specimens (rose-Bengal stained) of *Bolivina seminuda* were picked from the top 5 cm sections. The bigger and intact specimens (25 of each station and section) were selected for pore-size analysis. The entire specimen as well as the close-up view of the last chamber was taken by using Scanning Electron Microscope (SEM) (Figure 3.3A). For further measurements of detailed study of pore-patterns, all SEM images were processed to count the number of pores and pore-diameter in a fixed grid (180×180 pixel) by using NIS Element BR 4.10.00 software (Figure 3.3B The last formed chamber of each specimen was chosen for pore-size analysis because it is the true representative of gas exchange intensity (Richirt et al., 2019). The maximum diameter of all the pores within the grid (180×180 pixel) was measured. The average pore-diameter was calculated for each section at a station.

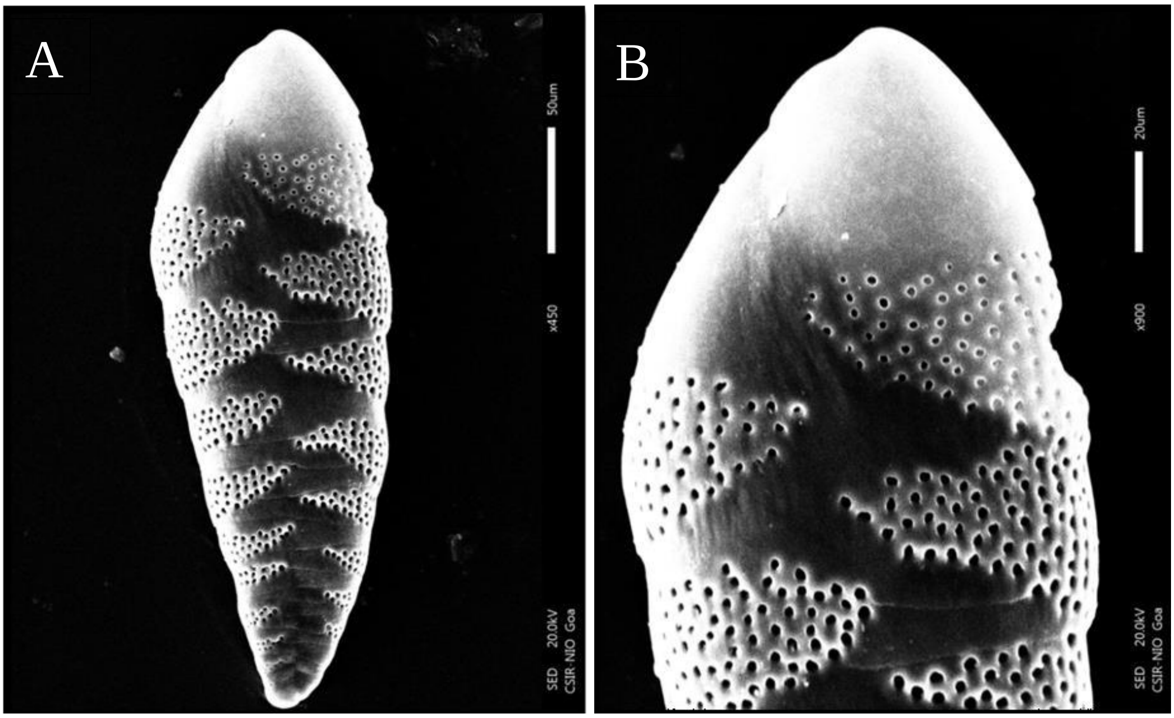

**Figure 3.3: Scanning Electron Micrograph of *Bolivina seminuda* (A) and magnified image of the last chamber for pore density and diameter measurements (B).**

## Total and inorganic carbon and nitrogen analysis

A small amount (~5 g) of sediment from unstained half was freeze-dried and powdered by using a clean agate mortar-pestle for carbon analysis. The total inorganic carbon (TIC) in the sediment was analysed by using coulometer (CM 5015 CO2) and the total carbon was analysed by using elemental analyser (FLASH 2000; Thermo Scientific). The organic carbon (%$C_{org}$) was calculated by subtracting TIC from total carbon. The dissolved oxygen concentration in the seawater, along with other physico-chemical parameters (salinity, temperature, pH) at the sediment-water interface were measured, wherever possible. The dissolved oxygen concentration at the sediment-water interface could not be measured at five stations as the multi-core tubes did not contain sufficient water. Additional bottom water parameters (temperature and dissolved oxygen) were downloaded from the World Ocean Circulation Experiment (WOCE) Global Hydrographic Climatology (Gouretski and Koltermann, 2004) by using Ocean Data View (ODV) software (Schlitzer, 2011) (Figure 3.1).

# Chapter-4: Response of inner shelf benthic foraminifera community to different concentrations of oxygen: A laboratory culture experiment

## Introduction

The dissolved oxygen concentration in seawater is one of the main environmental factors, that control marine community structure (Nigam et al., 2007; Gooday et al., 2010). The dissolved oxygen concentration in the ocean, especially shallow continental shelves, is likely to deplete in near future, due to anthropogenic eutrophication (Sarmiento et al., 1998; Keeling and Garcia, 2002; Meier et al., 2011). The dissolved oxygen is vital for the marine organisms, especially benthic organisms. The marine sediments on the shelf and slope are dominated by unicellular calcareous benthic foraminifera. Benthic foraminifera, form a substantial fraction of the marine benthic community and are an important driver of the global carbon cycling. Benthic foraminifera are strongly influenced by oxygen. In deeper regions, dissolved oxygen and organic matter are the dominant factors that control benthic foraminiferal distribution (Jorissen, 1995; 2007). The dissolved oxygen concentration affects the vertical distribution of a majority of benthic foraminifera, except for some deep infaunal species (Ernst and Zwaan, 2004). The abundance of infaunal benthic foraminifera, increases in low oxygen environments (Kaiho, 1994; Bernhard and Sen Gupta, 1999; Singh et al., 2006; 2015). The dissolved oxygen also modulates benthic foraminifera morphology. Benthic foraminiferal distribution along the western continental margin of India, suggests increased relative abundance of infaunal angular asymmetrical foraminifera in oxygen deficient zones (Nigam et al., 2007). Further, foraminifera in the oxygen deficient environment are characterized by high pore density (Glock et al., 2011; Kuhnt et al., 2013; Tetard et al., 2017). In view of the strong influence of dissolved oxygen, benthic foraminifera are often used to trace the geologic extent of both coastal and deep water oxygen deficient zones (Sen Gupta et al., 1996; Bernhard et al., 1999; den Dulk et al., 2000; Platon et al., 2005). The application of benthic foraminifera is also suggested to have an added advantage to delineate oxic (>1.5 mL/L $O_2$) and suboxic (0.3-1.5 mL/L $O_2$) facies, which is difficult from organic carbon/sulphur ratio, sulphur isotopes and trace elements (Kaiho, 1994).

The application of benthic foraminifera to reconstruct dissolved oxygen concentration in the past, is however, complicated by the fact that the dissolved oxygen, often co-varies with organic matter, in a majority of the marine settings. Therefore, several authors suggest that both dissolved oxygen and organic matter flux are the important factors controlling the abundance and distribution of benthic foraminifera (Douglas, 1981; Sen Gupta et al., 1981; Caralp, 1984; Lutze and Coulbourn, 1984; Bernhard, 1986; Corliss and Chen, 1988; Niensted and Arnold, 1988; Gooday, 1990; Jorissen et al, 1992; Sjoerdsma and van der Zwaan, 1992; Wahyudi and Minagawa, 1997; Jorissen, 1999, Caulle et al., 2014; Singh et al., 2018; Suokhrie et al., 2020). Therefore, from the field studies, it is difficult to delineate the effect of dissolved oxygen from that of the organic matter, on benthic foraminiferal community. The widely accepted TRophic conditions and Oxygen Concentrations (TROX) model also incorporated both the dissolved oxygen and organic matter content to explain the changes in benthic foraminifera community (Jorissen et al., 1995). A more efficient application of foraminifera to reconstruct the past dissolved oxygen concentration requires assessment of the effect of only dissolved oxygen on benthic foraminiferal community. Additionally, increasingly hypoxic to anoxic conditions have been reported from the marginal marine regions of several oceans (Diaz, 2001; Naqvi et al., 2010). The implications of such hypoxic to anoxic regions on benthic community have to be assessed (Vaquer-Sunyer and Duarte, 2008). Therefore, the objective of this work was to understand the effect of different concentrations of dissolved oxygen on marginal marine benthic foraminifera in controlled laboratory culture experiment.

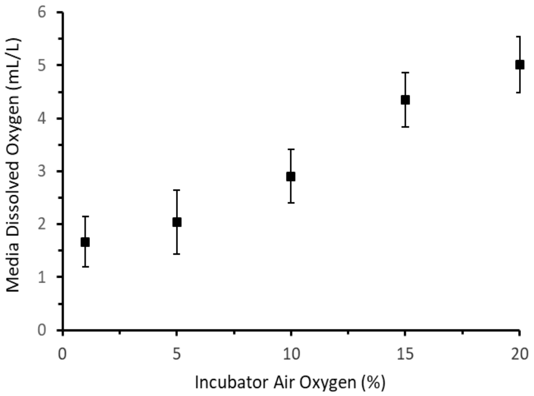

**Figure 4.1: Dissolved oxygen concentration in the seawater media at different percentage of oxygen in the air inside the incubators.**

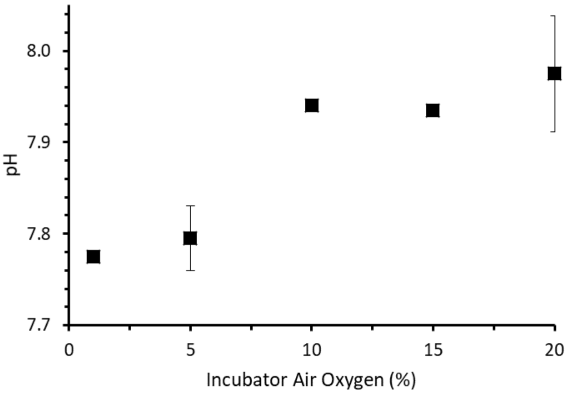

**Figure 4.2: The seawater pH in the flask with sediments, at different percentage of oxygen in the air inside the incubator.**

# Results

## Physico-chemical parameters

The dissolved oxygen concentration in the seawater media was measured at the respective oxygen percentage in the incubator air. The dissolved oxygen co-vary with ambient air oxygen (Figure 4.1). The linear relationship between ambient air and dissolved oxygen concentration was confirmed with the T-test.

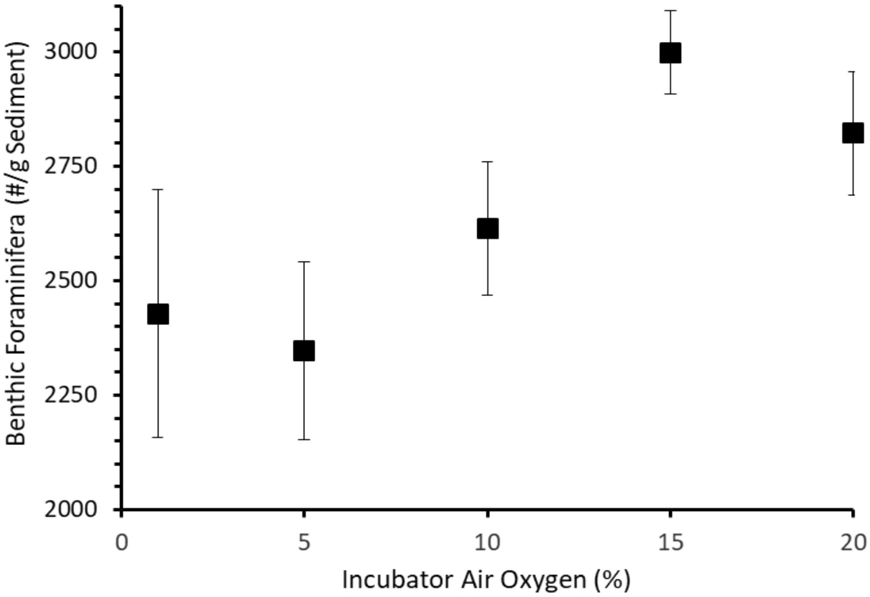

**Figure 4.3: Absolute abundance of benthic foraminifera (individual/g sediment) at different oxygen concentrations**.

The dissolved oxygen concentration varied from 1.67 mL/L at 1% to 5.01 mL/L at 20% air oxygen concentration. The pH was measured in the conical flasks that contained sediments. The pH decreased from 7.98 to 7.78, with a drop in oxygen percentage from ambient air concentration to 1% (Figure 4.2).

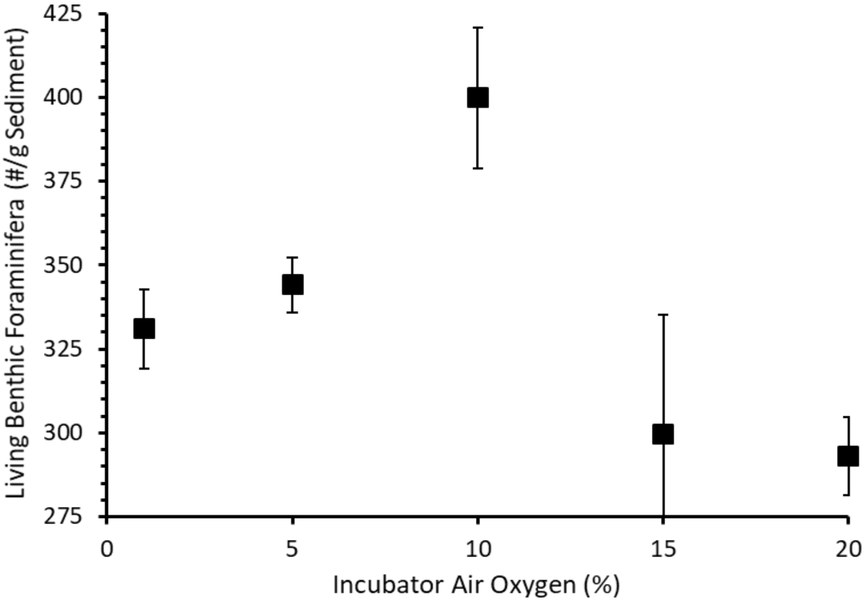

**Figure 4.4: Absolute abundance of living benthic foraminifera (individual/g sediment) at different oxygen concentrations.**

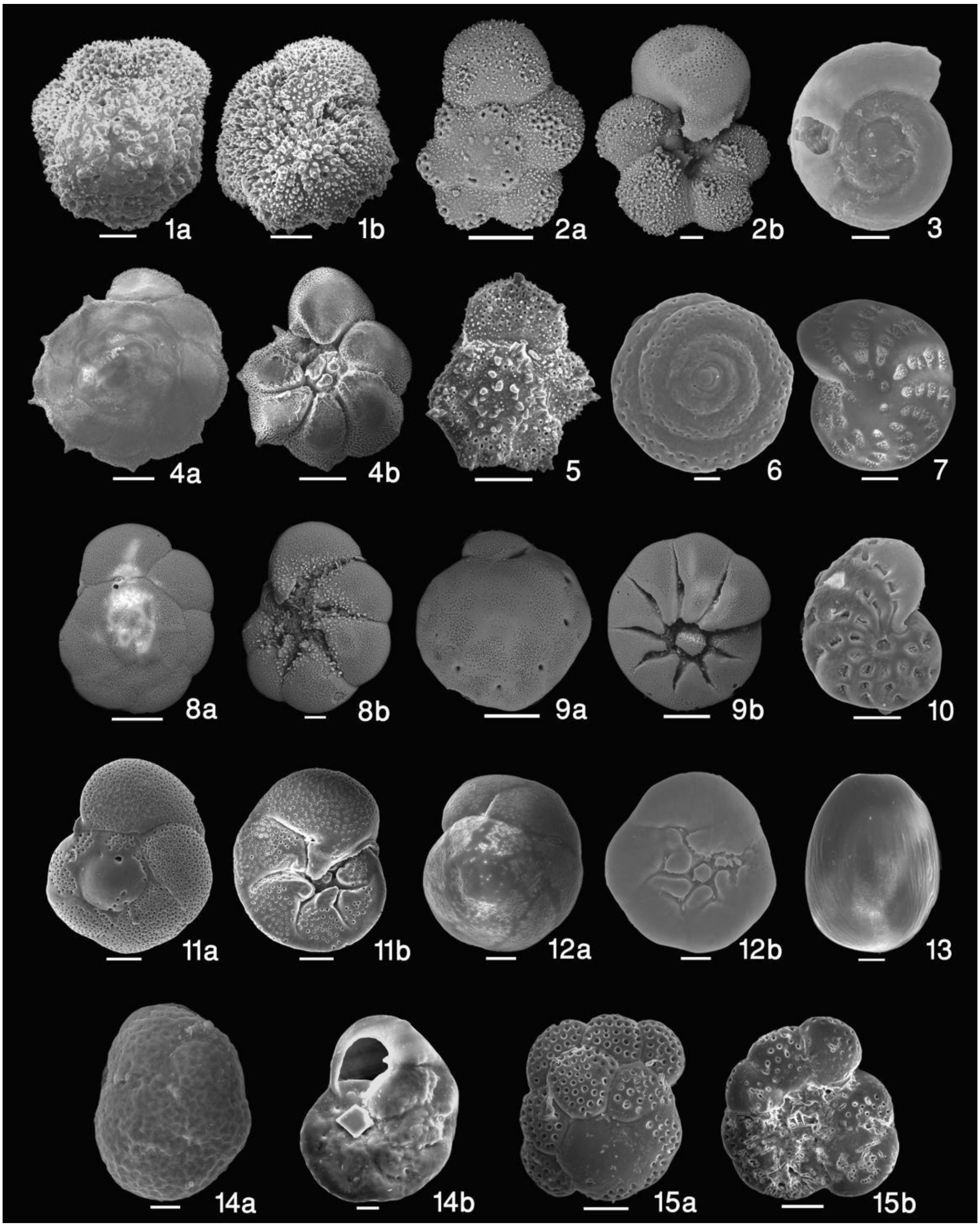

**Figure 4.5A: Living benthic foraminifera found in the sediments used for the experiment. 1. *Murrayinella murrayi,* a-dorsal view; b- ventral view; 2. *Murrayinella nicaraguaensis,* a-dorsal view; b-ventral view; 3. *Cornuspira involvens; 4. Pararotalia nipponica,* a-dorsal view; b- ventral; 5. *Pararotalia sp.;* 6. *Cornuspira sp.;* 7. *Elphidium crispum; 8. Ammonia tepida,* a-dorsal view; b- ventral view; 9. *Ammonia sobrina,* a-dorsal view; b- ventral view; 10. *Elphidium advenum 11. Rosalina leei,* a-dorsal view; b- ventral view; 12. *Rosalina globularis,* a-dorsal view; b- ventral view; 13. *Fissurina multicostata;* 14. *Rosalina sp.,* a-dorsal view; b- ventral view; 15. *Cymbaloporetta plana,* a-dorsal view; b- ventral view. The scale bar is 100 µm.**

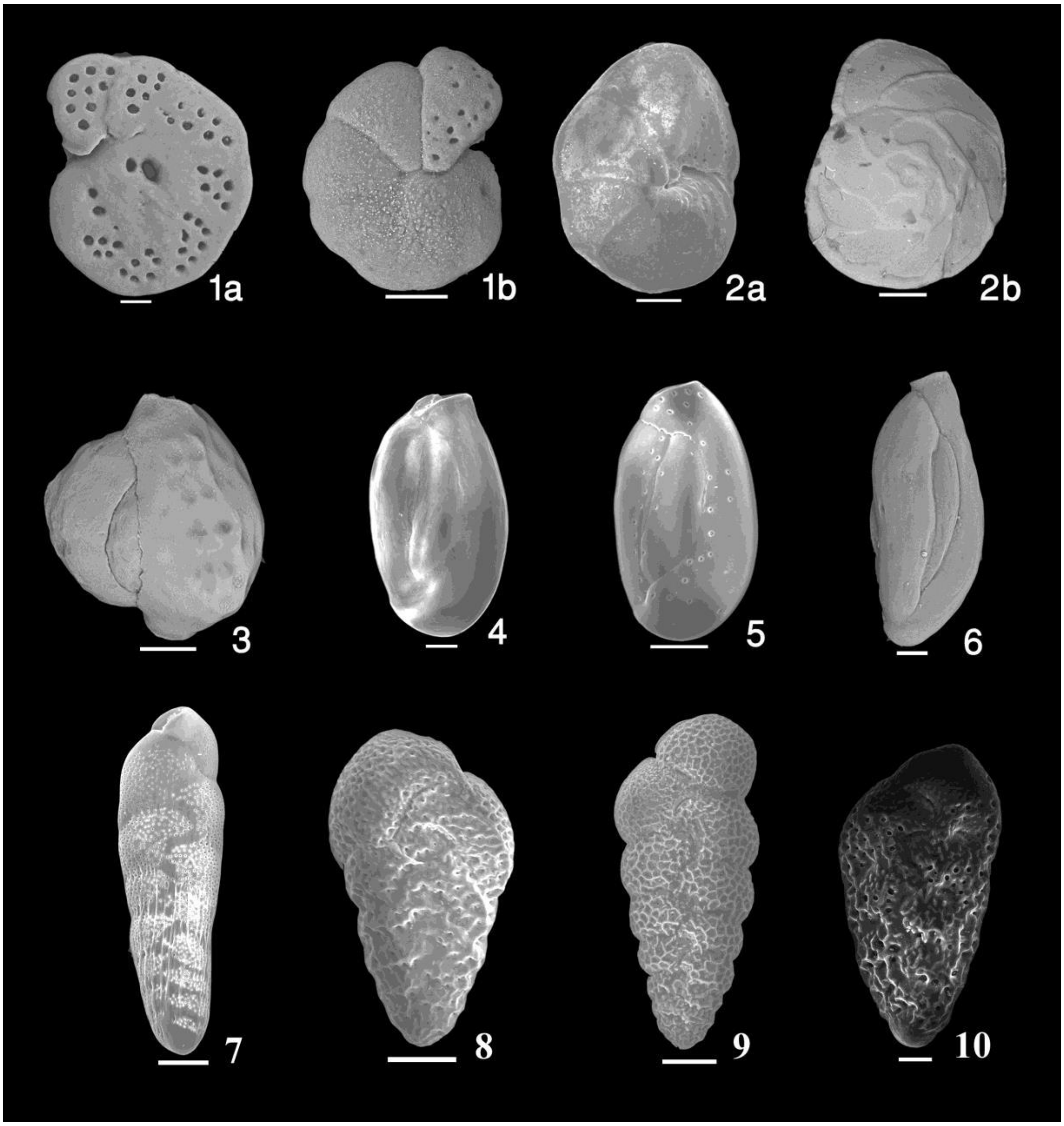

**Figure 4.5B: 1. *Cibicides refulgens,* a-dorsal view; b- ventral view; 2. *Eponides repandus,* a-dorsal view; b- ventral view; 3. *Quinqueloculina parkeri;* 4. *Quinqueloculina seminulum* 5. *Quinqueloculina oblonga*; 6. *Quinqueloculina sp*; 7. *Bolivina striatula*; 8. *Bolivina dilatata*; 9. *Bolivina subspinescens*; 10. *Bolivina sp*. The scale bar is 100 µm.**

## Dead and living (rose-Bengal stained) benthic foraminifera

The absolute abundance of dead benthic foraminifera varied from a minimum of 2348 individual/g sediment at 2.04 mL/L dissolved oxygen concentration to a maximum of 2998 individual/g sediment at 4.35 mL/L dissolved oxygen concentration. The dead benthic foraminiferal abundance decreased with decreasing dissolved oxygen concentration (Figure 4.3).

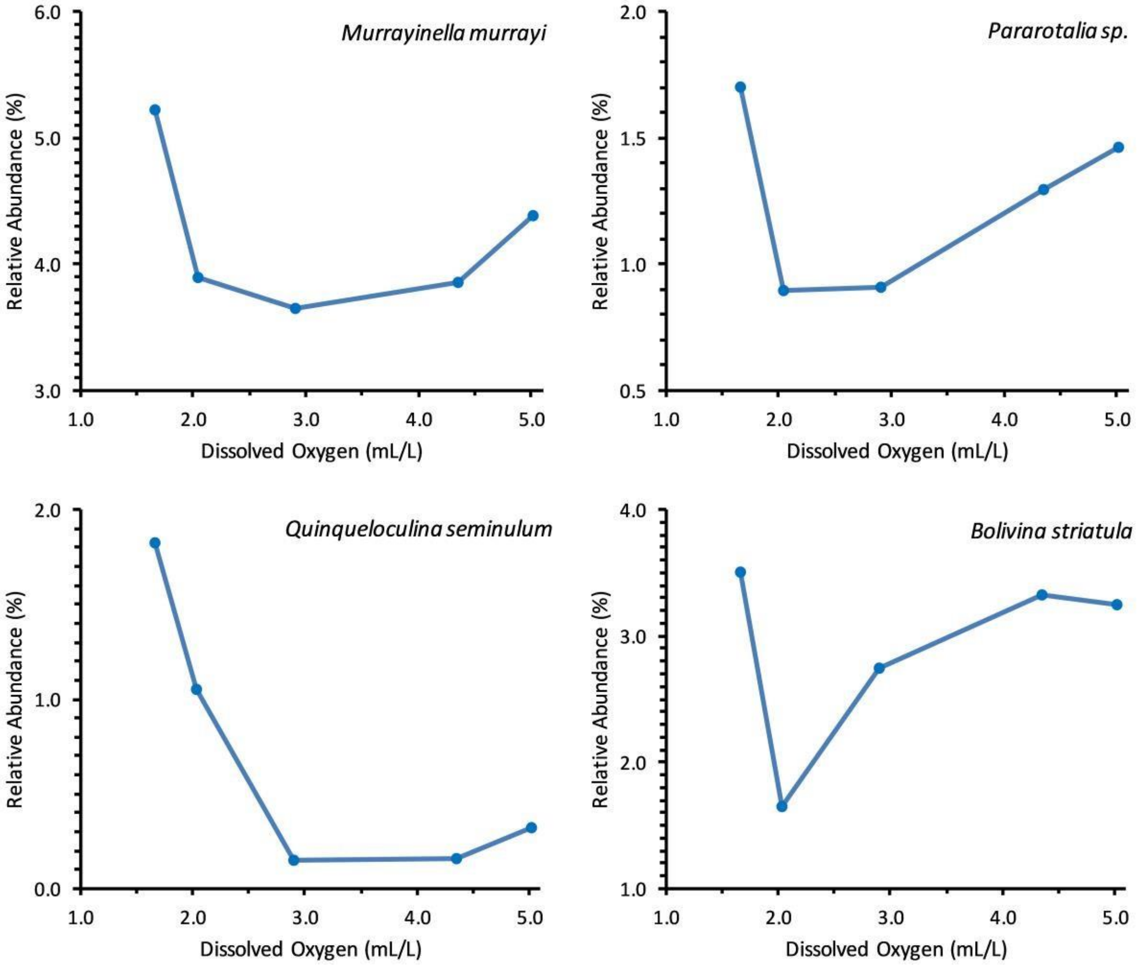

**Figure 4.6: Relative abundance of *Bolivina striatula, Murrayinella murrayi, Quinqueloculina seminulum* and *Pararotalia* sp. decreased with the initial decrease in dissolved oxygen concentration, but peaked at the lowest dissolved oxygen concentration.**

The living benthic foraminifera were an order of magnitude lower than dead benthic foraminifera (Figure 4.4). The living benthic foraminifera were abundant at 2.91 mL/L oxygen (400 individuals/g sediment) and the lowest in control set (293 individuals/g sediments). The living benthic foraminifera population increased from 1.67 mL/L to 2.91 mL/L oxygen concentration. However, a decreasing trend was observed in sets subjected to 4.35 mL/L, and 5.01 mL/L oxygen concentration (Figure 4.4). A significant variation from t-test for independent variables was seen at 1, 5 and 10% air oxygen, as compared to the control set.

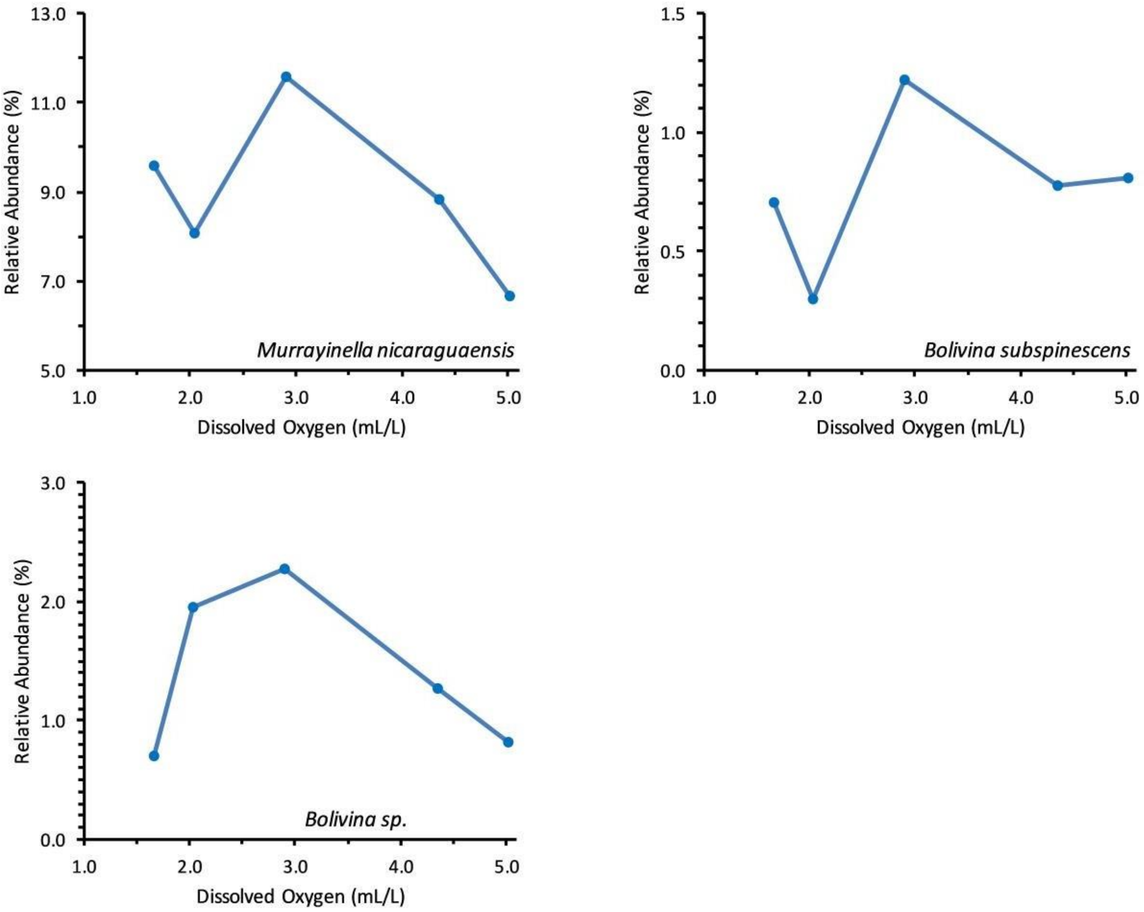

**Figure 4.7: Relative abundance of three living benthic foraminifera, namely *Murrayinella nicaraguaensis, Bolivina subspinescens* and *Bolivina* sp. was the maximum at the intermediate dissolved oxygen concentration (2.91 mL/L).**

## Relative abundance of benthic foraminifera

A total of 27 species (*Ammonia tepida, Ammonia sobrina, Bolivina variabilis, Bolivina striatula, Bolivina subspinescens, Bolivina dilatata, Bolivina sp., Cibicides refulgens, Cornuspira involvens, Cornuspira sp., Cymbaloporetta plana, Elphidium advenum, Elphidium crispum, Eponides repandus, Fissurina multicostata, Murrayinella murrayi, Murrayinella nicaraguaensis, Pararotalia sp., Pararotalia nipponica, Quinqueloculina seminulum, Quinqueloculina parkeri, Quinqueloculina oblonga, Quinqueloculina sp., Rosalina leei, Rosalina globularis, Rosalina sp.* and agglutinated) of living benthic foraminifera were found (Table 4.1; Figure 4.5A and 4.5B). Out of these 27 species, *Pararotalia nipponica* constitutes more than half of the total living benthic foraminifera at all dissolved oxygen concentrations. The relative abundance of *P. nipponica* varied from 65.5% at 2.91 mL/L dissolved oxygen to 74.5% at 2.0 mL/L dissolved oxygen concentration. *Murrayinella nicaraguaensis* was the second most dominant living benthic foraminifera, with the relative abundance varying from 6.7% at the highest dissolved oxygen concentration to 11.6% at 2.91 mL/L dissolved oxygen.

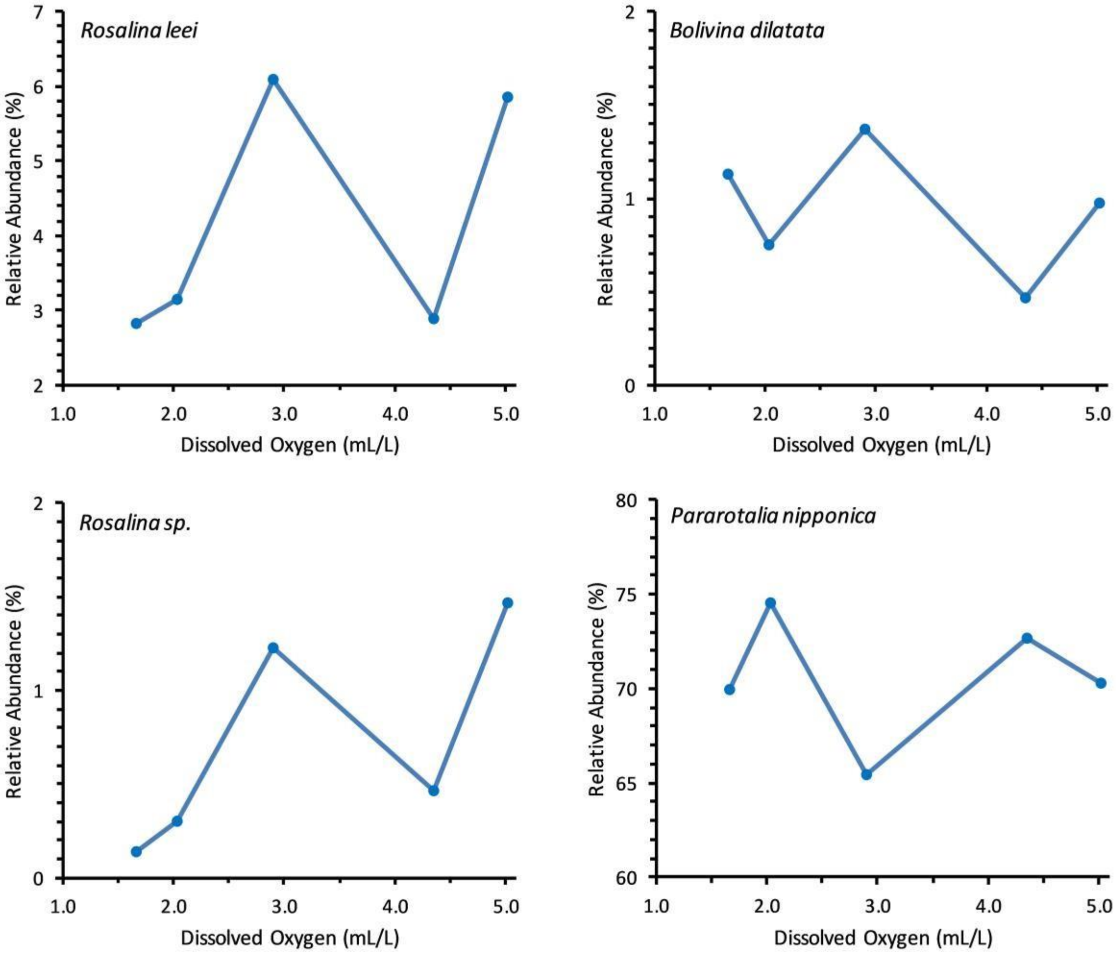

**Figure 4.8: Relative abundance of *Rosalina leei, Rosalina sp.*, *Bolivina dilatata* and *Pararotalia nipponica* does not show any definite trend with different dissolved oxygen concentrations.**

Three different patterns of benthic foraminiferal response to different concentrations of dissolved oxygen were observed. The relative abundance of *Bolivina striatula*, *Murrayinella murrayi*, *Quinqueloculina seminulum* and *Pararotalia* sp. decreased with the initial decrease in dissolved oxygen concentration, but peaked at the lowest dissolved oxygen concentration (Figure 4.6). The lowest relative abundance of all these species was at 2.04 mL/L or 2.91 mL/L dissolved oxygen concentration. In contrast to these species, the relative abundance of three living benthic foraminifera, namely *Murrayinella nicaraguaensis*, *Bolivina subspinescens* and *Bolivina* sp. was the maximum at the intermediate dissolved oxygen concentration (2.91 mL/L) (Figure 4.7). A few other dominant species *Pararotalia nipponica*, *Rosalina leei*, *Rosalina* sp. and *Bolivina dilatata* do not have any definite trend with different dissolved oxygen concentrations (Figure 4.8).

## Discussion

The dissolved oxygen concentration measured from the experimental and control sets were in the range of 1.67 to 5.01 mL/L. Kaiho (1994) recognized dissolved oxygen conditions depending on the oxygen concentration as anoxic (0-0.1 mL/L), dysoxic (0.1-0.3 mL/L), suboxic (0.3-1.5 mL/L), low oxic (1.5-3.0 mL/L) and high oxic (3.0-6.0 mL/L). Considering these different categories, our experimental sets were in the range of low oxic to high oxic conditions. The distribution and abundance of benthic foraminifera in the shallow water regions is influenced by the grain size, currents, temperature, salinity and organic matter flux (Mendes et al., 2004; Bouchet et al., 2009; Murray, 2006; Scott et al., 2001). All these parameters were similar for all the sets, thus ruling out any differential influence of these parameters on living benthic foraminifera in the experiment. The seawater salinity in all the sets was similar (34.5 to 35.5 psu). Therefore, any change in the size or loss of ornamentation or dissolution of foraminifera test because of salinity changes, as reported by Boltovskoy et al. (1991) and Kurtarkar et al. (2011) were ruled out. The pH increased from the experimental set (1-15%) to the control set from 7.78-7.98 psu. Therefore, the pH change was expected to significantly influence benthic foraminiferal assemblage, as low pH is detrimental to foraminiferal tests (Saraswat et al., 2015). A clear decrease in the absolute abundance of benthic foraminifera (dead + living) is thus attributed to a drop in pH with decreasing dissolved oxygen concentration. The thin walled, fragile benthic foraminifera tests are highly susceptible to dissolution in low pH seawater. Thus the decreasing dissolved oxygen concentration will result in poor preservation of dead benthic foraminifera tests due to a drop in pH.

**Table 4.1: List of all living benthic foraminifera found in the sediments along with their maximum relative abundance at the respective dissolved oxygen concentration in the culture experiment.**

| Species | Maximum Relative Abundance (%) | Dissolved Oxygen (mL/L) |
|---|---|---|
| *Ammonia sobrina* | 0.32 | 5.01 |
| *Ammonia tepida* | 0.30 | 2.04 |

| | | |
|---|---|---|
| *Bolivina striatula* | 3.51 | 1.67 |
| *Bolivina subspinescens* | 1.22 | 2.91 |
| *Bolivina variabilis* | 0.46 | 2.91 |
| *Bolivina sp.* | 2.27 | 2.91 |
| *Cibicides refulgens* | 0.48 | 4.35 |
| *Cornuspira involvens* | 0.65 | 4.35 |
| *Cornuspira sp.* | 0.33 | 5.01 |
| *Cymbaloporetta plana* | 0.65 | 5.01 |
| *Elphidium advenum* | 0.30 | 2.04 |
| *Elphidium crispum* | 0.00 | NA |
| *Eponides repandus* | 0.33 | 4.35 |
| *Fissurina multicostata* | 0.75 | 2.04 |
| *Murrayinella murrayi* | 5.23 | 1.67 |
| *Murrayinella nicaraguaensis* | 11.57 | 2.91 |
| *Pararotalia nipponica* | 74.55 | 2.04 |
| *Pararotalia sp.* | 1.70 | 1.67 |
| *Quinqueloculina oblonga* | 0.97 | 5.01 |
| *Quinqueloculina parkeri* | 0.30 | 2.04 |
| *Quinqueloculina seminulum* | 1.83 | 1.67 |
| *Quinqueloculina sp.* | 0.28 | 1.67 |
| *Rosalina globularis* | 0.60 | 2.04 |
| *Rosalina leei* | 6.08 | 2.91 |
| *Rosalina sp.* | 1.47 | 5.01 |
| Agglutinated | 0.64 | 4.35 |

The maximum abundance of living benthic foraminifera was at 10% air oxygen. The abundance at 1% and 5% air oxygen, although lower than that at 10% air oxygen, was higher than that at 15% and 20% air oxygen. Interestingly, the lowest abundance of living benthic foraminifera was at the highest oxygen concentration. This non-linear response of living benthic foraminiferal abundance is intriguing. The salinity, temperature and sediment organic carbon were similar and within the error limits in all the sets and thus are not the factors influencing the observed patterns in living benthic foraminifera. The very low abundance at the highest oxygen concentration is attributed to the high predatory pressure. The dissolved oxygen at the two highest concentrations was sufficient (high oxic) to support microbenthic community. The prevalence of macrobenthic community adversely affects benthic foraminifera (Levin, 2003, Enge et al., 2016). The dissolved oxygen concentration at 10% air oxygen dropped to low oxic levels. The low oxic concentration of dissolved oxygen is detrimental to macrobenthic community, thus leading to its decreased population and thus reduced predatory pressure. With this argument, the living benthic population should peak at the lowest dissolved oxygen levels. The living benthic foraminiferal abundance, however, decreased at the two lowest oxygen concentrations. We suggest that the macrobenthic community was already completely suppressed at low oxic levels and any further decrease in oxygen concentration was inconsequential. The living benthic foraminiferal abundance, then should have remained same as that at low oxic level, if not increase further. The further decline in living benthic foraminiferal population is attributed to the inability of the epifaunal benthic foraminifera to survive under low oxic and suboxic condition. The living benthic foraminiferal population was dominated by epifaunal *Pararotalia nipponica*. The other abundant species were *Murrayinella murayi, Murrayinella nicaraguaensis, Pararotalia sp*. and *Bolivina striatulata*. *Pararotalia nipponica* is a robust species and is present at almost all oxygen concentrations with >60% abundance. The epifaunal foraminifera are adapted to well oxygenated waters. The drop in oxygen to suboxic levels, adversely affected *P. nipponica*, leading to higher mortality and thus overall low living benthic foraminiferal population. In the marine oxygen deficient regions, population of infaunal forms increases significantly. Such a significant increase in this experiment was not observed as the original marginal marine benthic foraminiferal community had a very low abundance of infaunal foraminifera. Therefore, the overall response of benthic foraminifera to different oxygen concentrations will depend on the community structure, especially the abundance of infaunal and epifaunal foraminifera. As the marginal marine benthic foraminiferal community is dominated by robust epifaunal species, the initial impact of low dissolved oxygen will be minimal, unless the levels decease to a drastically low concentration.

All the living benthic foraminifera found in the waters off Goa, belong to 12 genera, namely *Ammonia, Bolivina, Cibicides, Cornuspira, Cymbaloporetta, Elphidium, Eponides, Fissurina, Murrayinella, Pararotalia, Rosalina, Quinqueloculina*. The agglutinated specimens could not be identified. A majority of these genera are widely reported from the shallow water inner shelf regions. *Ammonia* belonging to family Rotaliidae Ehrenberg, 1839, are infaunal and mostly found in muddy or sandy sediments on the inner shelf regions. They are herbivore and survive in brackish, marine as well as hypersaline waters. Their survival temperature range is from 0-30°C. *Ammonia sobrina* and *Ammonia tepida* were reported in the sediments. *Bolivina* d'Orbigny, 1839 belongs to family Bolivinidae Glaessner, 1937. *Bolivina* are infaunal – epifaunal and are found in muddy marine sediments on the inner (0-100 m) and outer shelf (100-200 m) (Murray, 1991). The species belonging to *Bolivina* show a negative response to light (Kitazato, 1981). They are found in (Murray, 1991). Four species, namely *Bolivina striatula*, *Bolivina dilatata*, *Bolivina subspinescens* and *Bolivina* sp. were found in the sediments collected from the inner shelf region of Goa. The genus *Cibicides* belongs to family Cibicididae Cushman, 1927. The epifaunal specimens of this genus are found attached to hard surface in shelf-bathyal region. The species belonging to this genus are reported from cold to warm temperatures and from 0-2000 m water depth (Murray, 1991). Only *Cibicides refulgens* was found in this study area. The genus *Cornuspira* belonging to family Cornuspiridae Schultze, 1854, is epifaunal and widely reported from the marginal marine and shelf environments (Murray, 2006). *Cornuspira involvens* was found in the present study. *Cymbaloporetta* belongs to family Cymbaloporidae Cushman, 1927 and is abundant on the shelf. The species of this genus are temporarily attached to seagrass and algae but are mobile in search of food or during reproduction. A few species of this genus also have special float chambers (Murray, 2006). *Cymbaloporetta plana* is abundant in the sediments. *Elphidium* belonging to family Elphidiidae has two types of species, namely keeled and non-keeled. The keeled specimens are epifaunal, and abundant on the inner shelf. They are found from 0-50 m water depth and can survive in temperate to warm temperatures and 35-40 psu salinity (Murray, 1991). The non-keeled specimens are infaunal and found in brackish to hypersaline marshes and lagoons. They are also found in inner shelf regions (Murray, 1991). We report *Elphidium advenum* (Cushman, 1922) and *Elphidium crispum* (Linnaeus, 1758) in the experimental sediments. *Eponides* belonging to family Eponididae Hofker, 1951 is a free or clinging epifaunal genus, abundant on the shelf to abyssal areas. The *Eponides* species can survive in cold to temperate regions (Murray, 1991). *Eponides repandus* was found in the study area. *Fissurina* genus belongs to family Ellipsolagenidae A. Silvestri, 1923. The specimens of this genus are infaunal and free living (Murray, 1991). Only one species, namely *Fissurina multicostata* was found in the sediments. *Murrayinella* belongs to family Glabratellidae Loeblich and Tappan, 1964. The specimens of this genus are common in shallow waters (Nomura and Takayaniagi, 2000). *Murrayinella murrayi* and *Murrayinella nicaraguaensis* were abundant in the sediments. *Pararotalia* belongs to family Rotaliidae Ehrenberg, 1839 and can survive in temperatures ranging from 22-29°C. *Pararotalia* are epifaunal and mostly found in very fine sand in the inner shelf region (Murray, 1991). We found a couple of species, namely *Pararotalia nipponica* (Asano, 1954) and *Pararotalia* sp. *Rosalina* belongs to family Rosalinidae Reiss, 1963. The specimens are epifaunal and are mostly clinging or attached to hard substrates. They are herbivore as well as omnivore and survive in temperate to warm marine waters on the inner shelf (Murray, 1991). We report three species namely *Rosalina leei*, *Rosalina globularis* and *Rosalina* sp.

Only those species, with relative abundance ≥1% are discussed in detail. Based on the relative abundance, species were categorized in a few distinct groups. One group comprised of the species with the maximum relative abundance at the lowest dissolved oxygen concentration. The relative abundance of *Bolivina striatula, Murrayinella murrayi, Quinqueloculina seminulum* and *Pararotalia sp.* decreased with the depleting oxygen concentration (Figure 4.6). Incidentally, the relative abundance of these species peaked at the lowest dissolved oxygen concentration. The relative abundance pattern suggests, either that the species belonging to this group prefer oxygen deficient environment, or the inability of other species to thrive at the lowest dissolved oxygen concentration. The severely detrimental effect of low dissolved oxygen on other species, will lead to the dominance of *B. striatula, M. murrayi, Q. seminulum* and *Pararotalia sp.*, although the overall population of these species may also have declined. Another group includes the species with the maximum relative abundance at the medium dissolved oxygen concentration. The relative abundance of three living benthic foraminifera, namely *Murrayinella nicaraguaensis*, *Bolivina subspinescens* and *Bolivina sp.* increases with the drop in dissolved oxygen concentration from 5.01 mL/L to 2.91 mL/L (Figure 4.7). Subsequently, the relative abundance decreases with the further drop in dissolved oxygen to 1.67 mL/L. The increase in the relative abundance of *M. nicaraguaensis*, *B. subspinescens* and *Bolivina sp.* with the initial decrease in dissolved oxygen concentration is attributed to reduced bioturbation due to declined macrobenthic activity. The subsequent drop in the relative abundance suggests that *M. nicaraguaensis*, *B. subspinescens* and *Bolivina sp.* do not prefer dissolved oxygen concentration ≤2.04 mL/L. No apparent trend was observed in the relative abundance of *Rosalina leei*, *Rosalina sp.*, *Bolivina dilatata* and *Pararotalia nipponica* at different dissolved oxygen concentrations (Figure 4.8). *Pararotalia nipponica* is the most dominant species at all dissolved oxygen concentrations. It is interesting to note that different species belonging to the same genus had a different response to various dissolved oxygen concentrations. Thus the benthic foraminiferal response to dissolved oxygen is species specific.

## Conclusions

We assess the response of marginal marine benthic foraminiferal community to different oxygen concentration. We report a non-linear response of the living benthic foraminiferal assemblage to different levels of oxygen concentration. The pattern is attributed to the combined effect of the presence of macrobenthic community as well as the dominance of epifaunal benthic foraminifera in the population. The dominance of epifaunal *Pararotalia nipponica* at all the oxygen concentrations, is attributed to its very high abundance in the original community as well as resilience to a wide range of oxygen levels. We report that the decreasing dissolved oxygen concentration will cause a poor preservation of calcareous benthic foraminifer shells due to a concomitant drop in pH.

# Chapter-5: Effect of phytodetritus on shallow-water benthic foraminifera under two warming scenarios

## Introduction

The dissolved oxygen and food are the two most important factors affecting benthic foraminifera. The organic matter remains of the dead macrofauna, as well as living diatoms, algae, are the food for benthic foraminifera. It has also been reported that many small organisms (algae and bacteria) were consumed by sub-surface foraminifera living in near shore sands. A few benthic species are very selective feeders where as others can survive on a variety of nutritional resources. The feeding habits change with the availability of food, as when fresh phytodetritus was unavailable, some species utilized more degraded food resources (Hegger, 1990). Many deep-dwelling species living beyond 5 cm within the sediments, can utilize more refractory organic matter than shallow infaunal/epifaunal species (Corliss and Emerson, 1990, Gooday et al., 1990). Deposit feeding, wherein sediments are collected and divided into small parcels and ingested, is one of the common feeding mechanisms of foraminiferida. Three types of food preferences are recognized, namely 1. Fresh phytodetritus, 2. Phytodetritus selectively but sedimentary organic matter as well when fresh phytodetritus is absent, and 3. Sedimentary organic matter at random (deposit feeders) (Nomaki et al., 2009).

Foraminifera adopt a variety of behavioural strategies to obtain their food (Lipps, 1983). They feed at low trophic levels, consuming mainly planktonic, other detritus and bacteria (Gooday et al., 1992) and sediment-dwelling species move actively across or within the substrate in search of food particles (Kitazato, 1988). Others are permanently attached to substrate and gather food from the surrounding area using their pseudopodia. Some epibenthic species can probably switch tactics from suspension to surface deposit feeding depending on flow conditions (Lipps 1983, Cedhagen, 1988). Response to the food is species specific as few species grow more when fed and others show increased growth when unfed (Lee et al. 1991). Foraminiferal response to phytodetritus was different to different depths in the ocean as well (Witte et al., 2003). Seasonal variation in foraminiferal population and assemblages are associated with the type and amount of food. Therefore, it is necessary to understand the effect of phytodetritus on foraminifera populations. Such studies will help to understand the reduced abundance of few species in low productivity conditions (Linshy et al., 2007).

The oxygen availability effected short term vertical distribution whereas long term benthic foraminiferal distribution depends on food availability (Ernst et al., 2005). In the tropical oceans, the organic matter and dissolved oxygen are closely coupled. The excessive organic matter flux in the regions of restricted water circulation, creates oxygen deficient zones. Therefore, it is difficult to assess the relative effect of dissolved oxygen and the organic matter flux on benthic foraminifera, from field studies. Foraminifers are consumed by a wide variety of organisms including selective and non-selective deposit feeders and specialized predators and probably represent an important link between lower and higher levels of deep-sea food webs. Thus the post-depositional changes significantly alter the living population, hindering the precise assessment of the effect of ambient parameters on living benthic population. Additionally, a few studies demonstrated that the foraminiferal growth, reproduction and thus abundance depends on food as well as the ambient temperature (Kurtarkar et al., 2019). Limited culture experiments have been conducted to understand the effect of various amount of food supply at different temperature, on foraminiferal growth and abundance. This laboratory experiment was an effort to understand the effect of different amount of organic matter on shallow water benthic foraminifera.

## Results

All weekly measurements were taken under inverted microscope and NIS- Element software to track their growth (Table 5.1).

**Table 5.1 – Details of weekly measurements.**

| No. of weeks | Temperature Range 27 - 32ºC | Temperature Range 25º - 30ºC |
|---|---|---|
| 1st week | All juveniles were of same size (~65-80 µm) at all the feed concentrations. | All juveniles were of same size (~63-72 µm) at all the feed concentrations. |
| 2nd week | The diameter of all fed as well as unfed specimens increased. However, | The diameter of all specimens fed 200 cells/mL was 116 µm and that |

| | | |
|---|---|---|
| | the growth was lowest in case of unfed specimens (98 µm) as compared to fed specimens (112 µm). | of the unfed specimens was 109 µm. The specimens fed 50 cells/mL were the smallest (101 µm). |
| 3rd week | The specimens fed 100 cells/mL and 25 cells/mL attained an average test-size of 151 µm. The specimens fed with 200 cells/mL and unfed specimens had similar test-size. The smallest test-size was of specimens fed with 50 cells/mL. | The maximum test diameter was in specimens maintained at 100 cells/mL. The specimens at other feed concentrations as well as unfed specimens also grew. Again smallest test-size was of the specimens fed with 50 cells/mL. |
| 4th week | The specimens of all four feed concentrations attained similar test diameter whereas the unfed specimens were comparatively smaller (144 µm). | The specimens at 50 cells/mL and all unfed specimens were smaller (148 µm) as compared to the specimens fed with 200 cells/mL (169 µm). |
| 5th week | Maximum test-size (168 µm) was in the specimens at 200 cells/mL. The unfed specimens did not grow well. | The maximum growth (189 µm) was in specimens fed with 100 cells/mL and unfed specimens were the smallest (154 µm). |
| 6th week | Again, the maximum growth (182 µm) was in the specimens fed with the maximum food (200 cells/mL). Unfed specimens grew up to 160 µm. | The specimens at 100 cells/mL had a larger test-size (92 µm). Other specimens also grew well. Unfed specimens did not grow well. |
| 7th week | All fed and unfed specimens grew well. | The maximum test diameter (200 µm) was attained by the specimens fed with 100 cells/mL. Unfed specimens did not grow. |
| 8th week | No noticeable growth was observed in fed and unfed specimens. | Some growth in the specimens fed with 200 cells/mL and 50 cells/mL. No growth in the unfed specimens. |
| 9th week | The test-size of some fed specimens increased to 205 µm (especially of | Growth was observed in all the specimens including fed and unfed. |

| | | |
|---|---|---|
| | 200 cells/mL). Unfed specimens also grew to 168 µm. | The maximum test diameter (213µm) was of the specimens fed with 200 cells/mL. |
| 10th week | The maximum test diameter (220 µm) was attained by specimens fed with 200 cells/mL. Unfed specimens also survived but their test-size was smaller than fed specimens. | All the fed specimens grew well. Although the unfed specimens also grew but their test-size was comparatively smaller (189 µm). |

### A. 27°C to32°C

After 1st week, all specimens of *Rosalina globularis*, including fed and unfed sets, grew well. The largest average diameter was attained by the specimens fed with 200 cells/mL and 25 cells/mL. The unfed specimens grew the least. Surprisingly, the unfed specimens continued to grow. By the 3rd week, all unfed specimens attained an average diameter of 142 µm, comparable with other sets. Subsequently, from 4th week onwards, a distinct difference was observed in the growth of unfed specimens, as compared to the fed specimens. Also, the specimens fed with the largest amount of food, grew the most. The average diameter of the all fed specimens was comparable until 8th week. A perceptible difference in the average diameter of the specimens fed with 200 cells/mL food, and other sets was observed from 9th week onwards (Figure 5.1).

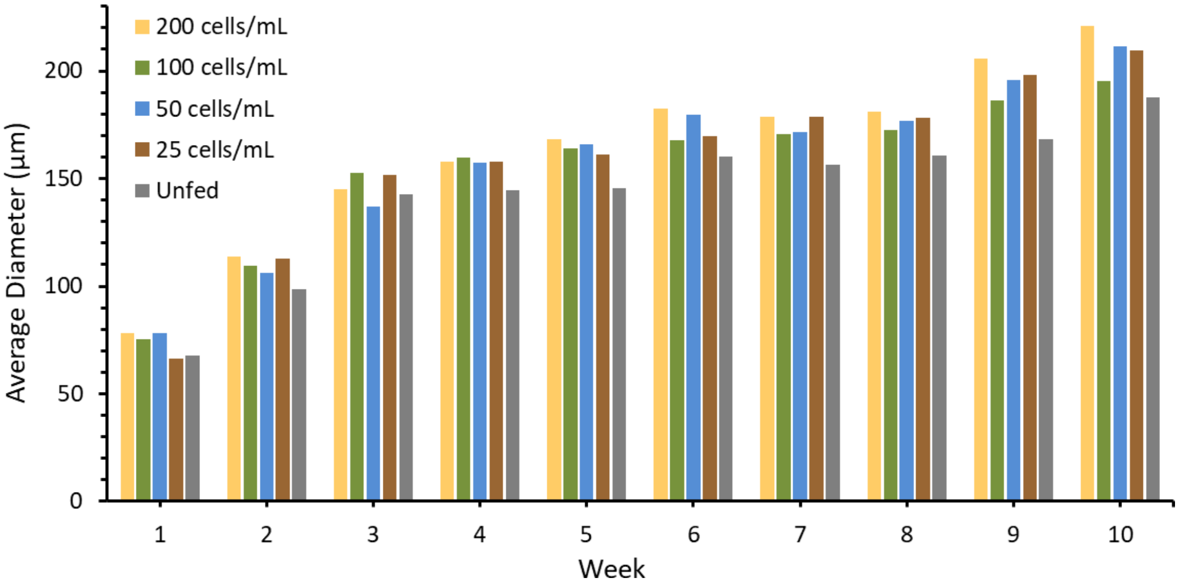

**Figure 5.1: The average maximum diameter of the specimens fed with different concentration of diatom cells at warm temperature (27°C to 32°C).**

At the end of the experiment, specimens fed with 200 cells/mL attained the maximum growth (220 µm). Surprisingly, the unfed specimens also grew and attained the average diameter of 187 µm. The growth of specimens fed with 25 cells/mL food was less as compared to the specimens fed with 200 cells/mL of food, but was comparable with those fed with 50 cells/mL food. A large increase in all sets was observed in the first 3 weeks of the experiment. A gradual but small increase in diameter was observed between 3rd to 5th weeks. The growth almost stopped between 6th to 8th week. A sudden spurt in growth was again observed in the 9th and 10th week. The difference in the growth rate of specimens during different weeks is attributed to the growth stages of foraminifera. The juveniles grow at a comparatively faster rate, than mature specimens.

### B. 25°C to30°C

A relatively more gradual growth until 5th week was observed in specimens maintained at 2°C lower temperature range. The growth of unfed specimens stopped after 5th week, whereas other fed specimens continued to grow until 9th week. A distinct gradation in the growth of unfed to the most fed specimens was observed at this temperature range (Figure 5.2). The unfed specimens attained an average diameter of 162 µm, whereas the specimens fed with 200 cells/mL food grew to an average diameter of 213 µm.

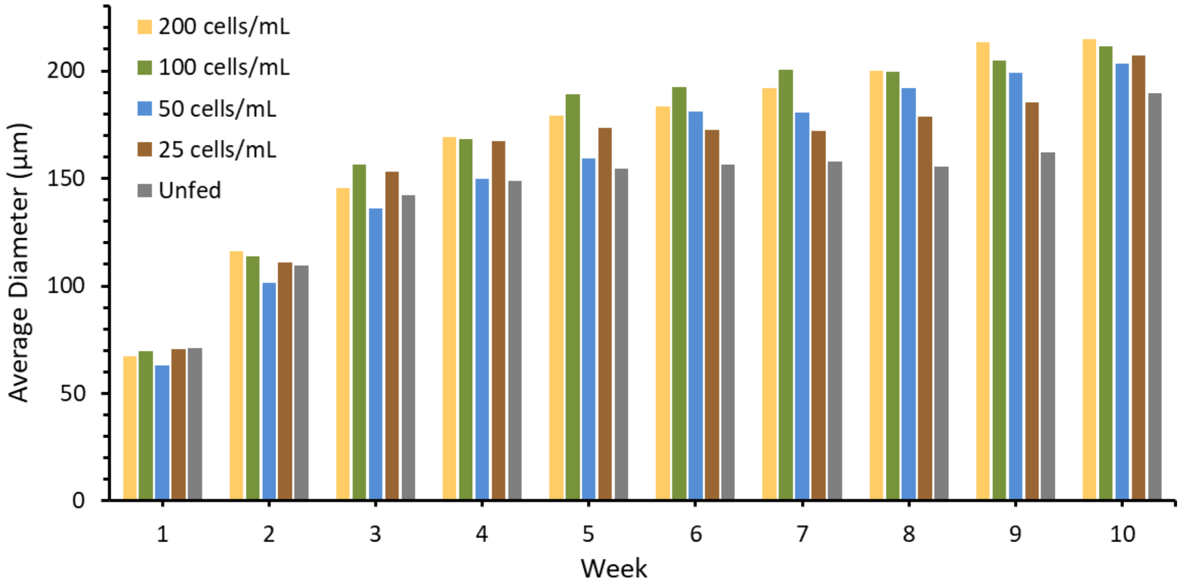

**Figure 5.2: The average maximum diameter of the specimens fed with different concentration of diatom cells at low temperature (25°C to 30°C).**

## Discussion

All specimens at all fed and unfed sets, as well as ambient temperatures grew during the experiment. The growth of unfed specimens was surprising. As 0.45 µm filtered seawater was used as culture media, the unfed specimens are likely to have fed on the bacteria and virus. Foraminifera feed on a variety of organic matter present in the sediments, including bacteria, small algae, cysts, pollen grains, plant and fungal fragments, protozoans, crustaceans, metazoans, algal endosymbiosis (Goldstein and Alve, 2011). Mostly they are omnivores, herbivores, carnivores or scavengers and few shallow water species show cannibalism, parasitism, mixotrophy and osmotrophy (Lipps, 1983, Capriulo et al., 1990, Gooday et al., 1990). There are several previous reports suggesting that benthic foraminifera feed on bacteria and virus. The growth of unfed specimens was stunted. Therefore, it can be concluded that *Rosalina globularis* test size would be smaller if specimens are in scarcity of food for long time.

The larger average test diameter attained by the specimens at the temperature range of 27°C to 32°C, suggests that *Rosalina globularis* prefers warmer environment for growth. However, the mortality rate was also high at 27°C to 32°C temperature range. In contrast to that, the reproduction was more in specimens grown at 25°C to 30°C temperature range. The different type of food and amount of phytodetritus play an important role in foraminiferal population and growth rate. Additionally, the survival rate is also governed by the food type. Food quantity is also responsible for foraminifera migrational activity and it is species specific (Gross, 2000). The increased supply of food increases foraminiferal abundance (Heinz et al., 2001).

The food supply and temperature modulated not only the growth, but also the mortality and reproduction in *Rosalina globularis.* Many previous culture studies on benthic foraminifera suggest that long term changes in foraminiferal diversity and abundance is closely associated with the amount of food and further that this response is species specific. Sometimes, foraminifera of same genus but different species show different food preferences. If there was no food supply for long duration, foraminifera survived even for longer time but reproduction rate reduced (Hemleben and Kitazato, 1995). If continuous food supply is available, foraminifera grew with higher reproduction rate. It was also seen that certain species belonging to the same genus responded differently when fed with living and dead cells. The food uptake rate was not only species specific, but even changed with individuals of different sizes of the same species. On the basis of this experiment, *Rosalina globularis* is likely to increase in abundance during summer monsoon when productivity is high and diatom flux is at their maximum.

## Conclusion

The high amount of phytodetritus (200 cells/mL) is responsible for the maximum growth in *Rosalina globularis* as this concentration represent the diatom flux during the summer monsoon in the field area. A good growth was also recorded in test-size of *Rosalina globularis* fed with pre-monsoon phytodetritus (50-100 cells/mL). Specimens which were fed 25 cells/mL (post-monsoon phytodetritus) were smaller than other specimens. The growth of unfed specimens of *Rosalina globularis* confirms the previous studies that unfed foraminifers can also survive for longer duration in the absence of phytodetritus and this response is species specific. The survival of *Rosalina globularis* specimens without additional food provides clues about how a few species could survive during low productivity in the sea. It is highly likely that the unfed *Rosalina globularis* fed on algae or bacteria present in sea water. From the relationship between temperature and *Rosalina globularis*, with the simultaneous change in phytodetritus, it can be concluded that *Rosalina globularis* prefers higher temperature range (27ºC-32ºC) for their growth. But in long term they prefer lower temperature range (25ºC-30ºC) as the mortality rate is higher at higher temperature. Therefore, it is clear that *Rosalina globularis,* a shallow water benthic species, prefers high productivity regions for their growth. As the mortality is higher at high temperature, summer monsoon is perfect season for their optimum growth, as during this time, phytodetritus flux is high and the temperature is also comparatively low. Although *Rosalina globularis* can survive in less phytodetritus flux, long term food scarcity could lead to smaller test size of *Rosalina globularis*.

# Chapter-6: Effect of dissolved oxygen and organic matter on benthic foraminifera

## Introduction

Foraminifera are a hugely successful group of predominantly marine, single-celled microorganisms (Saraswat and Nigam, 2013). Because of their excellent fossil record and their sensitivity to environmental conditions, they have been extensively used in paleoceanographic studies. Application of foraminifera in paleoecology requires a good understanding of the influence of different ambient parameters on their communities. Benthic foraminifera are influenced by a variety of parameters including dissolved oxygen, food availability (Corliss, 1985; Gooday and Turley, 1990; Jorissen et al., 1992; 1995; Sen Gupta and Machain-Castillo, 1993; Mackensen et al., 1995; McCorkle et al., 1997; Schmiedl et al., 1997; Van der Zwaan et al., 1999; Den Dulk et al., 2000; Nomaki et al., 2008; Mackensen, 2012; Mackensen and Schmiedl, 2016), temperature, salinity (Nigam et al., 1992; 2008; Kurtarkar et al., 2011; Saraswat et al., 2011; 2015; Manasa et al., 2016), depth (Corliss and Chen, 1988), sediment texture (Alve and Murray, 1999), and others (Boltovskoy et al., 1991; Murray, 2006; 1991). The response of benthic foraminifera to ambient parameters is studied by comparing the characteristics of recent fauna with the prevailing conditions. Benthic foraminifera in the top 1 cm of the sediments are usually studied for this purpose. As infaunal benthic foraminifera can survive up to 10-15 cm deep in the sediments (Corliss, 1985; Jannink et al., 1998), more attention is being paid to understand their sub-surface habitat. Ideally, living (i.e. rose-Bengal stained) benthic foraminifera are better suited than the dead assemblage, to understand the influence of prevailing physico-chemical conditions. Even though the surface distribution of ‘total’ (i.e. living and fossil) foraminiferal assemblages has been extensively studied from several parts of the northern Indian Ocean (see Bhalla et al., 2007 for extensive review; Gupta, 1994; Nigam and Khare, 1999; Saidova, 2007; De and Gupta, 2010; Jayaraju et al., 2010; Panchang and Nigam, 2014; Manasa et al., 2016), studies on the vertical distribution of living benthic foraminifera are still limited.

With the prevalence of both the seasonal shallow water hypoxia and perennial intermediate depth oxygen minimum zone, the northern Indian Ocean can help in understanding the effect of varying levels of oxygen and associated parameters on benthic foraminifera. Earlier, increase in relative abundance of angular asymmetrical benthic foraminifera (usually with serially arranged chambers) that corresponds with infaunal benthic foraminifera, at depths with low dissolved oxygen concentration, was reported from the eastern Arabian Sea, based on benthic foraminiferal distribution in the spade core-top samples (Nigam et al., 2007). The study was based on total benthic foraminifera and considered only top 2 cm of the sediments. The study of living benthic foraminiferal distribution in surface sediments, can help to better understand the effect of low oxygen on its abundance. But such studies are limited and have provided contrasting results. For example, a study from off Pakistan continental margin showed that infaunal benthic foraminifera, including *Uvigerina ex gr. U. semiornata* and *Bolivina aff. B. dilatata* dominate the upper few centimeters of sediments. The same study reported a major faunal changes at 300, 500 and 1000 m water depth (Schumacher et al., 2007). Contrary to that, no clear trend in benthic foraminifera with bathymetry and ecological parameters was found on the Murray ridge (Caulle et al., 2014), suggesting regional differences. The oxygen concentration in seawater and not the organic carbon related to primary productivity, was reported to be the prime factor influencing benthic foraminiferal abundance (Caulle et al., 2015). At the Oman margin, foraminiferal abundance in the oxygen minimum zone (OMZ) was higher as compared to a deeper well-oxygenated location (Gooday et al., 2000).

So far, only a handful of studies, on living (Rose-Bengal stained) benthic foraminiferal distribution, have been carried out from the Indian margin (Suresh Gandhi et al., 2007; Gandhi and Solai, 2010; Caulle et al., 2015; Suokhrie et al., 2017). Moreover, limited attempts have been made to understand sub-surface distribution of living benthic foraminifera from the northern Indian Ocean, except off the Pakistan margin (Caulle et al., 2014; Enge et al., 2014; Erbacher and Nelskamp, 2006; Gooday et al., 2009; Jannink et al., 1998; Larkin and Gooday, 2008; Schumacher et al., 2007) off Oman (Hermelin and Shimmield, 1990; Gooday et al., 2000) and off the Indian margin (Caulle et al., 2015). Additional studies on the vertical distribution of living benthic foraminifera across the OMZ of the northern Indian Ocean will help to improve the application of benthic foraminifera in paleoclimatic studies, especially to reconstruct past changes in intensity and spatial extent of OMZ. Therefore, the main objective of this work was to document the vertical distribution of living (stained) benthic foraminifera across the oxygen minimum zone in the Gulf of Mannar, western Bay of Bengal and the eastern Arabian Sea.

## Results

## Gulf of Mannar

### Dissolved oxygen (DO)

The WOCE seasonal (October) dissolved oxygen data downloaded by using ODV software was compared with the actual measurements at the time of sampling, wherever sufficient water from sediment-water interface was available. The values matched well. The dissolved oxygen varied from 3.48 ml/l at the deepest station (MC-58) to 0.53 ml/l at station MC-07 (Figure 6.1). The dissolved oxygen was ≤2.0 ml/l between 152 m and 1550 m, thus suggesting it to be the range of oxygen minimum zone in this region (shaded zone in Figure 6.1).

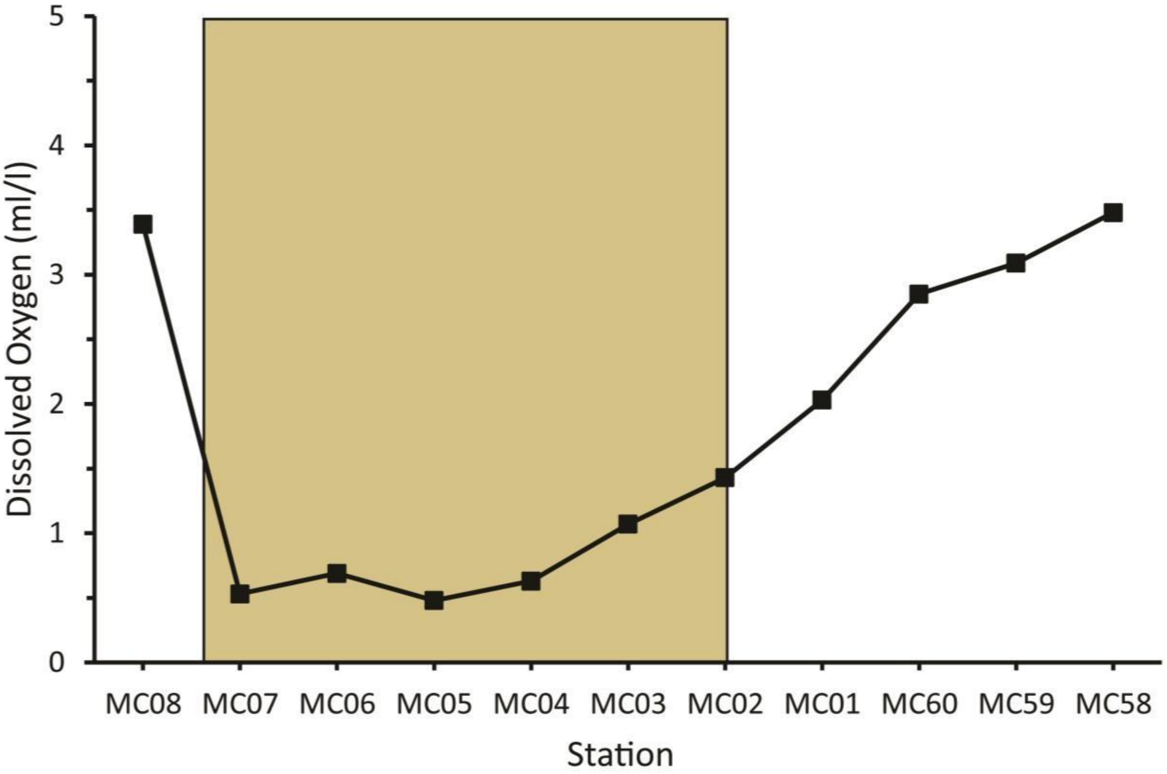

**Figure 6.1: The bottom water dissolved oxygen concentration at the sampling stations. The values are for the month of October when the sampling was done. The shaded region marks the oxygen minimum zone.**

### Organic carbon (%$C_{org}$)

The organic carbon increased with depth in both the core top (0-1 cm) and sub-surface (1-2 cm) samples, except MC-59 and MC-60 (Figure 6.2). The highest %$C_{org}$ (6.8%) in core top samples was at the deepest station (MC-58, 2750 m) and the lowest was at the shallowest station (MC-08, 58 m). The %$C_{org}$ was lower in the 1-2 cm section as compared to top sediment layer. Interestingly, %$C_{org}$ in both the core top (0-1 cm) and 1-2 cm section was same at station MC-59 (Figure 6.2).

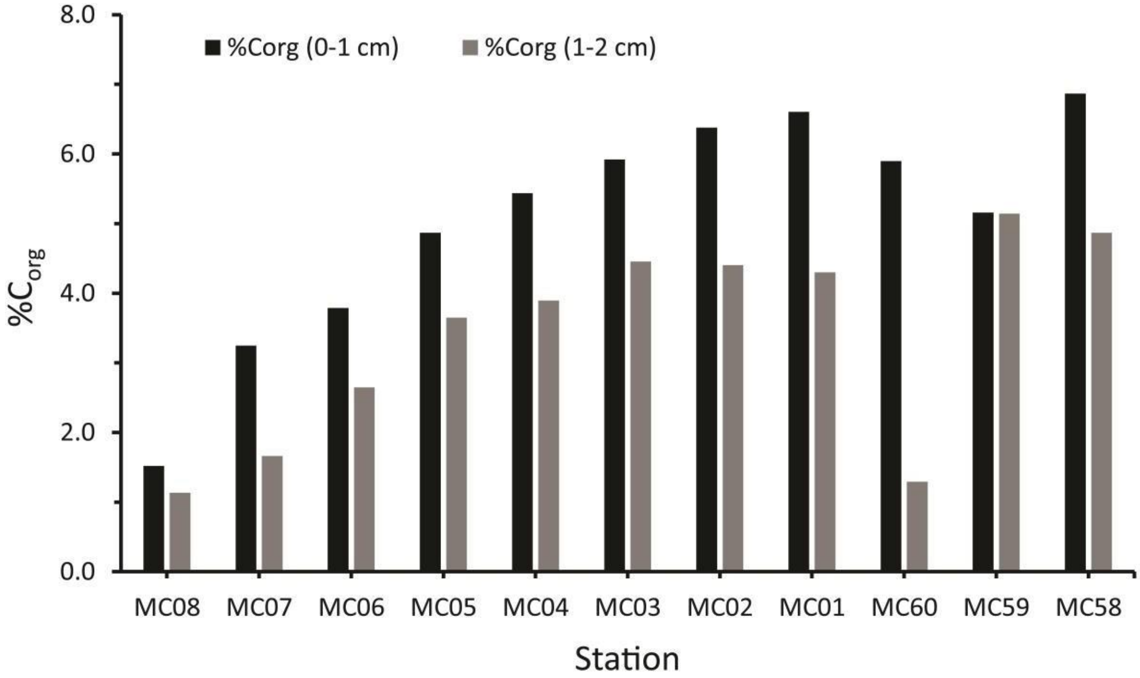

**Figure 6.2: The organic carbon (%$C_{org}$) in core top (0-1 cm) and sub-surface (1-2 cm) samples, at the sampling stations.**

### Absolute abundance of benthic foraminifera

The vertical foraminifera stock (sum of top 5 cm sediment) varied from 46 specimen/g sediment to 3480 specimen/g sediment (Figure 6.3). The highest abundance of 3480 specimen/g sediment was at station MC-06 (215 m water depth). The vertical foraminifera stock was relatively more in intermediate than in shallow and deeper depths.

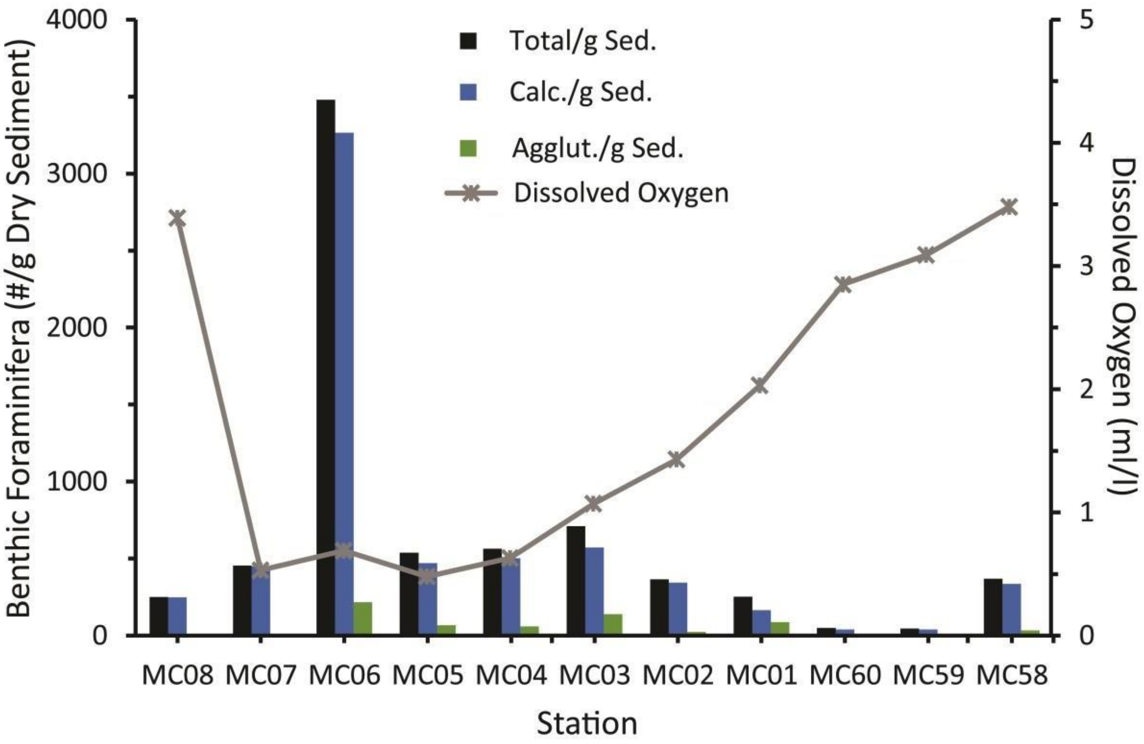

**Figure 6.3: Absolute abundance of vertical stock of living total, calcareous and agglutinated benthic foraminifera. The dissolved oxygen concentration at each station is plotted as line diagram.**

### Contribution to the vertical stock

The core top section of MC-03 contained the highest percentage (95%) of total vertical foraminiferal stock and the lowest abundance in core-top section was in MC-60 (Figure 6.4). In the majority of the core top samples (0-1 cm), the living foraminiferal abundance was more (>85%), as compared to sub-surface samples, except a couple of deeper stations (Figure 6.4). It is interesting to note that foraminiferal abundance in 1-2 cm section was almost an order of magnitude lower than the core top section. Further deeper sections (>2 cm) contained much less living fauna, except a few stations. Most of the sub-surface samples (1-2 cm, 2-3 cm, 3-4 cm, 4-5 cm), contained <10% living benthic foraminiferal population, except a few station in the shelf (MC-07 and MC-08) and slope (MC-58, MC-59 and MC-60). At these stations, the deeper sections contain >10%, and in a few cases ≥60% of the total living population. The evident exceptions were stations MC-59, where 30% of the living benthic population was in 3-4 cm section and MC-07 where 15% of the fauna was in the 3-4 cm and 22% fauna was in the 4-5 cm section. Incidentally, all of these stations with a substantially abundant living benthic foraminiferal population in deeper sections were outside the OMZ.

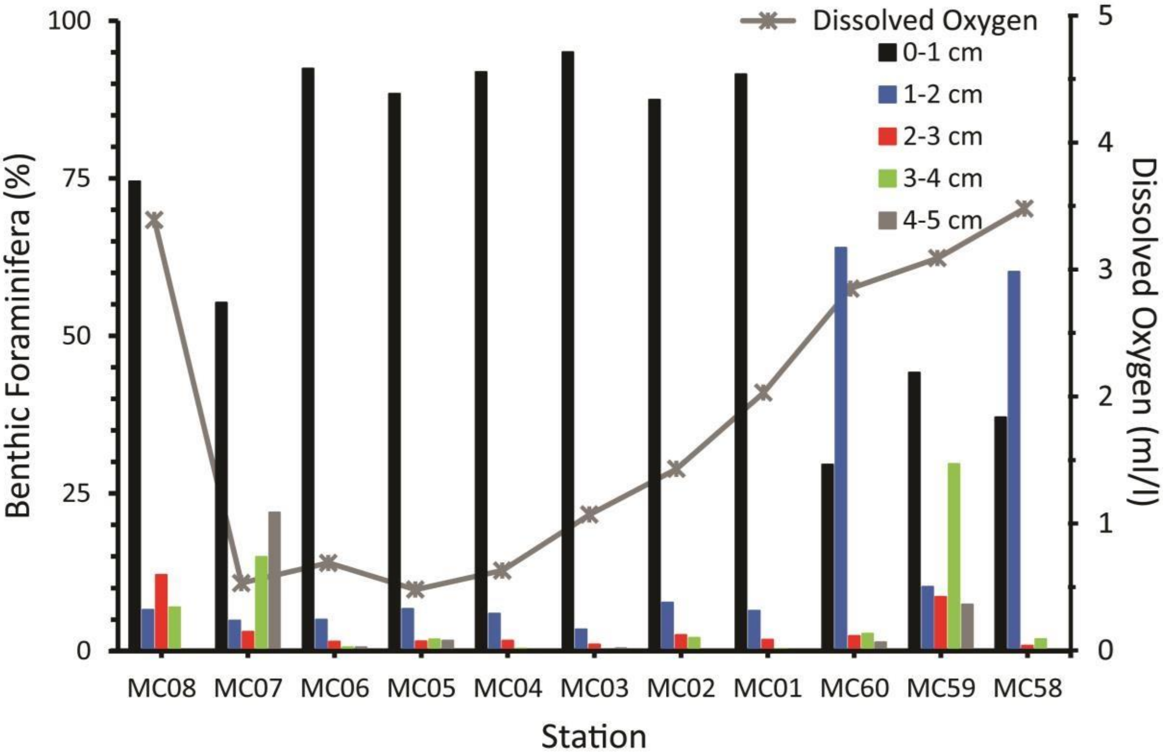

**Figure 6.4: The relative contribution of benthic foraminifera in different sections of the sediments, to the total vertical stock. The dissolved oxygen concentration at each station is plotted as line diagram.**

### Living calcareous and agglutinated benthic foraminifera (Vertical Stock)

The calcareous foraminifera dominated the vertical foraminifera stock at all the stations. They constituted ~80% of the living fauna at all but one station (Figure 6.5). The calcareous foraminifera constitute the entire living benthic foraminiferal population at the shallowest station (MC-08, 58 m). The lowest calcareous abundance (65%) is at MC-01 (1550 m water depth). On the other hand, agglutinated foraminifera are much less abundant, with an average ~12% of total living population in vertical foraminifera stock. The agglutinated foraminiferal abundance is relatively high in the slope region (stations between 215 m to 2080 m), with a maximum (~35%) at MC-01 (1550 m) (Figure 6.5).

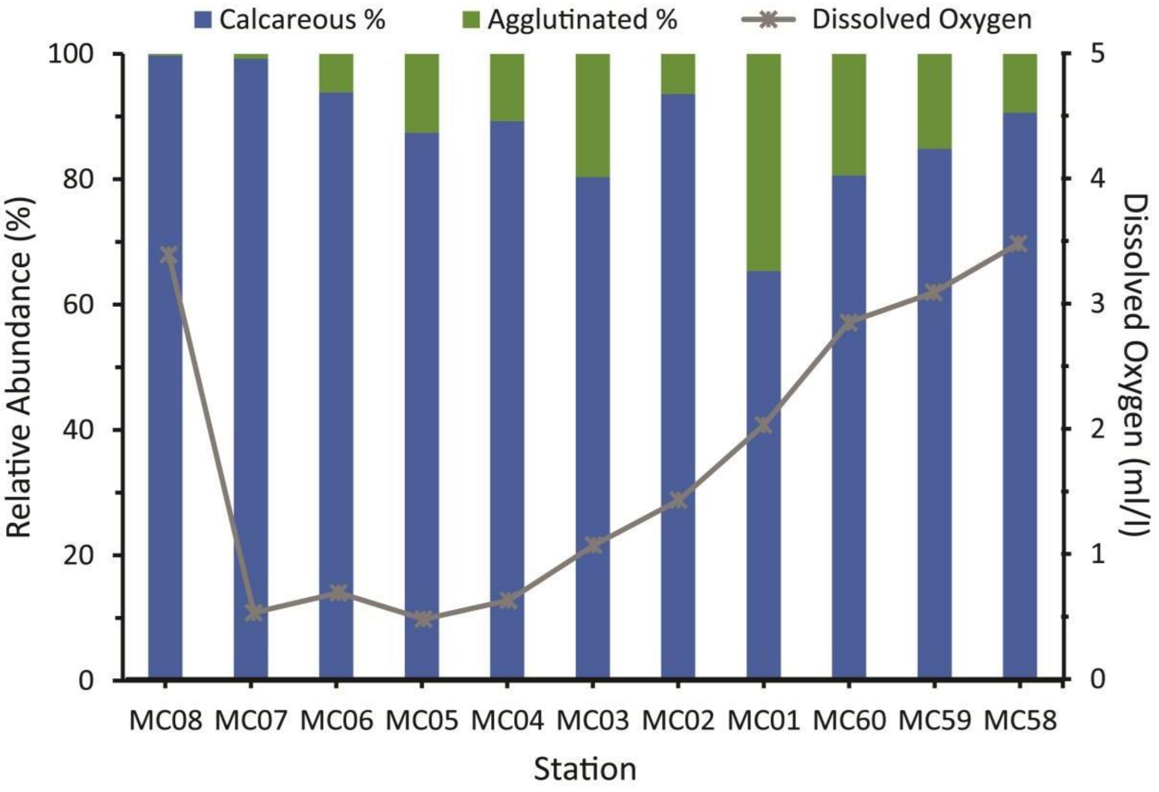

**Figure 6.5: The relative abundance of living calcareous and agglutinated benthic foraminiferal morpho-groups in the vertical stock in the Gulf of Mannar, southeastern Arabian Sea. The dissolved oxygen concentration at each station is plotted as a line diagram.**

### Calcareous benthic foraminifera (Living)

A comparison of living benthic foraminiferal distribution in surface (0-1 cm) and sub-surface (>1 cm) sediments indicates that on an average, calcareous foraminifera in core-top (0-1 cm) samples constitute ~62% of the vertical foraminifera stock (Figure 6.6). The contribution of living calcareous foraminifera to the vertical stock drastically decreases in sub-surface samples (average 14% in 1-2 cm section and ≤5% in subsequent sections) (Figure 6.6). However, calcareous benthic foraminifera are more abundant than agglutinated foraminifera in all sub-surface (2-3 cm, 3-4 cm, 4-5 cm) sections, except one deeper station (MC-59) where agglutinated foraminifera are more abundant (Figure 6.7).

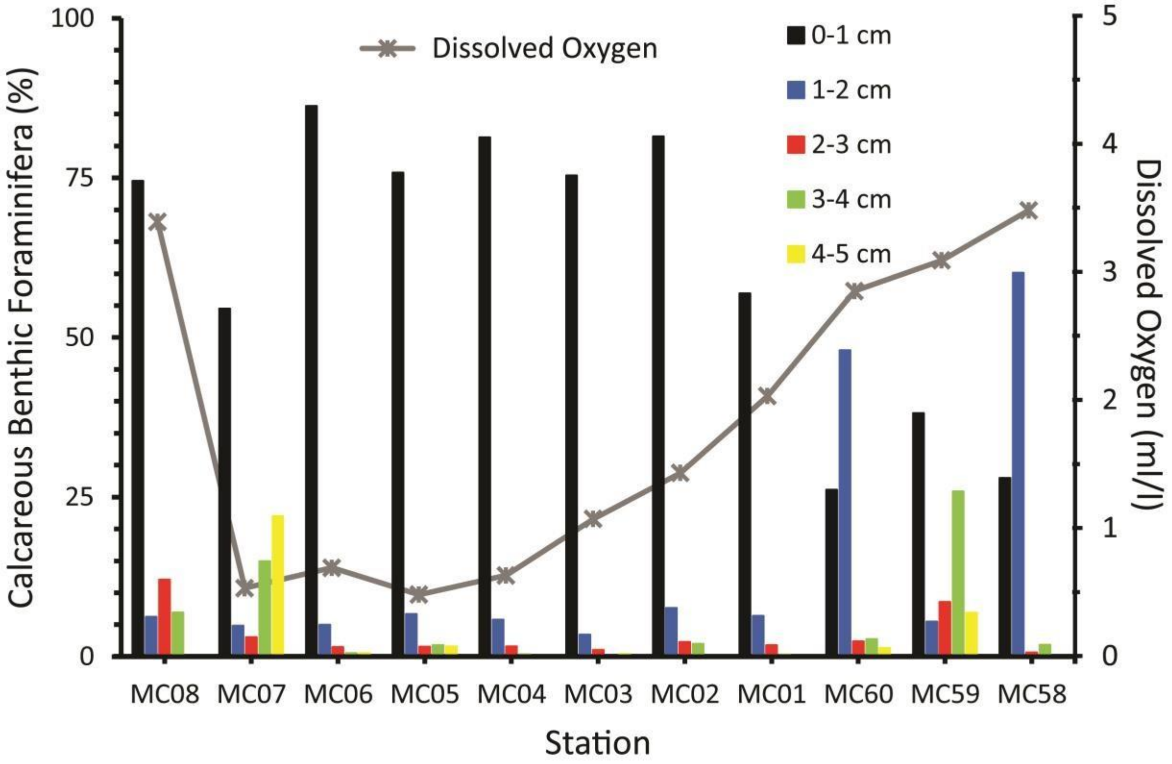

**Figure 6.6: The relative contribution of living calcareous benthic foraminifera in the top 5 cm sections, to the vertical stock at different stations. The dissolved oxygen concentration at each station is plotted as a line diagram.**

### Agglutinated benthic foraminifera (Living)

The living agglutinated benthic foraminifera are also relatively more abundant in core top (0-1 cm) section than sub-surface samples (Figure 6.7). The maximum abundance (37%) of living agglutinated benthic foraminifera is in MC-01, at 1550 m and no agglutinated foraminifera were found in the core-top section at 58 m (MC-08). In sub-surface samples (1-2 cm), agglutinated foraminiferal abundance is drastically lower as compared to core top samples. In fact, agglutinated foraminifera are absent in 1-2 cm section of all but a couple of stations (MC-59 and MC-60). A higher relative abundance of agglutinated foraminifera (25% and 46%) is, however, observed in sub-surface samples at two of the deepest stations, namely MC-60 (1887 m) and MC-59 (2080 m), respectively. Finally, agglutinated foraminiferal abundance drastically decreases with increasing sediment depth, and they are completely absent in the deepest sediment layer (4-5 cm) at all the stations except at MC-59 (Figure 6.7).

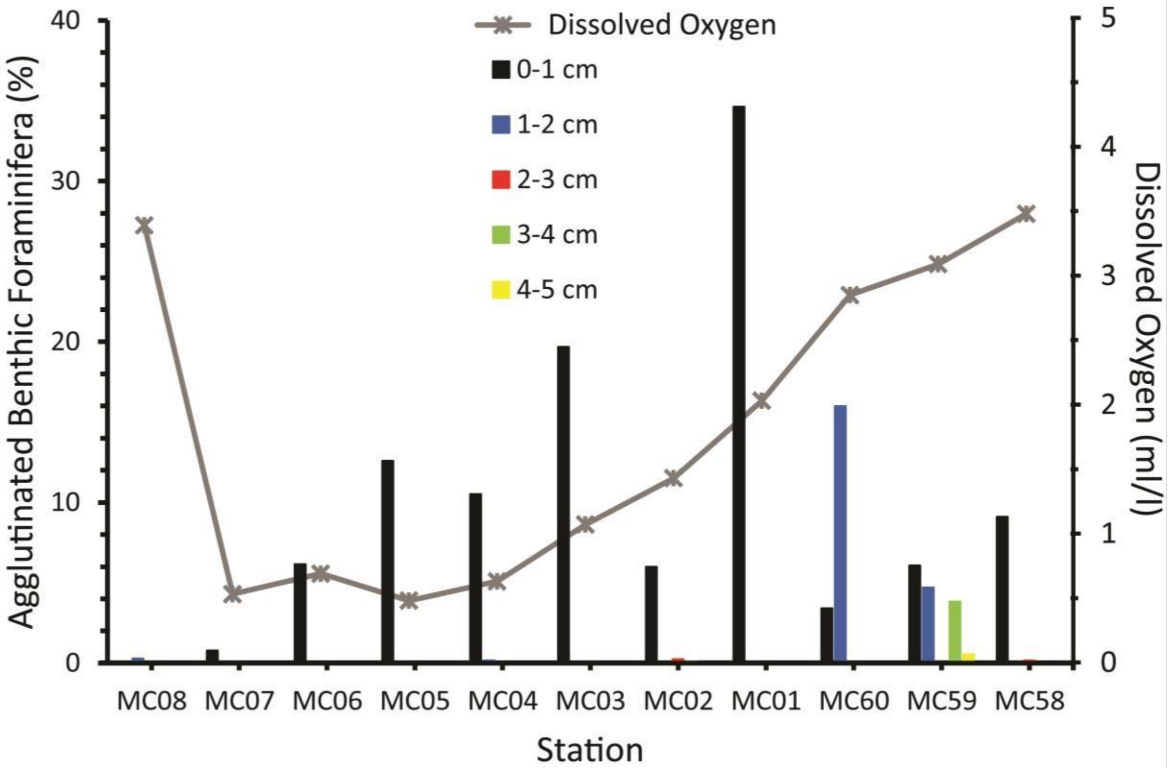

**Figure 6.7: The relative contribution of living agglutinated benthic foraminifera in the top 5 cm sections, to the vertical stock at different stations. The dissolved oxygen concentration at each station is plotted as a line diagram.**

### Calcareous epifaunal and infaunal benthic foraminifera

The specimens were segregated into epifaunal and infaunal morpho-groups, based on the morphology, following Nigam et al., (2007). The epifaunal calcareous foraminifera are dominant in the middle slope and relatively less abundant in both the shelf and outer slope region (Figure 6.8). The lowest relative abundance of calcareous epifaunal foraminifera (~6%) is at station MC-60 (1887 m water depth), and the highest (61%) is at MC-05 (510 m water depth). The calcareous infaunal forms dominate the total living benthic foraminiferal assemblage (Figure 6.8). The relative abundance of living infaunal calcareous benthic foraminifera in vertical stock is comparatively less in the upper slope, marked by low dissolved oxygen (Figure 6.8). The lowest relative abundance of infaunal calcareous foraminifera (26%) is at station MC-05 (510 m water depth), and the highest is at shallow water station MC-07 that falls at the continental shelf and slope boundary (Figure 6.8).

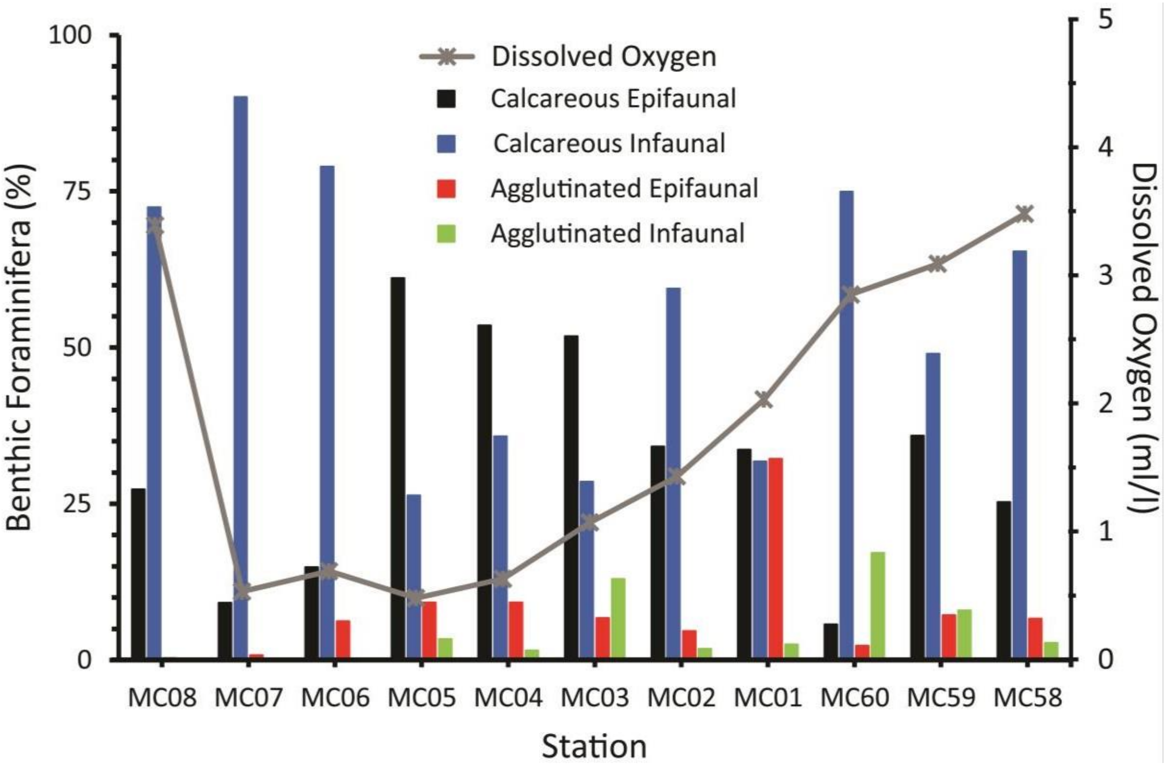

**Figure 6.8: The relative abundance (%) of living benthic foraminiferal morpho-groups in the vertical stock. The dissolved oxygen concentration at each station is plotted as a line diagram.**

The core top (0-1 cm) samples contain almost the entire living epifaunal calcareous benthic foraminifera at all the stations except MC-59 (water depth 2080 m) (Figure 6.9A). Surprisingly, infaunal calcareous foraminifera are also abundant only in the top 0-1 cm section at a majority of the stations in the shelf and upper slope, suggesting their shallow depth habitat (Figure 6.9B). However, in contrast with negligible epifaunal benthic foraminifera, the sub-surface samples, especially 1-2 cm section, also contain substantial living calcareous infaunal benthic foraminifera. Only at a couple of deeper stations, infaunal foraminiferal abundance in 1-2 cm section is higher than that in the top section (0-1 cm). Further, at MC-59 (2080 m water depth), the maximum abundance of living infaunal calcareous benthic foraminifera is in 3-4 cm section. The lowest relative abundance of living calcareous infaunal benthic foraminifera (~5%) in core top section (0-1 cm) is at the deepest station (MC-58, 2750 m water depth) and the highest (72%) is at MC-06. The living calcareous infaunal benthic foraminifera dominate benthic foraminiferal assemblage in sub-surface samples at all the stations (Figure 6.9B).

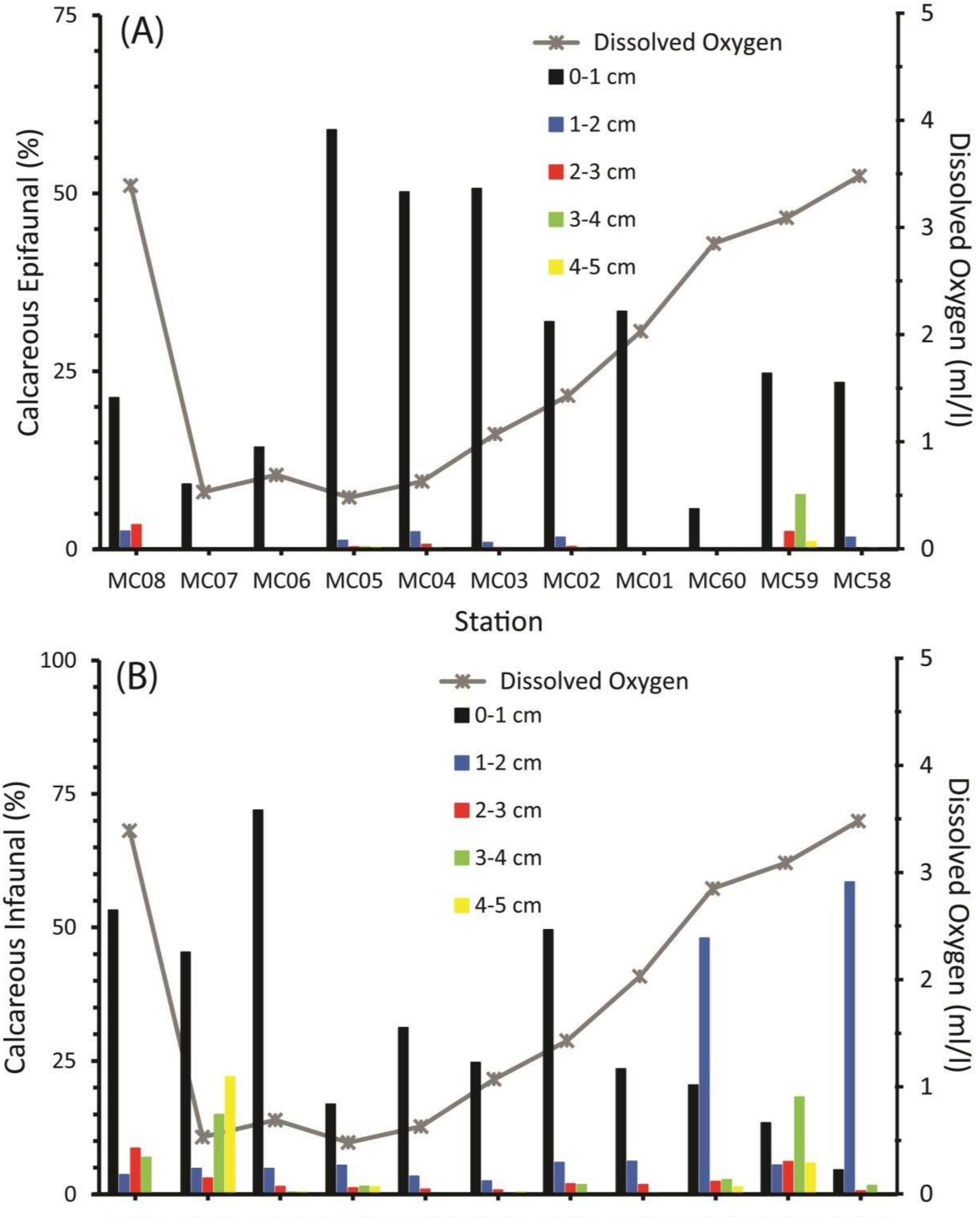

**Figure 6.9: The relative contribution of living calcareous epifaunal (A) and infaunal (B) benthic foraminifera in top 5 cm sections, to the vertical stock at different stations. The dissolved oxygen concentration at each station is plotted as a line diagram.**

### Agglutinated infaunal and epifaunal benthic foraminifera

The epifaunal agglutinated foraminifera are present only in the core top samples (0-1 cm) of all stations except MC-59, where it is also present in 1-2 cm section (Figure 6.10A). Surprisingly, even the infaunal agglutinated foraminifera are present only in the top 0-1 cm section at a majority of the stations (Figure 6.10B). The infaunal agglutinated benthic foraminifera are absent on the continental shelf and appear in core top samples only at 510 m water depth onwards. The infaunal agglutinated foraminifera do not have a clear water depth related trend (Figure 6.10B). In contrast with the calcareous foraminifera, the relative abundance of infaunal agglutinated foraminifera is less than that of epifaunal forms at a majority of the stations.

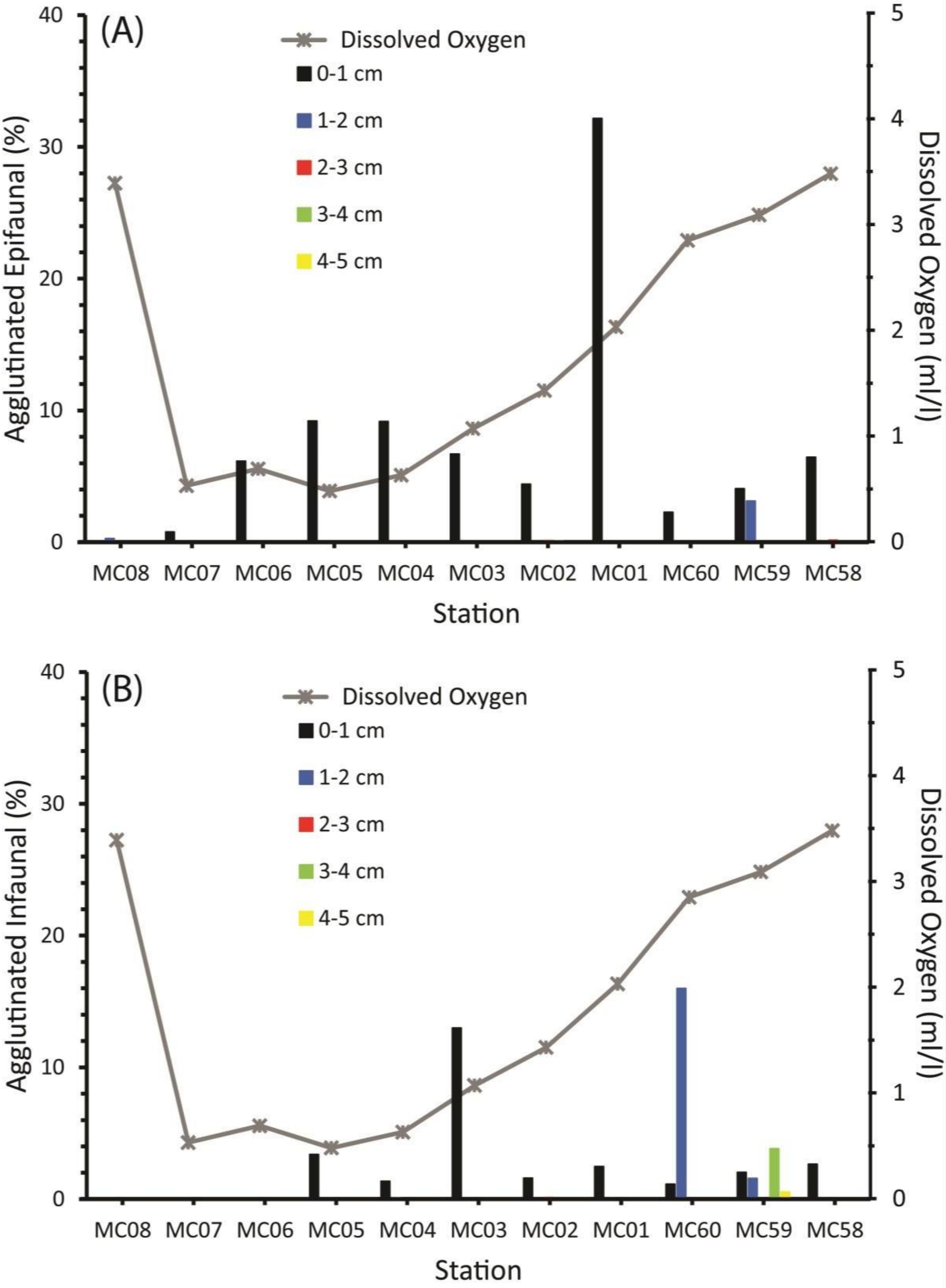

**Figure 6.10: The relative contribution of living agglutinated epifaunal (A) and infaunal (B) benthic foraminifera in top 5 cm sections, to the vertical stock at different stations. The dissolved oxygen concentration at each station is plotted as a line diagram.**

### Principle component analysis (PCA)

The absolute abundance of total benthic foraminifera as well as that of both the calcareous and agglutinated foraminifera is positively correlated with salinity and negatively correlated with bottom water dissolved oxygen and water depth (Figure 6.11). None of these and even other ambient parameters, however, seem to have a dominant significant effect on the absolute abundance of benthic foraminifera.

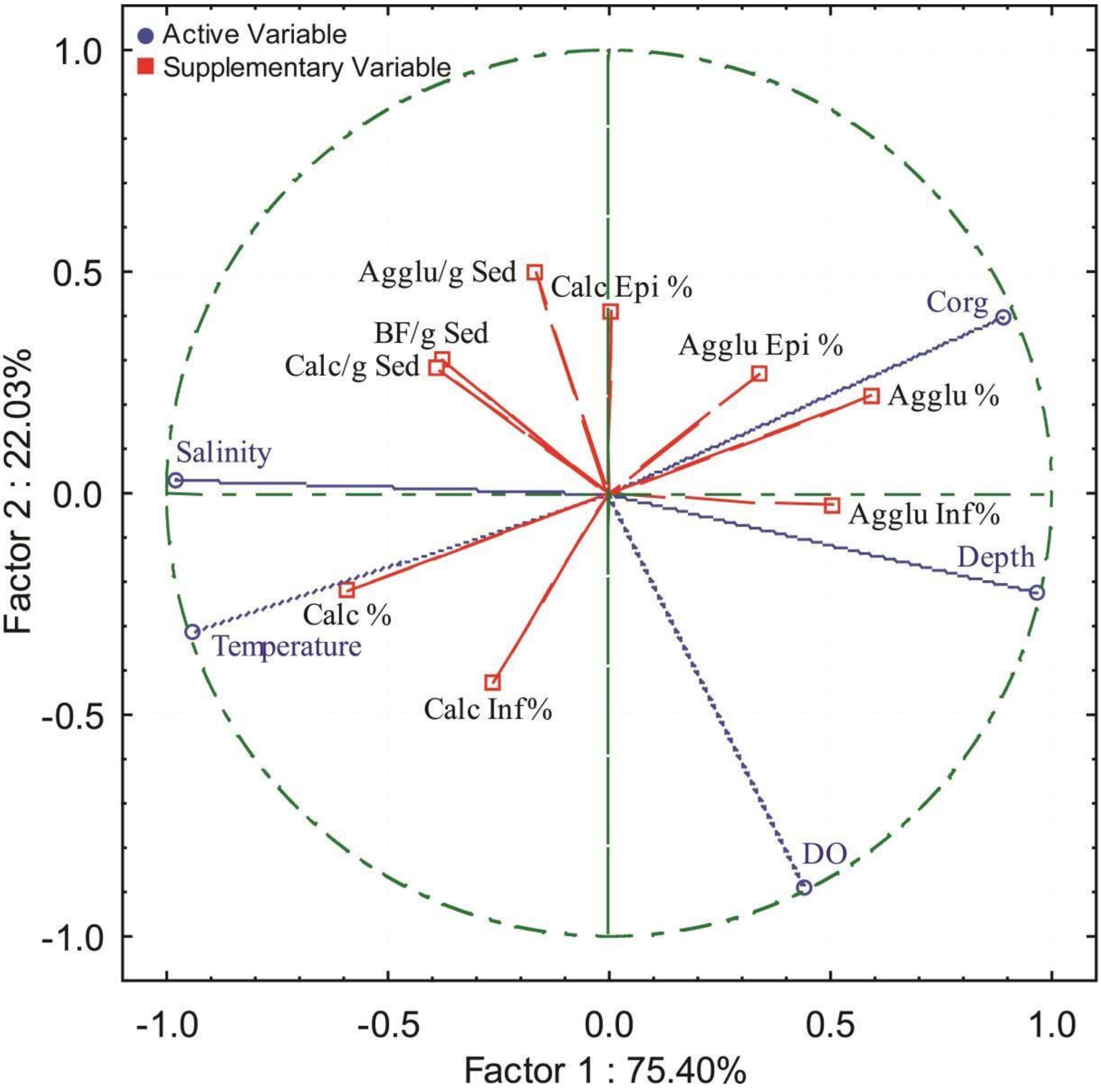

**Figure 6.11: The principle component analysis (PCA) of different living benthic foraminiferal groups with the ambient physico-chemical conditions. DO: Dissolved Oxygen, $C_{org}$: Organic Carbon, BF/g sed: Benthic foraminifera/g dry sediment, Calc/g Sed: Calcareous benthic foraminifera per gram sediment; Agglu/g Sed: Agglutinated benthic foraminifera per gram sediment; Calc%: Relative abundance of calcareous benthic foraminifera, Agglu%: Relative abundance of agglutinated benthic foraminifera, Calc Epi: Calcareous Epifaunal, Calc Inf: Calcareous Infaunal, Agglu Epi: Agglutinated Epifaunal, Agglu Inf: Agglutinated Infaunal.**

The relative abundance of agglutinated benthic foraminifera is significantly positively correlated with $\%C_{org}$ and negatively correlated with bottom water temperature (Figure 6.11). The relative abundance of calcareous benthic foraminifera has an opposite relationship with these two parameters (negatively correlated with $\%C_{org}$ and positively correlated with bottom water temperature) (Figure 6.11). Interestingly, the organic matter content of the sediment has a different relationship with the infaunal and epifaunal forms of agglutinated and calcareous benthic foraminifera. The epifaunal agglutinated and epifaunal calcareous foraminifera are positively correlated with $\%C_{org}$. In contrast with that, the infaunal calcareous foraminifera are negatively correlated with $\%C_{org}$. Infaunal agglutinated benthic foraminifera do not have any relationship with $\%C_{org}$. The temperature of seawater is positively correlated with the infaunal calcareous benthic foraminifera and negatively correlated with epifaunal calcareous and agglutinated foraminifera (Figure 6.11).

## Western Bay of Bengal

### Dissolved oxygen concentration

The dissolved oxygen concentration in the western Bay of Bengal varies from 0.35 mL/L to 4.20 mL/L. The dissolved oxygen concentration gradually decreases across the continental shelf. The oxygen deficient zone ranges from ~100 m to ~1000 m (Figure 6.12).

### Organic carbon (%Corg)

The organic matter concentration is low on the continental shelf and gradually increases towards the slope (Figure 6.13). The concentration is also high at the deeper waters. Although the organic carbon concentration is high within the oxygen deficient zone, the increase from the oxygenated shelf waters to the oxygen deficient slope waters is gradual. The organic matter concentration, however, decreases, below the deeper boundary of the oxygen deficient zone in the western Bay of Bengal. The organic matter concentration in core-top section (0-1 cm) is similar to that in the subsequent four sections, without any systematic increase or decrease at a majority of the stations.

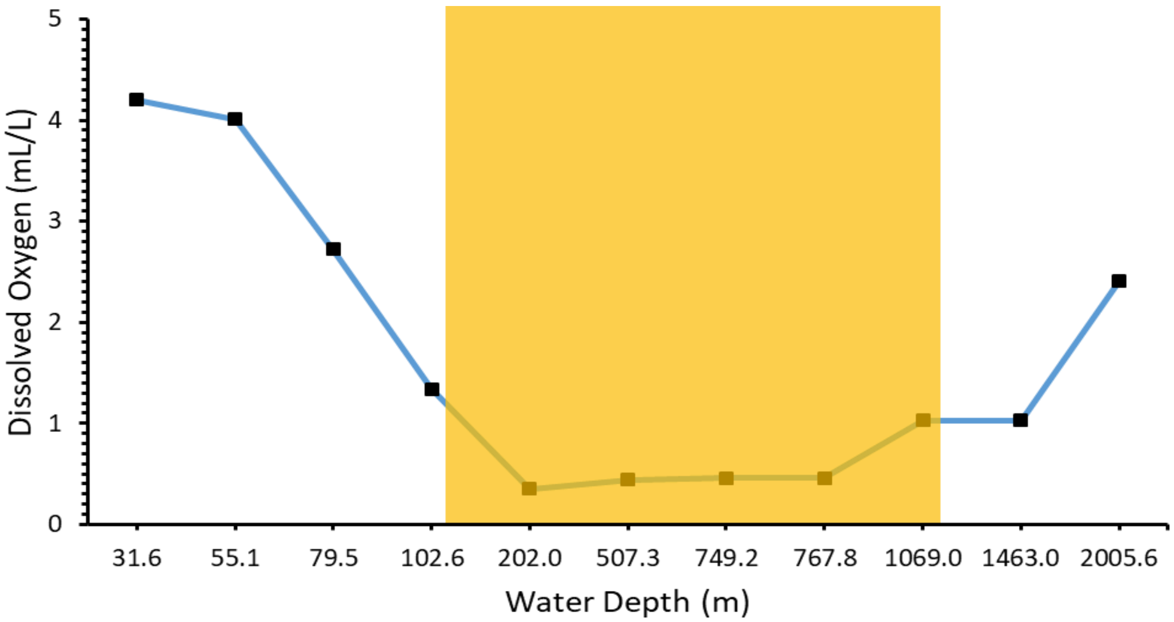

**Figure 6.12: The bottom water dissolved oxygen concentration at the sampling stations. The values are for the month of October when the sampling was done. The shaded region marks the oxygen minimum zone.**

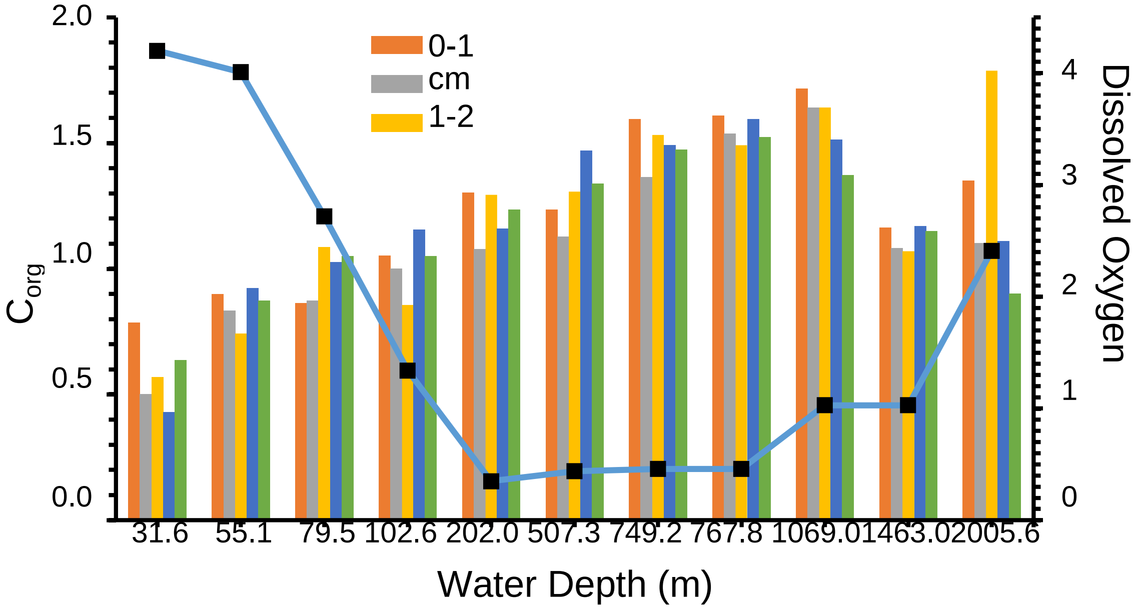

**Figure 6.13: The organic carbon (%Corg) in core top (0-1 cm) and sub-surface (1-2, 2-3, 3-4, 4-5 cm) samples, in the western Bay of Bengal.**

### Nature of the organic matter (Corg/N)

As expected, the $C_{org}$/N ratio is very high on the continental shelf of the western Bay of Bengal. The ratio decreases towards the outer shelf and is very low on the slope. The lowest $C_{org}$/N is at the core of the oxygen deficient zone. A minor increase in $C_{org}$/N is observed at the deeper stations. Unlike the organic carbon, a large difference is observed between the $C_{org}$/N ratio in the 0-1 cm section and deeper sections, especially on the shelf. The trend of change in $C_{org}$/N from core top section to deeper section, is inconsistent (Figure 6.14).

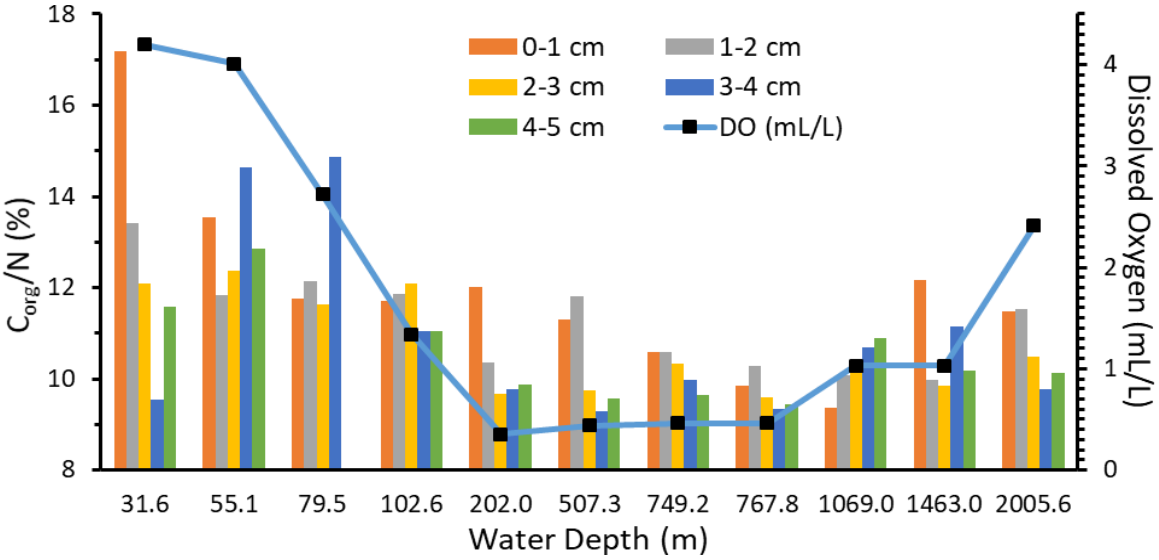

**Figure 6.14: Corg/N ratio in the surface sediments of the western Bay of Bengal. The dissolved oxygen at the stations is plotted as line diagram.**

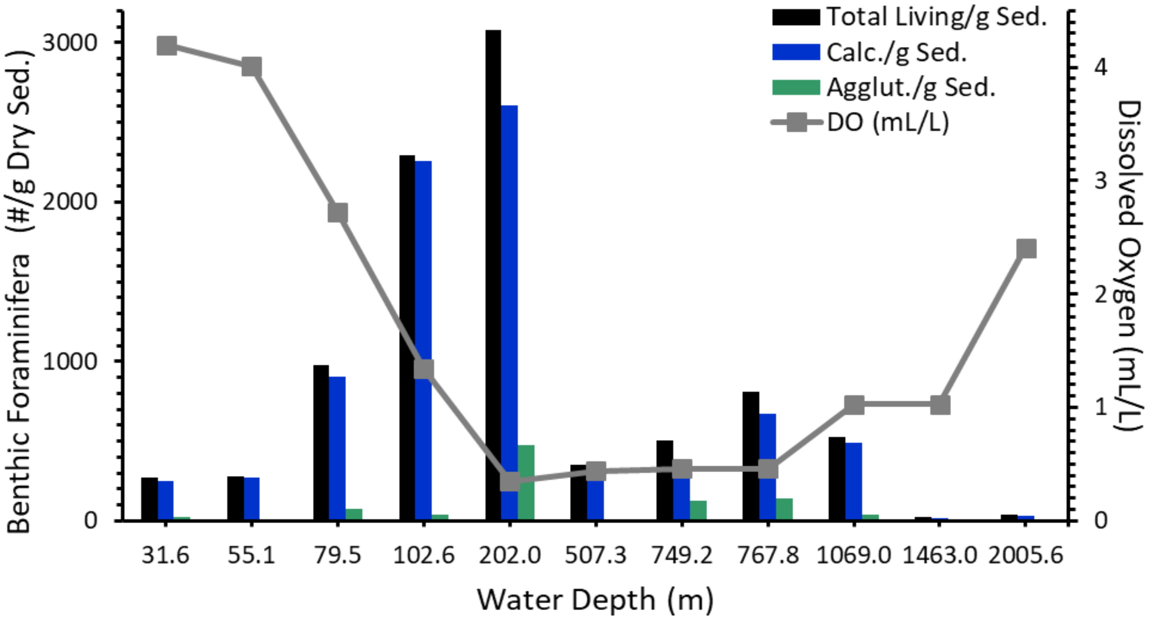

**Figure 6.15: Absolute abundance of vertical stock of living total, calcareous and agglutinated benthic foraminifera in the western Bay of Bengal. The dissolved oxygen concentration at each station is plotted as line diagram.**

### Absolute abundance of living benthic foraminifera

The living benthic foraminiferal abundance is high on the outer shelf and upper slope (Figure 6.15). The living benthic foraminifera were rare in the lower slope. The highest living benthic foraminiferal abundance (2866/g sediment) is at 202 m. A substantial fraction of the living benthic foraminifera population is calcareous at a majority of the stations. Agglutinated benthic foraminifera are rare throughout the transect, except at a few stations within the oxygen deficient zone.

### Contribution to the vertical stock (Living Benthic Foraminifera)

The living benthic foraminiferal abundance is the highest in top 0-1 cm section, at all depths (Figure 6.16). The living benthic foraminifera are generally confined to the upper 2 cm section, at a majority of the stations. Only at 102.6 m depth, a substantial number of living benthic foraminifera are present in 3-4 cm section. The fraction of living benthic foraminiferal population in the top 0-1 cm section increases within the oxygen deficient zone. Within the oxygen deficient zone, living benthic foraminifera were rare below the top 2 cm.

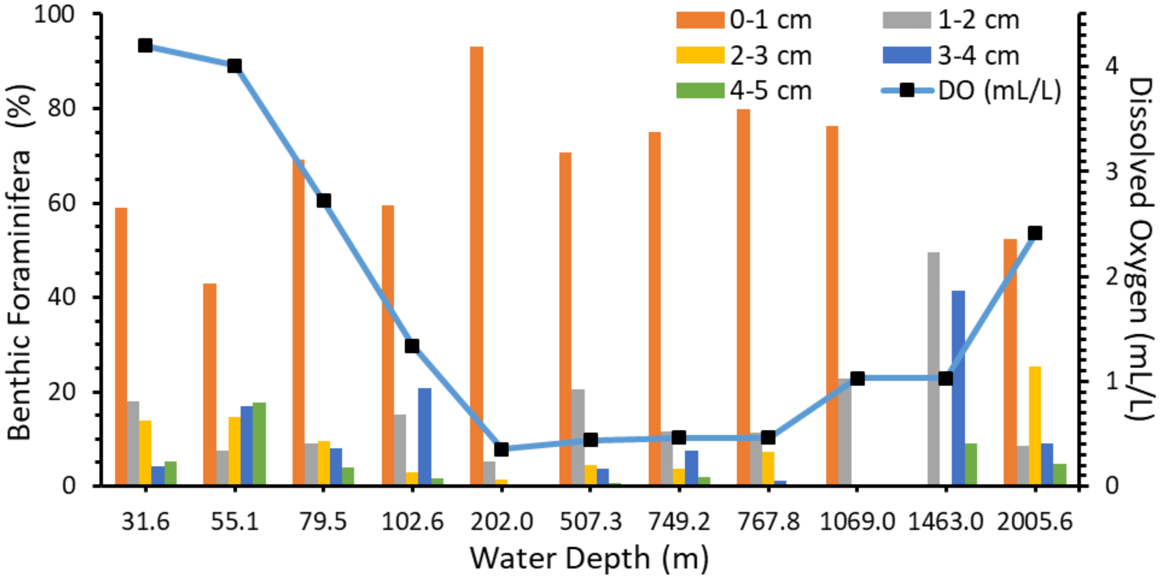

**Figure 6.16: The relative contribution of benthic foraminifera in different sections of the sediments, to the total vertical stock. The dissolved oxygen concentration at each station is plotted as line diagram.**

### Living calcareous and agglutinated benthic foraminifera (Vertical Stock)

The living calcareous foraminifera are dominant at all the stations, in all sections. The relative abundance of living calcareous benthic foraminifera is however, comparatively lower on the slope than that on the shelf (Figure 6.17). However, the living agglutinated foraminifera are rare on the shelf and comparatively more on the slope. The highest relative abundance of living agglutinated benthic foraminifera is at 749.2 m (Figure 6.17). The calcareous benthic foraminifera dominate all the sections of the top 5 cm of the sediments at all depths (Figure 6.18). Interestingly, at a few stations, although the relative abundance of calcareous benthic foraminifera is low in the top section (0-1 cm), the subsequent sections are dominated by calcareous forms. The agglutinated benthic foraminifera are rare in all the sections of the top 5 cm sediments at all the stations. The relative abundance significantly decreases at deeper sections. The relative abundance of living agglutinated benthic foraminifera in the deeper sections is comparatively more in the oxygen deficient zone (Figure 6.19).

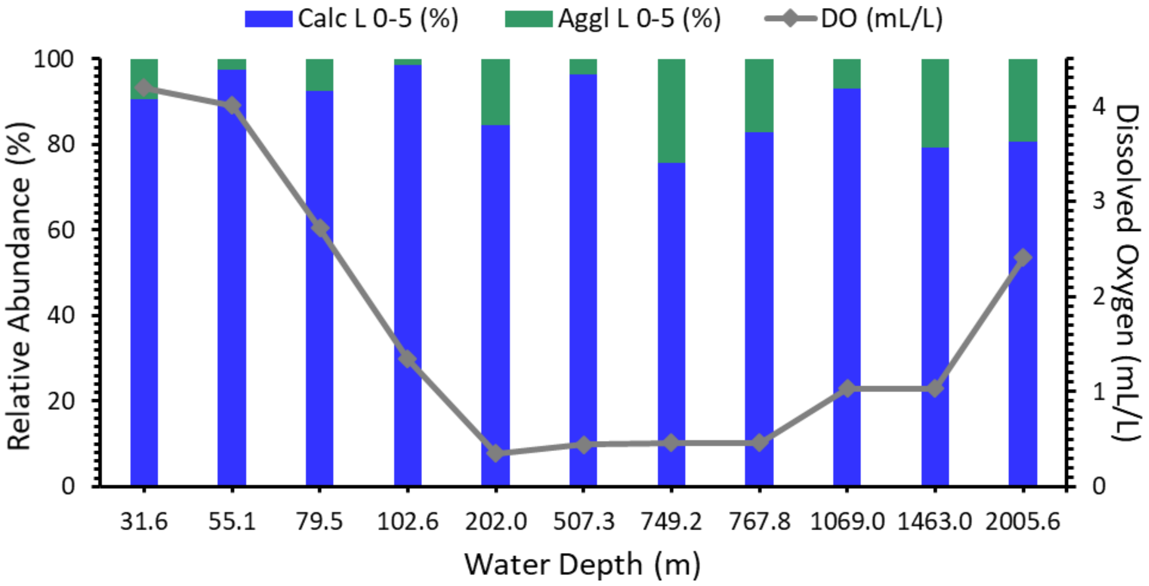

**Figure 6.17: The relative abundance of living calcareous and agglutinated benthic foraminifera in the western Bay of Bengal. The dissolved oxygen concentration at each station is plotted as a line diagram.**

### Relative abundance of angular asymmetric and rounded symmetric benthic foraminifera (0-1 cm)

The relative abundance of angular asymmetrical benthic foraminifera increases with depth on the continental shelf. The relative abundance and trend of both the living and dead angular asymmetric foraminifera is similar on the shelf. The abundance is, however, low within the oxygen deficient zone, but still higher than that of the rounded symmetrical foraminifera (Figure 6.20).

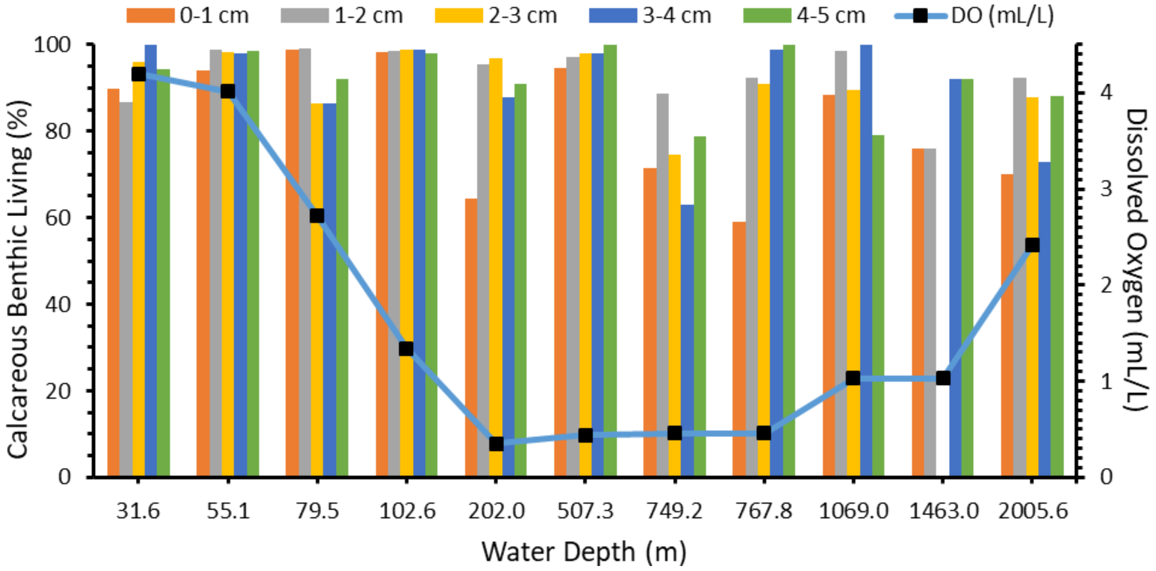

**Figure 6.18: The relative abundance of living calcareous benthic foraminifera in different sections of the top 5 cm sediments the western Bay of Bengal. The dissolved oxygen concentration at each station is plotted as a line diagram.**

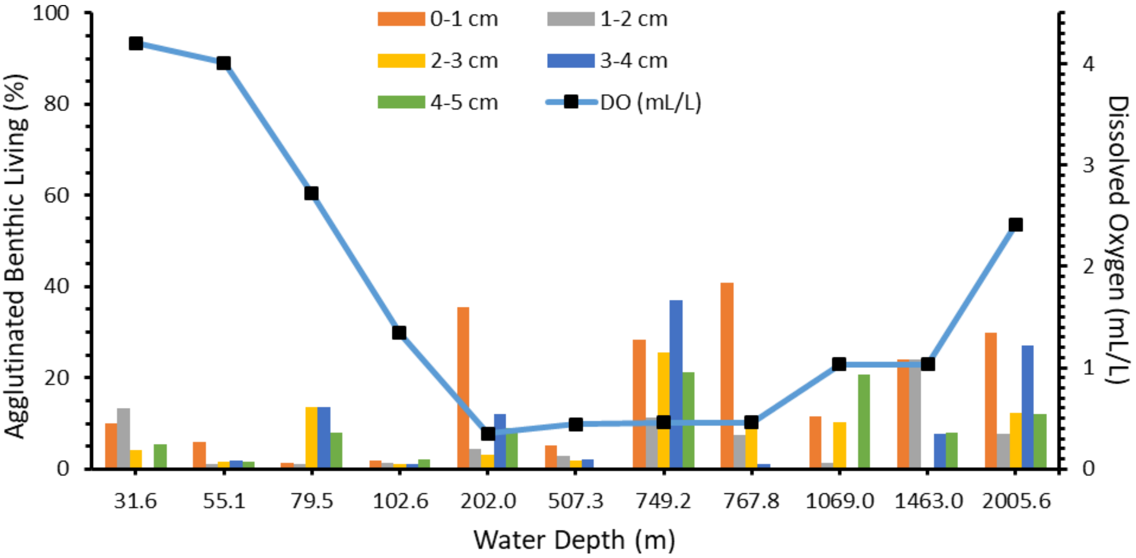

**Figure 6.19: The relative abundance of living agglutinated benthic foraminifera in different sections of the top 5 cm sediments in the western Bay of Bengal. The dissolved oxygen concentration at each station is plotted as a line diagram.**

The relative abundance of rounded symmetrical benthic foraminifera decreases from the inner shelf to outer shelf. However, the relative abundance increases within the oxygen deficient zone. But, the abundance is still lower than that of the angular asymmetric benthic foraminifera. Interestingly, the relative abundance of living rounded symmetrical forms is higher than that of the angular asymmetrical benthic foraminifera, within the oxygen deficient zone. The dead population is, however, dominated by the angular asymmetrical benthic foraminifera (Figure 6.21).

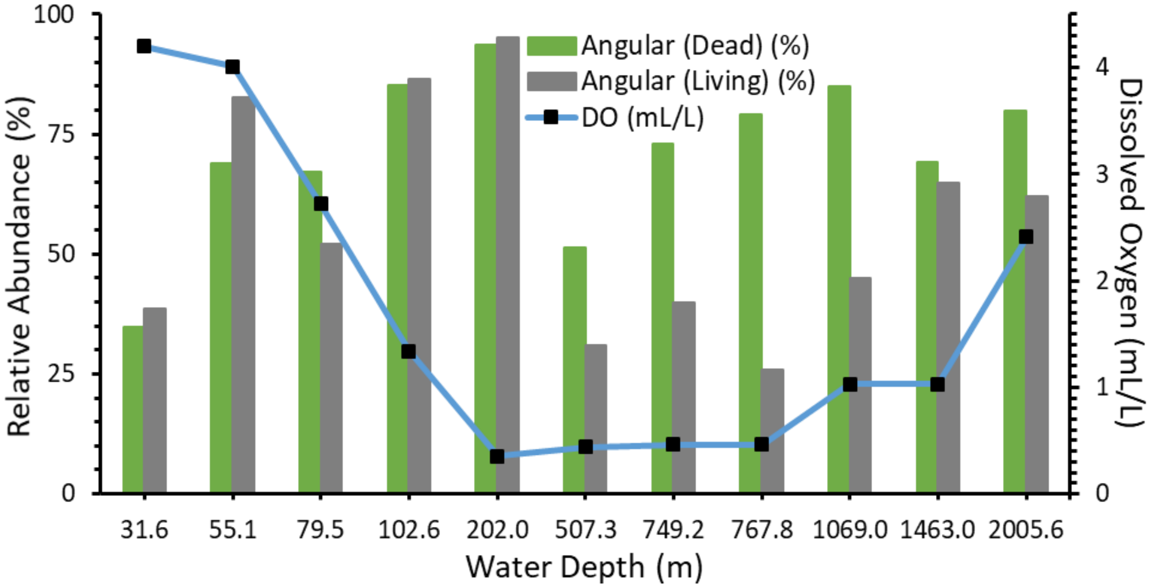

**Figure 6.20: The relative abundance (%) of living and dead angular asymmetric benthic foraminiferal morpho-group in the core top section (0-1 cm). The dissolved oxygen concentration at each station is plotted as a line diagram.**

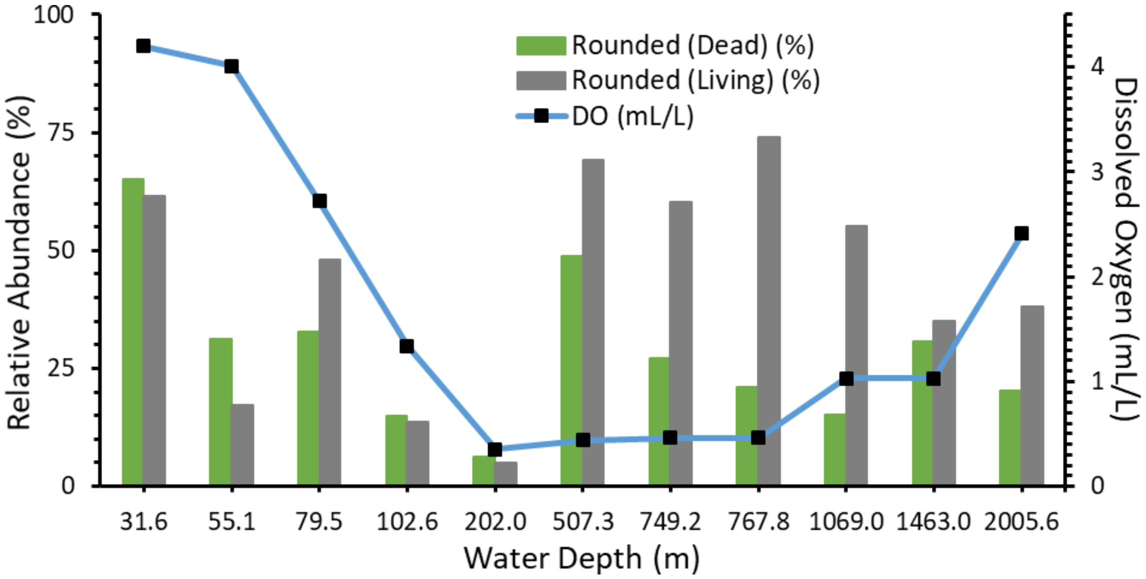

**Figure 6.21: The relative abundance (%) of living and dead rounded symmetric benthic foraminiferal morpho-group in the core top section (0-1 cm). The dissolved oxygen concentration at each station is plotted as a line diagram.**

## Eastern Arabian Sea

### Dissolved oxygen concentration

The lowest dissolved oxygen at the sediment-water interface is in the eastern Arabian Sea. The oxygen deficient zone extends from the shelf-slope boundary to the slope. The dissolved oxygen at deeper depths is comparable with that at the continental shelf in the eastern Arabian Sea (Figure 6.22).

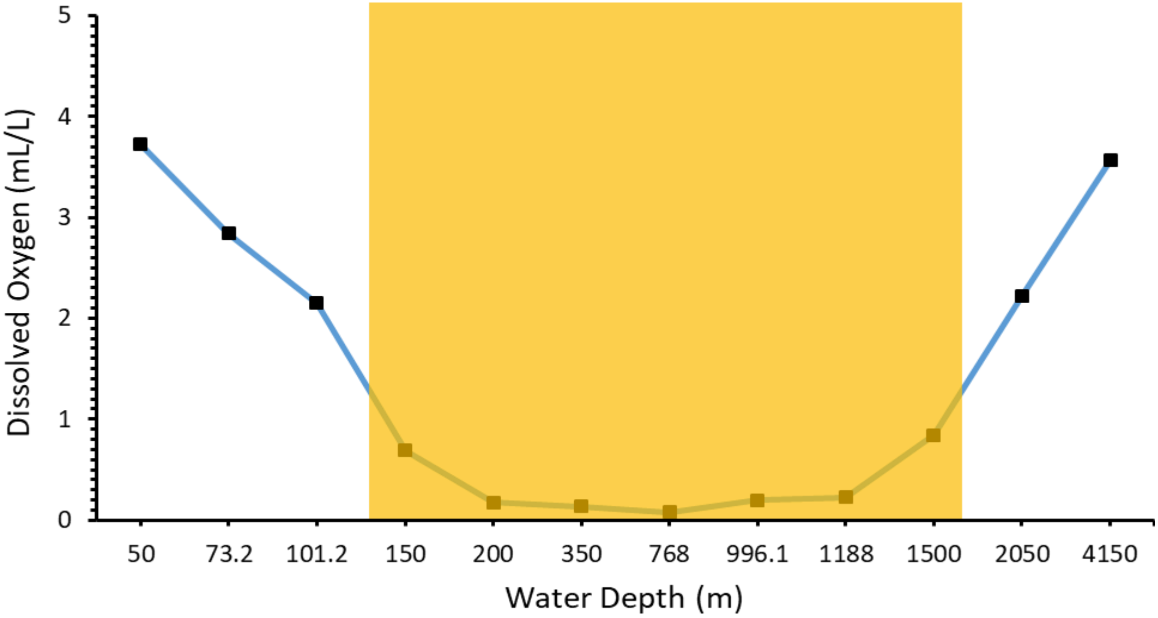

**Figure 22: The bottom water dissolved oxygen concentration at the sampling stations in the eastern Arabian Sea. The shaded region marks the oxygen minimum zone.**

### Organic carbon (%Corg)

The organic matter concentration in the surface sediments of the eastern Arabian Sea is almost double that in the western Bay of Bengal, but lower than that in the Gulf of Mannar. The organic matter concentration is low on the shelf and increases abruptly on the slope. The organic matter concentration again decreases in the deeper waters. The zone of high organic matter concentration in the eastern Arabian Sea coincides with the oxygen deficient zone (Figure 6.23).

### Nature of the organic matter (Corg/N)

The organic matter to nitrogen concentration ratio is often used to understand the origin and nature of the organic matter. The ratio is comparatively higher on the shelf than on the slope. A peculiar observation is the consistent $C_{org}/N$ (~9) throughout the slope. A distinct decrease in $C_{org}$/N ratio matches with the oxygen deficient zone. $C_{org}$/N ratio is higher at deeper depths (Figure 6.24).

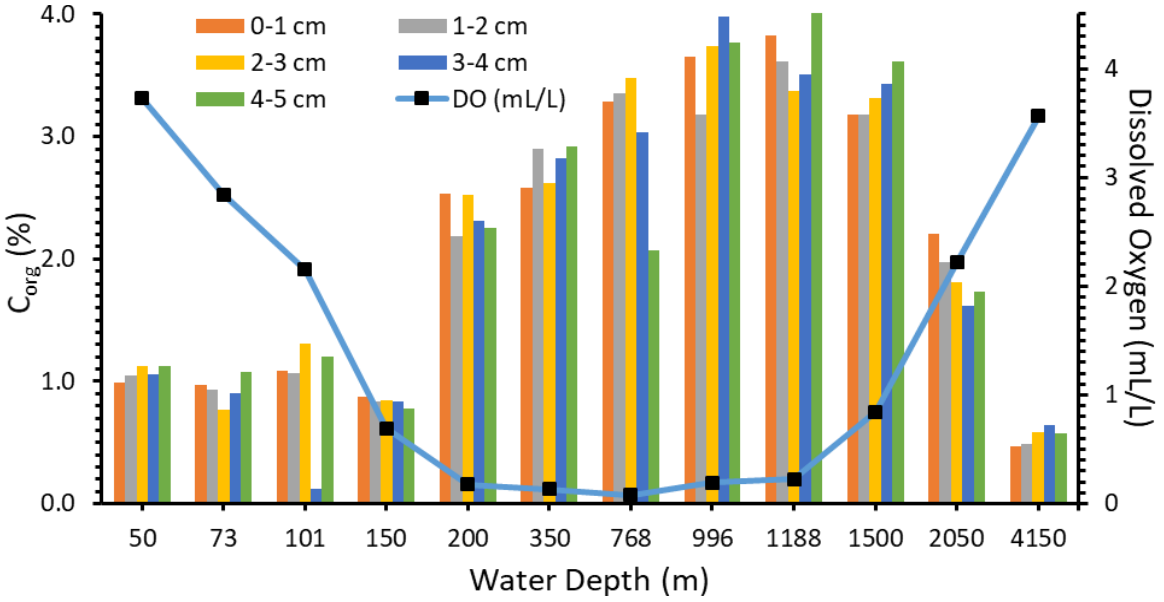

**Figure 6.23: The organic carbon (%$C_{org}$) in core top (0-1 cm) and sub-surface (1-2, 2-30, 3-4, 4-5 cm) samples, in the eastern Arabian Sea.**

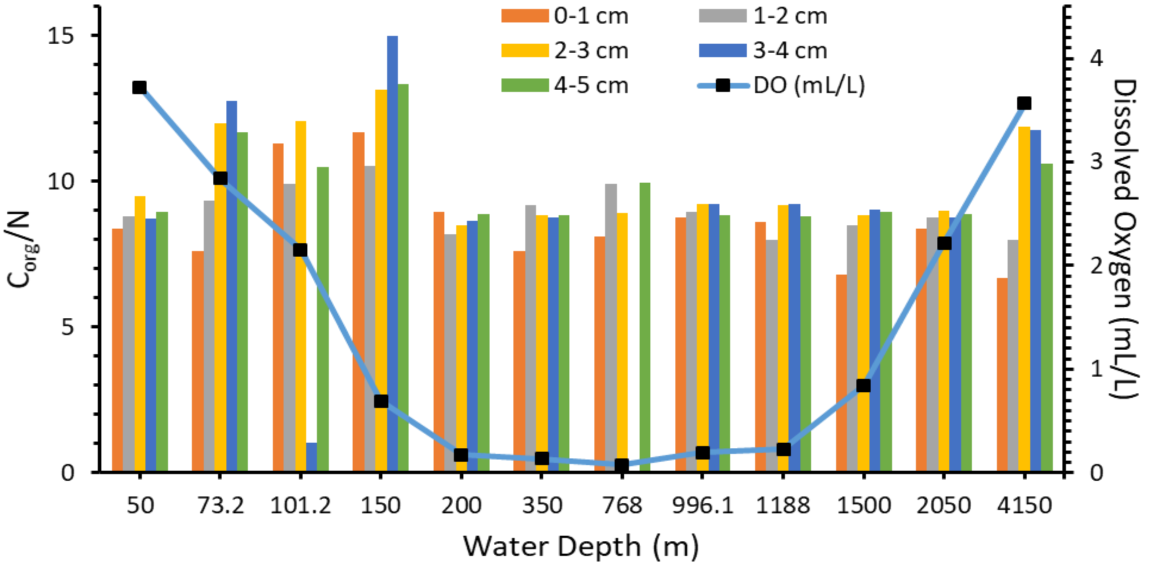

**Figure 6.24: $C_{org}$/N ratio in the surface sediments of the eastern Arabian Sea. The dissolved oxygen at the stations is plotted as line diagram.**

### Absolute abundance of living benthic foraminifera (0-1 cm)

The absolute abundance of living benthic foraminifera varies significantly from the shelf to slope. Living benthic foraminiferal are negligible on the shelf. A large population is observed on the slope. The increase in living benthic foraminiferal population on the slope coincides with the decrease in dissolved oxygen concentration. The living benthic foraminiferal population again decreases at deeper depths (Figure 6.25).

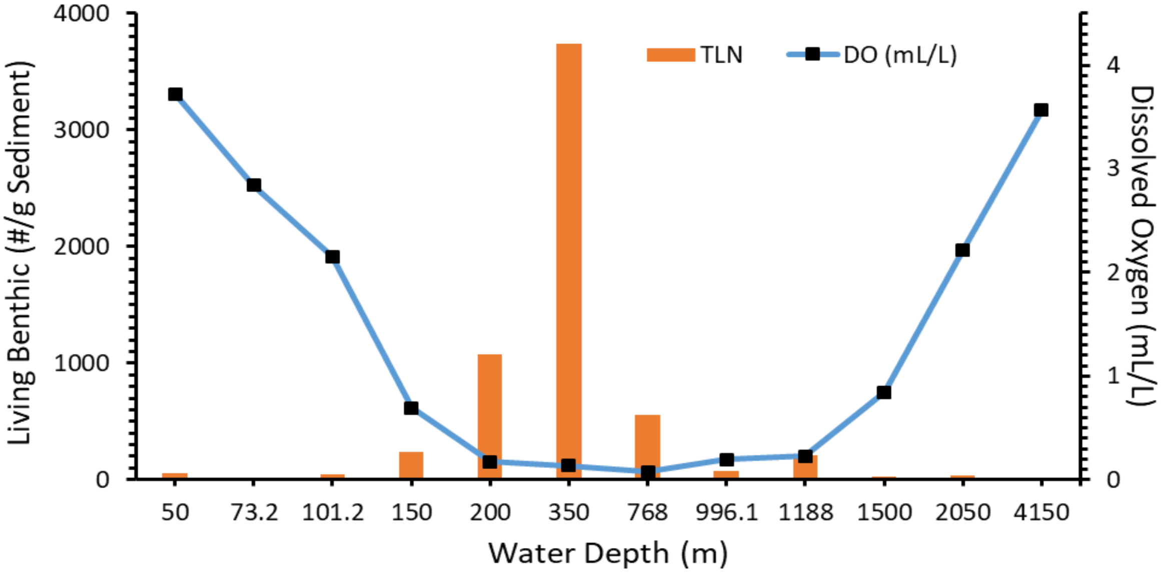

**Figure 6.25: Absolute abundance of living benthic foraminifera in the core top section in the eastern Arabian Sea. The dissolved oxygen concentration at each station is plotted as line diagram.**

### Calcareous and agglutinated benthic foraminifera (Living, 0-1 cm)

Calcareous benthic foraminifera dominate the living population comprising of more than 70% of the total assemblage. The highest relative abundance of calcareous benthic foraminifera is on the continental shelf. The relative abundance decreases on the slope and the lowest abundance is at the core of the oxygen deficient zone. A comparatively lesser abundance is also observed at the deeper stations. Agglutinated benthic foraminifera constitute less than 30% of the total living population in 0-1 cm section. Agglutinated benthic foraminifera are the least abundant on the shelf. A substantial fraction of the living benthic foraminiferal population is agglutinated only on the slope. The highest relative abundance of agglutinated benthic foraminifera is at the core of the oxygen deficient zone. The relative abundance of agglutinated benthic foraminifera is high, even at deeper stations (Figure 6.26).

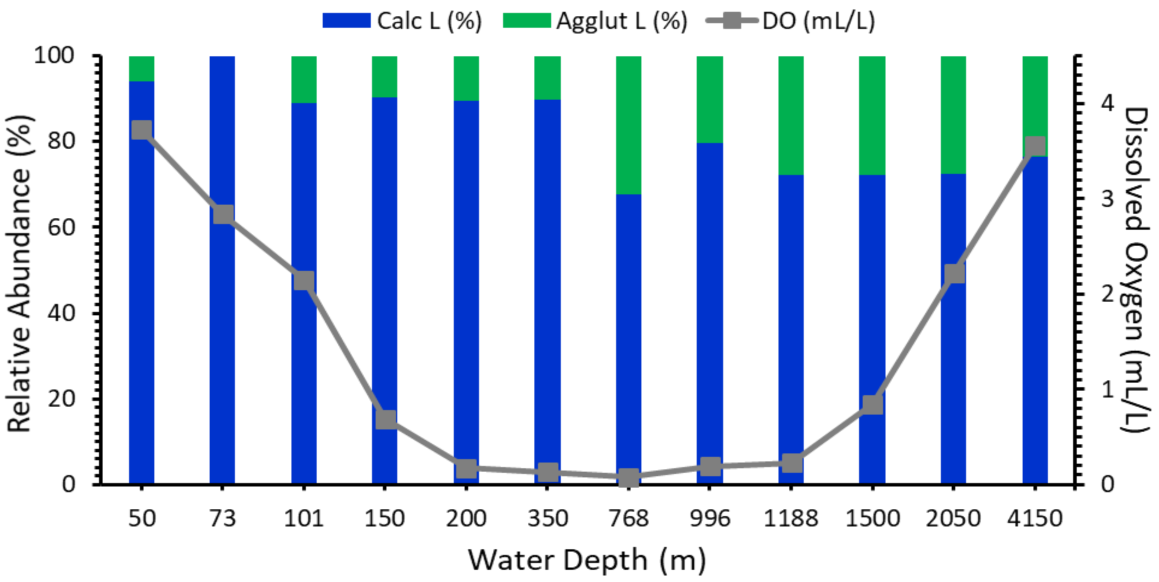

**Figure 6.26: The relative abundance of living calcareous and agglutinated benthic in the eastern Arabian Sea. The dissolved oxygen concentration at each station is plotted as a line diagram.**

### Relative abundance of angular asymmetric and rounded symmetric benthic Foraminifera (0-1 cm)

The angular asymmetric benthic foraminifera constitute ~40% of both the living and dead benthic foraminiferal population at a majority of the stations. The abundance is very low at the deepest station. The relative abundance of angular asymmetric benthic foraminifera is comparatively more in the oxygen deficient zone. Within the oxygen deficient zone, angular asymmetric benthic foraminifera constitute as high as 80% of the living benthic foraminiferal population. The relative abundance of angular forms decreases at stations below the deeper boundary of the oxygen deficient zone (Figure 6.27).

The rounded symmetrical benthic foraminifera dominate the population on the shelf and deeper waters. The relative abundance of rounded symmetrical benthic foraminifera is comparatively low on the slope. The decrease in the relative abundance of rounded symmetrical benthic foraminifera matches with the oxygen deficient zone. The relative abundance of both the dead and living rounded symmetrical foraminifera has a similar pattern from the shelf to the slope and further deeper waters (Figure 6.28).

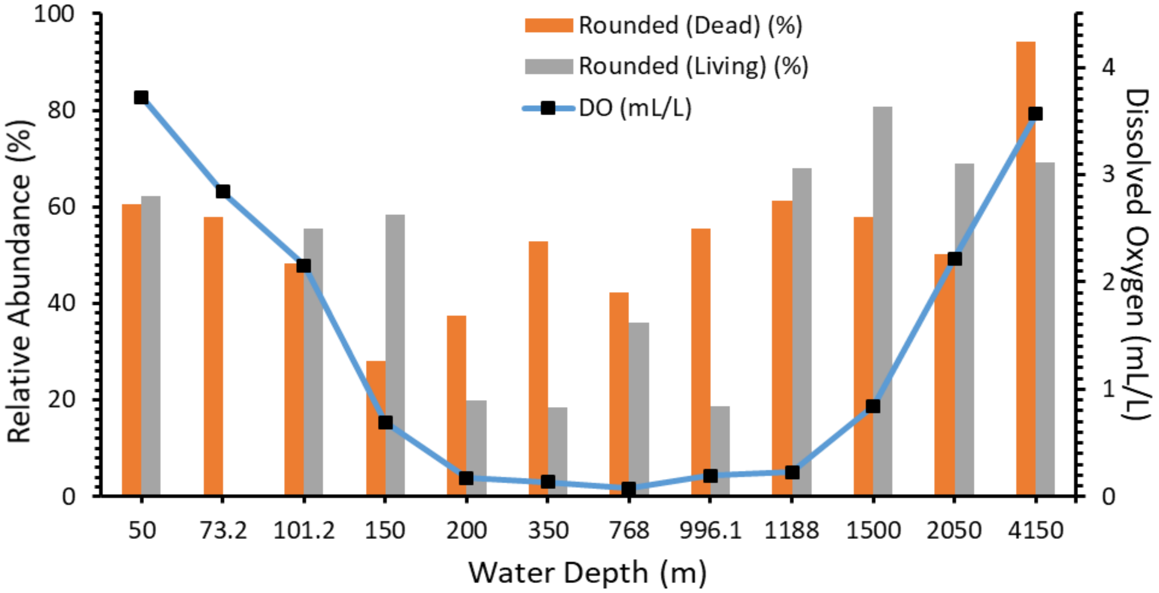

**Figure 6.27: The relative abundance (%) of living and dead angular asymmetric benthic foraminiferal morpho-group in the core top section (0-1 cm) in the eastern Arabian Sea. The dissolved oxygen concentration at each station is plotted as a line diagram.**

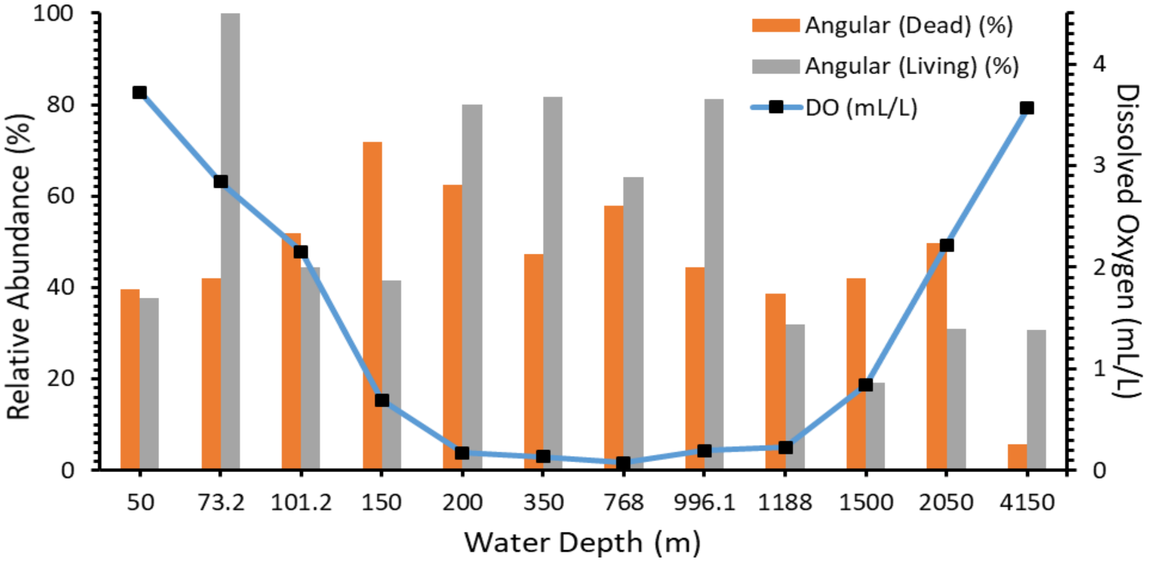

**Figure 6.28: The relative abundance (%) of living and dead rounded symmetric benthic foraminiferal morpho-group in the core top section (0-1 cm) in the eastern Arabian Sea. The dissolved oxygen concentration at each station is plotted as a line diagram.**

## Discussion

### Organic matter and dissolved oxygen

The organic matter content of the sediments increases in the oxygen deficient zone of both the Gulf of Mannar as well as the eastern Arabian Sea. The sediments in the well oxygenated zone on the shelf and at in the region deeper than the oxygen deficient zone has comparatively lesser organic matter, in both the Gulf of Mannar and the eastern Arabian Sea, suggesting a close link between the dissolved oxygen concentration and the preservation of the organic matter. Such a relationship between the organic matter and the dissolved oxygen is, however, not observed in the western Bay of Bengal. Although the organic matter content of the sediments is relatively higher in the oxygen deficient zone of the western Bay of Bengal, the difference is very low. The organic matter content of the sediments distinctly decreases in the well oxygenated waters only towards the deeper boundary of the oxygen deficient zone. The negligible difference in the organic matter content of the sediments on the well oxygenated outer shelf, as compared to the sediments within the oxygen deficient zone is due to the additional factor of grain-size and sediment influx. The huge influx of finer grains quickly buries the sediments, thus favouring the preservation of the organic matter on the well oxygenated shelf. The low $C_{org}$/N within the oxygen deficient zone as well as at further deeper depths, in both the western Bay of Bengal as well as the eastern Arabian Sea transect, is due to the increased marine organic matter contribution at relatively deeper depths, as compared to the shelf. The nitrogen deficient terrestrial organic matter contribution results in higher $C_{org}$/N on the inner shelf.

**Benthic foraminiferal abundance**

As the dissolved oxygen decreases to ≤1 ml/l at 152 m water depth in the Gulf of Mannar, foraminiferal abundance increases. The dissolved oxygen concentration remains low (≤2 ml/l) up to 1500 m, and increased foraminiferal abundance is observed in this depth range (Figure 6.3). The living benthic foraminiferal population drastically decreases at stations MC-59 and MC-60, where dissolved oxygen concentration is comparatively high, and $\%C_{org}$ is low (Figures 6.3, 6.4). A further increase in living benthic foraminiferal population is observed at further deeper stations where both the dissolved oxygen as well as $\%C_{org}$ are high (Figure 6.3). A similar pattern in the abundance of living benthic foraminifera is also observed in the eastern Arabian Sea. The living benthic foraminiferal abundance increases within the organic matter rich sediments of the oxygen deficient zone in the eastern Arabian Sea. The relationship however, is not so robust in the western Bay of Bengal. Here, although the absolute abundance of living benthic foraminifera increases with an initial decrease in the dissolved oxygen, several stations with very low dissolved oxygen have a comparatively lower benthic foraminiferal population. Interestingly, the decrease in dissolved oxygen does not result in any major change in organic carbon.

The living benthic foraminiferal abundance in surface and sub-surface sediments depends on various ecological parameters, out of which dissolved oxygen concentration in bottom water and $\%C_{org}$ in sediment, are considered to be the major ones (Jorissen et al., 1995; 2007; Jannink et al., 1998; Schumacher et al., 2007). The oxygen availability in the northern Indian Ocean, in general, is controlled by monsoon winds induced productivity and water circulation (Naqvi et al., 2003). The upwelling induced episodic injection of nutrients stimulates rapid biological production in the eastern Arabian Sea during the later phase of the summer monsoon (Rejomon et al., 2013). The organic matter produced is degraded by microbes by consuming the available oxygen, thus lowering the dissolved oxygen content of the seawater. When low oxygenated water comes in contact with the seafloor, it can have an effect on the abundance and diversity of the benthic foraminiferal fauna. Benthic foraminifera are one of the major faunal elements that respond to low oxygen condition (Den Dulk et al., 2000; Gooday and Turley, 1990; Jorissen et al., 1992; 1995; McCorkle et al., 1997; Nomaki et al., 2008). Since only a few foraminifera species tolerate low oxygen conditions, foraminiferal diversity in hypoxic settings is generally depressed (Sen Gupta and Machain-Castillo, 1993; Van Der Zwaan et al., 1999). However, given that the number of foraminiferal predators is also reduced, and since available food supply is high, the few foraminiferal species that live under these conditions, increase their abundance significantly (Jorissen et al., 1995). Consequently, the abundance of oxygen tolerant benthic foraminifera under low predatory pressure is the major factor responsible for the increased absolute abundance of living benthic foraminifera in the oxygen minimum zone of the Gulf of Mannar. Although we do not have species data (neither for foraminifera and nor for other macrofauna/megafauna predators), it is likely that in our case too, the assemblages might be dominated by a few oxygen tolerant foraminifera that can thrive due to reduced predation. The lack of food, as evident from a drop in $\%C_{org}$ combined with potentially increased predator pressure as inferred from comparatively high dissolved oxygen at a couple of stations (MC-59, MC-60) in the lower slope region, can adversely affect living benthic foraminifera. Similar trends have also been reported from other parts of the Arabian Sea where vertical foraminifera stock increases within OMZs (Jannink et al., 1998; Schumacher et al., 2007; Caulle et al., 2015). The difference in living benthic foraminiferal abundance within the OMZ and the deeper regions of the Gulf of

Mannar is similar to that off Oman (Gooday et al., 2000), Pakistan (Gooday et al., 2009) and central-eastern Arabian Sea (Caulle et al., 2015). In all of these regions, benthic foraminiferal abundance is relatively higher at stations falling within the OMZ than that at deeper depth. Such a clear trend in benthic foraminiferal abundance within and outside OMZ is, however, not observed in the northeastern Arabian Sea (Caulle et al., 2014). The difference might be due to the difference in sampling as we sampled the regions starting from very shallow to a deeper depth covering the OMZ, whereas, in other studies, sampling began within the OMZ and continued to greater depths. The difference is also observed in %$C_{org}$ in all three zone. In Gulf of Mannar, %$C_{org}$ initially increases with depth, but is constant (~5%) from intermediate to deeper depth. But, off Pakistan margin, %$C_{org}$ increases in intermediate depth and decreases in deeper depths (Gooday et al., 2009; Koho et al., 2013). The same is true at a few locations off Indian margin (Caulle et al., 2015). Contrary to that, %$C_{org}$ off Oman region decreases with depth (Gooday et al., 2009). The exact cause of difference in %$C_{org}$ with depth in various Indian Ocean regions is although not clear, is often ascribed to dissolved oxygen concentration, quantity and quality of organic matter flux as well as benthic macro- and megafauna population (Gooday et al., 2010).

In the Gulf of Mannar, as well as the western Bay of Bengal, a significant fraction (up to >90%) of the total benthic foraminiferal population in the OMZ is confined to the core-top (0-1 cm) section. Only at a few stations falling above and below the low dissolved oxygen zone, a sizable fraction of the living population was observed in deeper sections. $ALD_5$ is less than 0.6 in OMZ as compared to >1.0 in both the shallow and deeper depths suggesting that low bottom water dissolved oxygen concentration, is most likely the major factor leading to decreased $ALD_5$ in the Gulf of Mannar. Previously, living benthic foraminifera have been reported to survive up to 10-15 cm down in the sediments (Corliss, 1985; Jannink et al., 1998).

### Calcareous and agglutinated foraminifera

The calcareous foraminifera dominate all the depths. The dominance of calcareous foraminifera over that of the agglutinated foraminifera, continues even within the OMZ, a finding that has been commonly reported from a few other regions as well (Gooday et al., 2000; Caulle et al., 2014). The agglutinated foraminifera comprise only ~12 % (varying from 0-35%) of the vertical foraminifera stock (total living benthic foraminifera in top 5 cm of the sediments). The high absolute abundance of agglutinated benthic foraminifera in the upper slope region, as compared to the lower slope, is the result of a combination of low dissolved oxygen and high %$C_{org}$. The microbial processes under low dissolved oxygen are often associated with more %$C_{org}$ and a resultant low pH (Ben-Yakoov, 1973). The agglutinated benthic foraminifera are more tolerant to low pH as compared to their calcareous counterparts. A relatively more food availability at deeper stations, as evident from high %$C_{org}$, increases the relative abundance of agglutinated benthic foraminifera at stations where dissolved oxygen is also very high. The drastic drop in living calcareous foraminifera and absence of agglutinated benthic foraminifera in deeper sections at almost all the stations is also ascribed to a combination of a drop in dissolved oxygen and %$C_{org}$ with increasing depth in the sediments (Ben-Yakoov, 1973; Kristensen, 2000; Taylor et al., 2015). The reduction and subsequent removal of iron, in the organic cement of agglutinated foraminifera, from ferric to ferrous form, in the deeper sections causes a drastic decline in agglutinated benthic foraminiferal population (Sidner and McKee, 1976; Schröder, 1988). The negative influence of water depth and dissolved oxygen concentration on absolute abundance of calcareous benthic foraminifera in the Gulf of Mannar is also evident from the PCA plot (Figure 6.11). The higher abundance of both the calcareous and agglutinated benthic foraminifera in 1-2 cm section as compared to that in the core top (0-1 cm) section at station MC-60 (water depth 1887 m) is intriguing. The only striking characteristic at this station is much lower %$C_{org}$ in the sub-surface section (1-2 cm) than in the core top section (0-1 cm).

The calcareous foraminifera dominate the living benthic assemblage (>80% at almost all the stations) in the Gulf of Mannar, western Bay of Bengal as well as the eastern Arabian Sea. Our findings are partially in line with the Oman margin, where calcareous foraminifera are abundant in core OMZ as compared to the well oxygenated deeper area (Gooday et al., 2000). In a clear contrast to this, much higher abundance (40-80%) of agglutinated foraminifera has been reported from the OMZ off Pakistan and western Indian margin (Caulle et al., 2014; 2015).

### Epifaunal and Infaunal benthic foraminifera

Several attempts have been made to understand the ecological preferences of benthic foraminiferal morpho-groups, both from the shallow as well as deeper regions (Corliss, 1985, Corliss and Chen, 1988, Nigam et al., 2007; Manasa et al., 2016; Suokhrie et al., 2017). Benthic foraminiferal morpho-groups are not only influenced by turbulence, but also by productivity, oxygenation (Naik et al., 2017). Here we've tried to understand the possible factors affecting benthic foraminiferal morpho-groups in the Gulf of Mannar. The calcareous infaunal forms dominate the living benthic foraminiferal assemblage in the shelf as well as the lower slope of the Gulf of Mannar (Figure 6.20). Both of these regions are marked by high dissolved oxygen. Interestingly, both the calcareous and agglutinated epifaunal forms are abundant in the OMZ. Surprisingly, the spatial distribution trend of both the calcareous and agglutinated infaunal morpho-group in the Gulf of Mannar is opposite to that reported from other regions. The previous studies suggest an increase in infaunal benthic foraminifera in low oxygen environment (Kaiho, 1994; Bernhard and Sen Gupta, 1999; Singh et al., 2015). The distribution of recent benthic foraminifera in surface sediments along the western continental margin of India, also suggests an increase in the relative abundance of angular asymmetrical benthic foraminifera, all of which are infaunal in nature, in OMZ (Nigam et al., 2007). The surface sediments collected from the eastern Arabian Sea, as a part of this doctoral work, also has high abundance of angular asymmetrical forms in the OMZ. The possible reason for the high abundance of infaunal foraminifera in the core-top sections of the Gulf of Mannar, can be the temporal migration of infaunal species towards the top, due to a seasonal change in dissolved oxygen and food availability (Van der Zwaan et al., 1999).

At 1550 m water depth, a station at the lower boundary of OMZ, calcareous infaunal, calcareous epifaunal and agglutinated epifaunal forms equally contribute to the benthic foraminiferal assemblage. Here, %$C_{org}$ is relatively high and dissolved oxygen is >2 ml/l, suggesting a combination of physico-chemical parameters that equally support all these forms. At 1887 m water depth, agglutinated infaunal forms, substantially contribute to the total living benthic assemblage. This station is marked by high dissolved oxygen but a distinct drop in %$C_{org}$, especially in the sub-surface section (1-2 cm) as compared to both the immediate shallow and deep stations, suggesting that low %$C_{org}$ at this station facilitated the abundant infaunal agglutinated foraminifera. The findings are in contrast with California Borderland basins, where agglutinated infaunal forms dominated the station with high %$C_{org}$ (Kaminski et al., 1995). Incidentally, the ratio of infaunal (angular asymmetrical) to epifaunal (rounded symmetrical) benthic foraminifera has also been suggested as a proxy to reconstruct past monsoon (Nigam et al., 1992; Nigam et al., 2009; Manasa et al., 2016). The application arises from the fact that the abundance of rounded symmetrical (epifaunal) forms increases in a turbulent environment when a river drains into the sea (Nigam et al., 1992; Nigam et al., 2009; Manasa et al., 2016). We, however, report that the distribution of infaunal and epifaunal calcareous and agglutinated benthic foraminifera shows a different trend, suggesting a differential effect of ambient conditions. Therefore, the relative abundance of infaunal and epifaunal forms of calcareous and agglutinated benthic foraminifera should not be combined while using changes in benthic foraminiferal morpho-group to reconstruct past climate.

Based on this work, it is clear that not all the living benthic foraminifera are confined to the core-top section (0-1 cm). What is more important is the changes in average living depth with the difference in ambient physico-chemical parameters. It implies that during any particular time, depending on prevailing conditions, living benthic foraminifera will contribute differently to the core-top and sub-surface sections, in the same region. Therefore, it is apparent that the average living depth will vary temporally, in tandem with the ambient conditions. In view of it, we suggest that precaution must be taken when using benthic foraminiferal characteristics for paleoceanographic studies that rely on the assumption that at any given time, core-top sediments contain all the living benthic foraminifera.

## Conclusions

The effect of ambient conditions, especially dissolved oxygen and organic matter on the vertical habitat of living benthic foraminifera has been documented from the Gulf of Mannar, western Bay of Bengal and eastern Arabian Sea. We report that the top 0-1 cm section of the sediment contains >85% of the total living benthic foraminifera at stations within the oxygen minimum zone. The low oxygen in the upper slope region affect the vertical living of foraminifera as the average living depth in this region reduced more than a centimeter, as compared to both the shallow and deeper stations. At stations with high dissolved oxygen, especially in the lower slope, a substantial fraction of the total living benthic foraminiferal population inhabits deeper sections of the sediments. Therefore, it is evident that vertical distribution of benthic foraminifera depends on bottom water oxygen concentration and organic matter quantity. The calcareous benthic foraminifera dominate the foraminiferal population both within and outside the oxygen minimum zone, suggesting their higher adaptability in all types of marine environments. The relative abundance of agglutinated benthic foraminifera is higher in the continental slope as compared to the shelf. All the agglutinated foraminifera are confined to the top 0-1 cm of the sediments in the shelf and upper slope. We further report that infaunal and epifaunal morpho-groups of calcareous and agglutinated foraminifera show a different trend.

# Chapter-7: A unique highly diverse living benthic foraminiferal assemblage in the oxygen deficient zone of the southeastern Arabian Sea

## Introduction

The eukaryotic life on Earth developed only after the great oxygenation event. But, the first billion years of eukaryotic life on earth was under severely oxygen depleted conditions, not comparable to today, suggesting sustenance under oxygen deficient environment (Zimorski et al., 2019). However, a majority of the extant marine organisms are critically influenced by the dissolved oxygen and food (Wishner et al., 2018; Laffoley and Baxter, 2019). The restricted circulation and water column stratification leading to limited replenishment, coupled with high marine primary productivity results in excessive utilization of the available oxygen and thus creates oxygen deficient zones (ODZ) (Naqvi et al., 2009). Post-industrialization global warming is creating life threatening challenges for the terrestrial as well as marine biospheres. In the ocean ecosystem, increasing sea surface temperature (SST) is suggested as the leading factor for the decrease in dissolved oxygen and thus the expanding ODZs (Moffitt et al., 2015). Anthropogenic activities have contributed towards the expansion of ODZs (Breitburg et al., 2018), by facilitating oxygen loss from warm waters and increased nutrient load (Bouwman et al., 2005) supporting primary productivity (Reed et al., 2017). The decreased dissolved oxygen in the sea surface water increases the mortality of planktic fauna (Takarina et al., 2017) and causes vertical compression of benthic habitat (Stramma et al., 2010; McCormick and Levin, 2017). The decreased dissolved oxygen also alters marine elemental cycling (Naqvi et al., 2010; Lei et al., 2017). Therefore, it is important to understand the dynamics of ODZs. The record of spatio-temporal variability of ODZs helps in understanding its dynamics.

Biologically productive regions like the eastern Pacific Ocean (off Peru and off California margin), continental margin off Western Africa and the Arabian Sea are the key zones to understand the oceanographic processes depleting the dissolved oxygen at certain depth in the ocean. In the Arabian Sea, a strong coastal upwelling induced primary productivity, sluggish circulation coupled with water column stratification, creates an intense perennial ODZ at intermediate depths. The well-defined ODZ in the Arabian Sea is the deepest ODZ (150-1500 m) in the world ocean (Naqvi et al., 2009). Additionally, a seasonal hypoxic zone also develops on the continental shelf (Naqvi et al., 2006). The intense ODZs of the Arabian Sea include the region off Oman, off Pakistan and off the southern tip of India. A low dissolved oxygen zone has also been reported from the western Bay of Bengal (Bristow et al., 2017). Interestingly, the Bay of Bengal ODZ is not as intense as that in the Arabian Sea. The influx of Arabian Sea high salinity water is suggested to sustain the dissolved oxygen in the Bay of Bengal (Jain et al., 2017). The water between the Arabian Sea and the Bay of Bengal is exchanged through the region off the southern tip of India, creating a strong seasonal contrast in the ambient parameters, including a low dissolved oxygen zone in this region. Therefore, the southeastern Arabian Sea, can provide insight into the effect of the change in cross basin exchange of seawater in modulating ODZ in both the Arabian Sea and Bay of Bengal.

The low dissolved oxygen affects living benthic fauna, in the region, where it impinges on bottom sediments (Levin, 2003; Levin et al., 2000). Benthic foraminifera (marine unicellular protists) are very sensitive to change in the ambient dissolved oxygen (Kaiho, 1994; Kaminski et al., 1995; Jorissen et al., 1995; Gooday et al., 2000; Singh et al., Filipsson and Nordberg, 2004; 2010; 2006; Bhaumik and Gupta, 2005; Nigam et al., 2007; Filipsson et al., 2011; Kaminski, 2012; Mackensen et al., 1985; Caulle et al., 2015; Manasa et al., 2016; Singh et al., 2018). Thus, benthic foraminifera have been extensively used to reconstruct the past ODZ strength in the world ocean (Reichart et al., 1998; Den Dulk et al., 2000; Aksu et al., 2002; Nigam et al., 2009; Singh et al., 2015; Naik et al., 2017). Benthic foraminifera include a few thousands of species worldwide, with unique microhabitat preference (Lei et al., 2017; 2019). Different species thrive in different ODZ regions in the world Ocean. Therefore, it is imperative to document the unique benthic foraminiferal assemblage and/or species characteristic of the different ODZs.

From the Arabian Sea, living benthic foraminifera have been documented from ODZ off Pakistan margin (Caulle et al., 2014; Enge et al., 2014; Erbacher and Nelskamp, 2006; Gooday et al., 2009; Jannink et al., 1998; Larkin and Gooday, 2008; Schumacher et al., 2007), off Oman (Hermelin and Shimmield, 1990; Gooday et al., 2000) and off the Indian margin (Caulle et al., 2015). So far, there is no such detailed study documenting living benthic foraminifera from the ODZ off the eastern and western margin of India. Additionally, a majority of paleo-ODZ studies relied on the application of benthic foraminifera identified in the top one or two cm of the sediments recovered from the modern ODZ. However, benthic foraminifera frequently migrate up or down in the sediments (Mackensen and Douglas, 1989), especially in response to the changing ambient dissolved oxygen. Therefore, the living benthic foraminifera in a substantial section of the top sediments must be documented for more precise identification of assemblage characteristic of the ambient ODZ. Here we assess the influence of strong seasonal stress on benthic foraminifera living in the top 5 cm of the sediments within the ODZ of the southeastern Arabian Sea.

## Results

The multicore samples cover the region from the very shallow-continental shelf to deep continental slope. The sediments were mainly clayey-mud except at station MC07 and MC08, where it was mainly coarse sand. The main source of clay in this region is input from the Bay of Bengal water as it brings a lots of clay as a result of higher monsoon sediment influx. The coarse sand on the continental shelf is derived from the broad carbonate shelf. This heterogeneity in sediment type also influences the living habitat of benthic fauna in the region.

### Ecological parameters

The seawater temperature at the sediment-water interphase varied between 2.06-25.96°C. The salinity varied between 34.75-35.19 psu and both decreased with increasing depths. Bottom water dissolved oxygen varied between 0.48-3.48 mL/L (21-155 µM) and ODZ (<2.00 mL/L or <90 µM) lies between 152- 1550 m water depth. The organic carbon concentration varied from 1.52% to 6.86% in core-tops. In the top 5 cm sediment

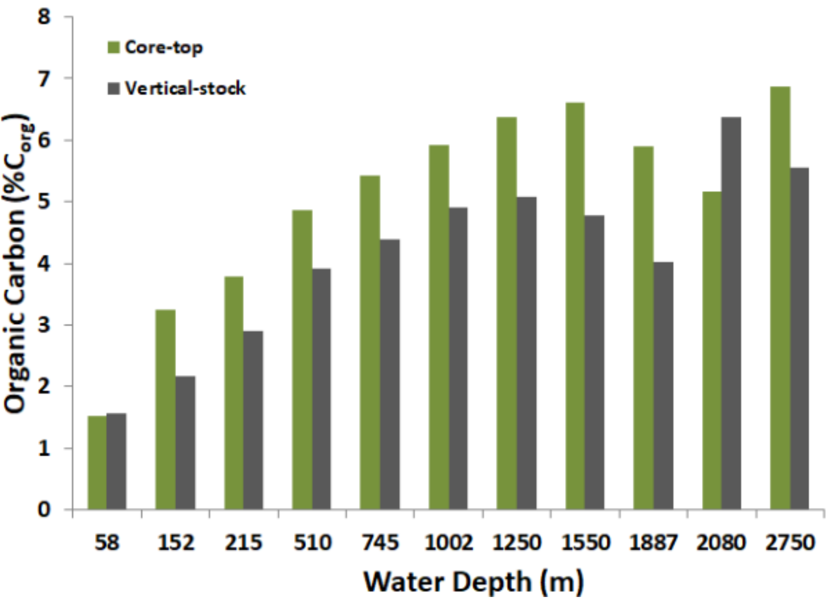

**Figure 7.1: The organic carbon variation with depth in the core-top (0-1cm) and 0-5 cm section.**

section, %$C_{org}$ varied between 1.57-6.37%. Organic carbon increased from shallow to deeper depths with slight decrease after MC01 (1550 m) (Figure 7.1). %Corg/TN varied between 8.84-16.43 in the core-top and 6.64-15.19 in the 0-5 cm section. In the 0-5 cm section, %$C_{org}$/TN was lower at intermediate depths as compared to the shallower and deeper depths. Such a trend was not observed in core-top section (Figure 7.2).

**Faunal abundance**

The living benthic foraminiferal abundance varied between 14-3216 specimen/g sediment in the core-top section (Singh et al., 2018) (Figure 7.3a). The abundance decreased to 8-48 specimen/g sediment in the top 5 cm section of the sediment (Figure 7.3b). The reduced abundance in the 0-5 cm section was mainly due to the rare presence of living benthic foraminifera in deeper sections (2-3 cm, 3-4 cm and 4-5 cm). We found the highest abundance of living benthic foraminifera at 215 m (MC06) and the minimum was at 1887 m (MC60) in the core-top sections. The same is also true for the 0-5 cm section (Figure 7.3a, b). In the core-top sections, the absolute abundance increased many folds at Intermediate water depth stations (MC03, 04, 05, 06), as compared to shallower/deeper non ODZ depths. Such an abundance trend was, however, not as prominent in the 0-5 cm section.

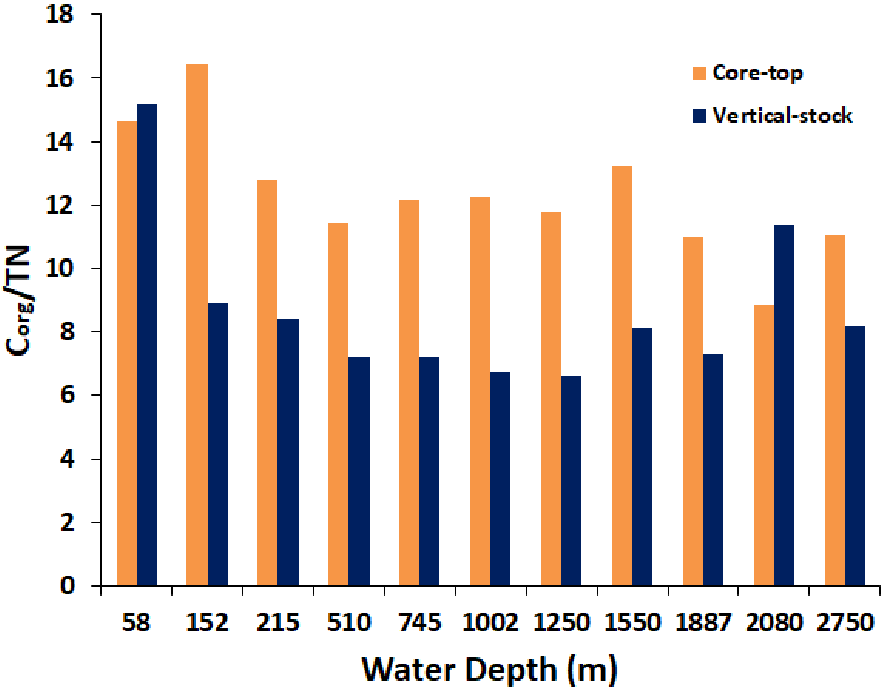

**Figure 7.2: $C_{org}$/Nitrogen variation with depth in core-top (0-1 cm) and 0-5 cm section.**

We found 112 living benthic foraminifera in the south-eastern Arabian Sea (Table 7.1). In terms of the species composition at the shallowest station (MC08; 58 m), *Cassidulina laevigata* (45%), *Eponides umbonatus* (20%) and *Cassidulina carinata* (11%) were the top three contributors in the core top as well as the 0-5 cm section. The relative abundance of these species was, however, lower in the 0-5 cm section [*Cassidulina laevigata* (35%), *Eponides umbonatus* (15%) *Cassidulina carinata* (9%)] (Figure 7.4). In the core-top section of station MC07 and MC06, with the lowest dissolved oxygen, *Bolivina seminuda* dominates the assemblage with 31% and 49% relative abundance, respectively. Besides this, the abundant presence of *Bulimina elegans*, *Bolivina dilatata* and *Hopkinsinella glabra*, represents the low dissolved oxygen assemblage in this region. *Bolivina seminuda* dominates the 0-5 cm section also, with 40% abundance at MC07 and 57% at MC06 (Figure 7.4). At MC05 and MC04, *Rotaliatinopsis semiinvoluta* (23% and 25% respectively) was the dominant species along with *Bolivina currai* (5% and 13% respectively) and *Epistominella exigua* (5% and 13% respectively), whereas *Hopkinsinella*

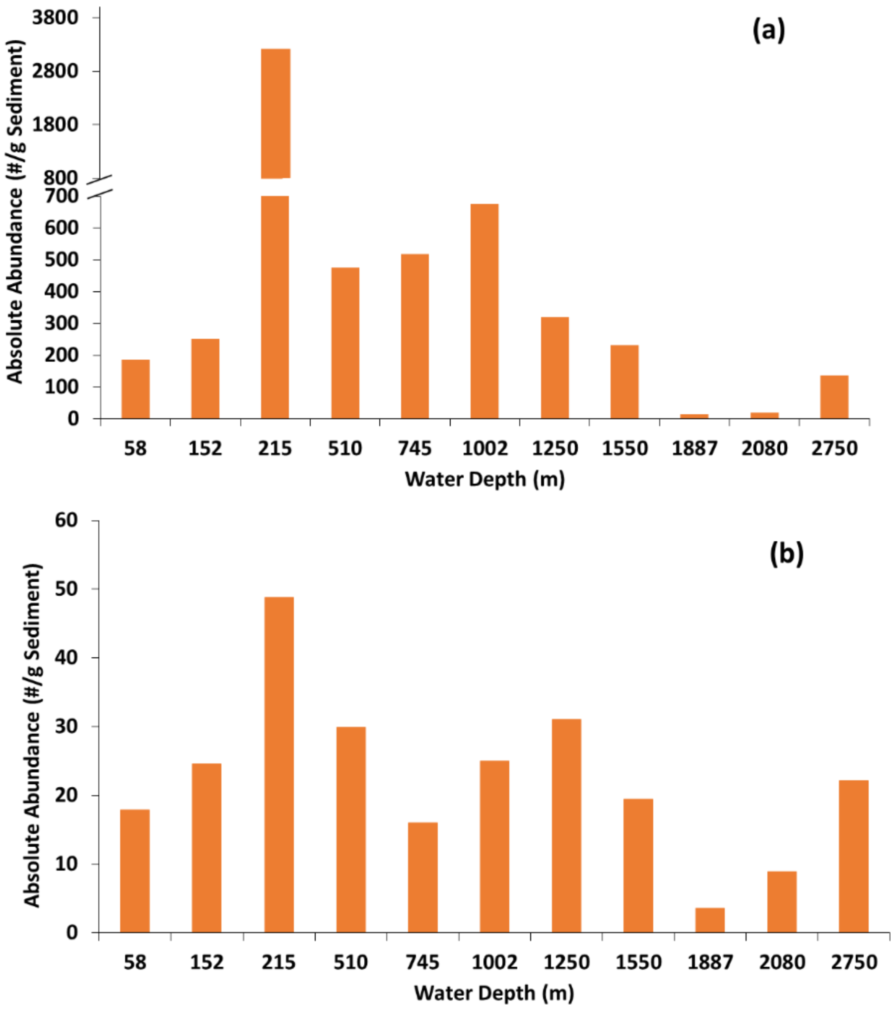

**Figure 7.3: The absolute abundance of living benthic foraminifera (#/g Sediment) in the a) core-top (0-1 cm) and b) 0-5 cm section.**

*glabra* (19% and 6% respectively) and *Rotaliatinopsis semiinvoluta* (13% and 14% respectively) were abundant in the 0-5 cm section. *Bolivina currai* was also present at MC07 (12%) in the core-top (Figure 7.4). At MC03, *Epistominella exigua* (39%) *Bolivina dilatata* (14%) and *Bolivina currai* (10%) were dominant in both the core-top as well as the 0-5 cm section with 26%, 10% and 6% abundance, respectively. At MC02, *Bolivina dilatata* (18%), *Bolivina churchi* (13%) and *Pullenia salisburyi* (6%) were abundant in the core-top and *Bolivina dilatata* (15%), *Bolivina*

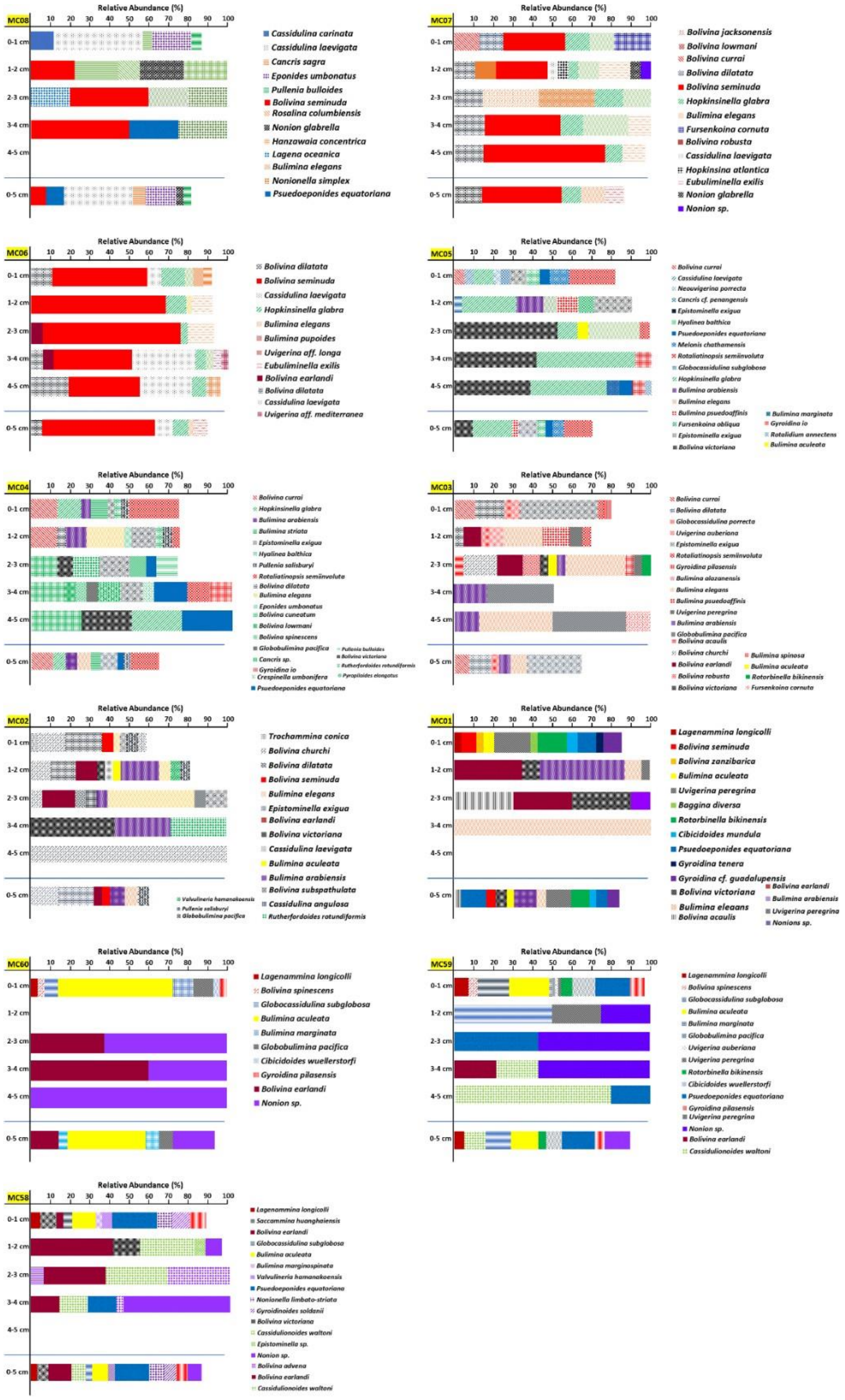

**Figure 7.4: The relative abundance of benthic foraminifera species in each section up to 5 cm depth as well as in the 0-5 cm section. The species having >3% relative abundance are illustrated in the graph.**

*churchi* (12%) and *Bulimina arabiensis* (6%) were abundant in the 0-5 cm section (Figure 7.4). At MC01, *Uvigerina peregrina, Rotorbinella bikinensis* and *Pseudoeponides equatoriana* were the most dominant species in the core-top, whereas *Bolivina earlandi, Bulimina arabiensis* and *Uvigerina peregrina* were abundant in the 0-5 cm section. At the deeper stations (MC60, 59 and 58), *Bulimina aculeata, Globocassidulina subglobosa, Pseudoeponides equatoriana* were abundant in the core-top section, whereas 0-5 cm section was dominated by *Bolivina earlandi, Bulimina aculeata* and *Pseudoeponides equatoriana* (Figure 7.4).

The depth habitat of the dominant species in the south-eastern Arabian Sea was defined from its vertical distribution (Figure 7.4, Table 7.2). Amongst the dominant living benthic foraminifera in the south-eastern Arabian Sea, 17 (*Baggina diversa, Bulimina marginospinata, Bulimina pupoides, Bulimina striata, Cancris cf. penangensis, Cassidulina carinata, Cibicidoides mundula, Cibicidoides wuellerstorfi, Eponides umbonatus, Gyroidina cf. guadalupensis, Gyroidina tenera, Gyroidinoides soldanii, Lagenammina longicolli, Melonis chathamensis, Neouvigerina porrecta, Saccammina huanghaiensis, Trochammina conica*) were strictly epifaunal (found only in the top 0-1 cm section). Only one species (*Bolivina acaulis*) was shallow-infaunal (found in 1-3 cm section of the sediments). The depth habitat of a majority (23) of the species (*Bolivina churchi, Bolivina currai, Bolivina dilatata, Bolivina earlandi, Bolivina seminuda, Bulimina aculeata, Bulimina pseudoaffinis, Cancris sagra, Cassidulionoides waltoni, Globocassidulina porrecta, Globocassidulina subglobosa, Gyroidina pilasensis, Hyalinea balthica, Nonion glabrella, Nonionella limbato-striata, Pullenia bulloides, Pullenia salisburyi, Rotaliatinopsis semiinvoluta, Rotorbinella bikinensis, Uvigerina aff. Longa, Uvigerina auberiana, Uvigerina peregrina, Valvulineria hamanakoensis*) varied from epifaunal to shallow-infaunal. Only four species, namely *Bulimina marginata, Eubuliminella exilis, Globobulimina pacifica*, and *Nonion* sp., were shallow to deep-infaunal (living at 1-5 cm depth) in the south-eastern Arabian Sea. A few species (*Bolivina victoriana, Bulimina arabiensis, Bulimina elegans, Cassidulina laevigata, Epistominella exigua, Hopkinsinella glabra, Pseudoeponides equatoriana*) were found in all top 5 cm of the sediments, suggesting a variable depth habitat from epifaunal to deep-infaunal. Interestingly, one species, namely *Fursenkoina cornuta* was found in epifaunal and deep-infaunal habitats and not within shallow-infaunal depths.

Among all the living benthic foraminifera, only those species with ≥3% relative abundance, are used for the detailed statistical analysis. MVSP run between ambient parameters and species abundance, is discussed below. The ecological preferences in the core-top and 0-5 cm section are discussed separately. The comparison with ambient parameters in both the core top section as well as the 0-5 cm section, helps to understand species' living depth habitat/vertical movement and their ecological preferences.

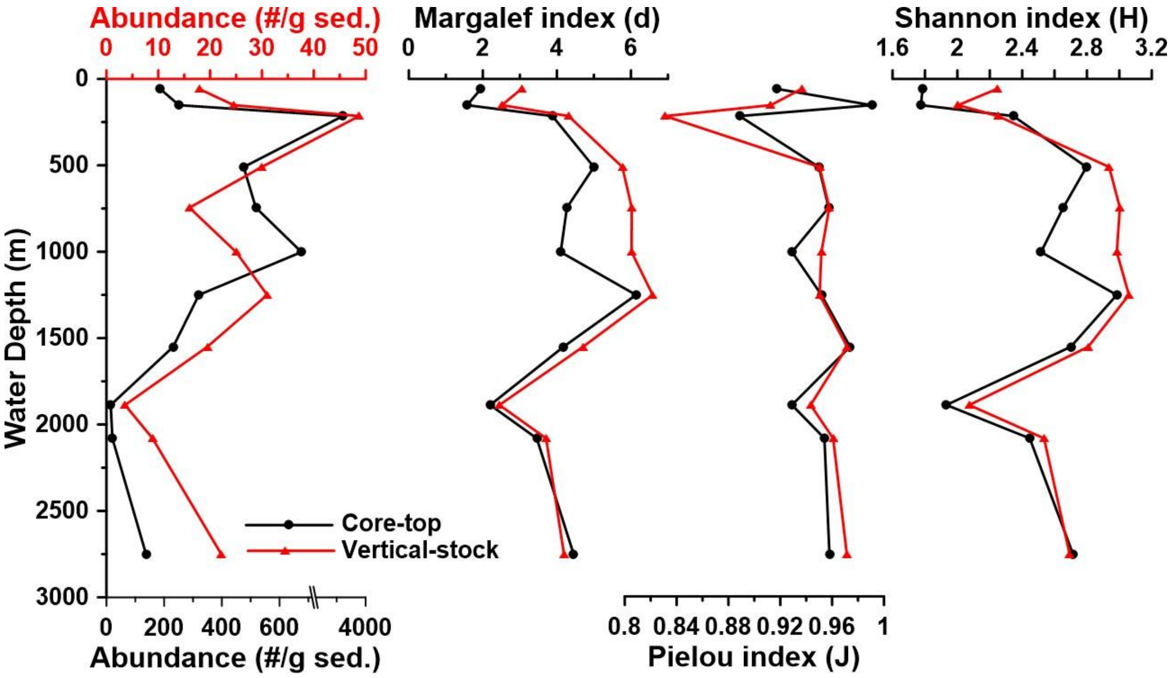

**Figure 7.5: Biodiversity indices [Margalef index (d) for richness, Pielou index (J) for evenness and Shannon index (H) for diversity] of the living benthic foraminifera in the core-top (0-1 cm) and 0-5 cm section.**

### Biodiversity index

From the surface distribution of living benthic foraminifera, Margalef index (d) for richness, Pielou index (J) for evenness and Shannon index (H) for diversity was calculated by using PRIMER software. The species richness, diversity and evenness were high at the intermediate depths, within the ODZ. In the core-top section, Margalef index varies between 1.5-6.1 with maximum value at MC02 (1250 m) and minimum at MC07 (152 m) (Figure 7.5). Pielou index varied between 0.88-0.97 with the maximum value at MC01 (1550 m) and the minimum at MC06 (215 m). Shannon index (H) varied between 1.77-2.98, with the maximum value at MC02 (1250 m) and the minimum at MC07 (152 m).

The same pattern is also observed in the 0-5 cm section also with higher d, J and H index at the intermediate depths (Figure 7.5).

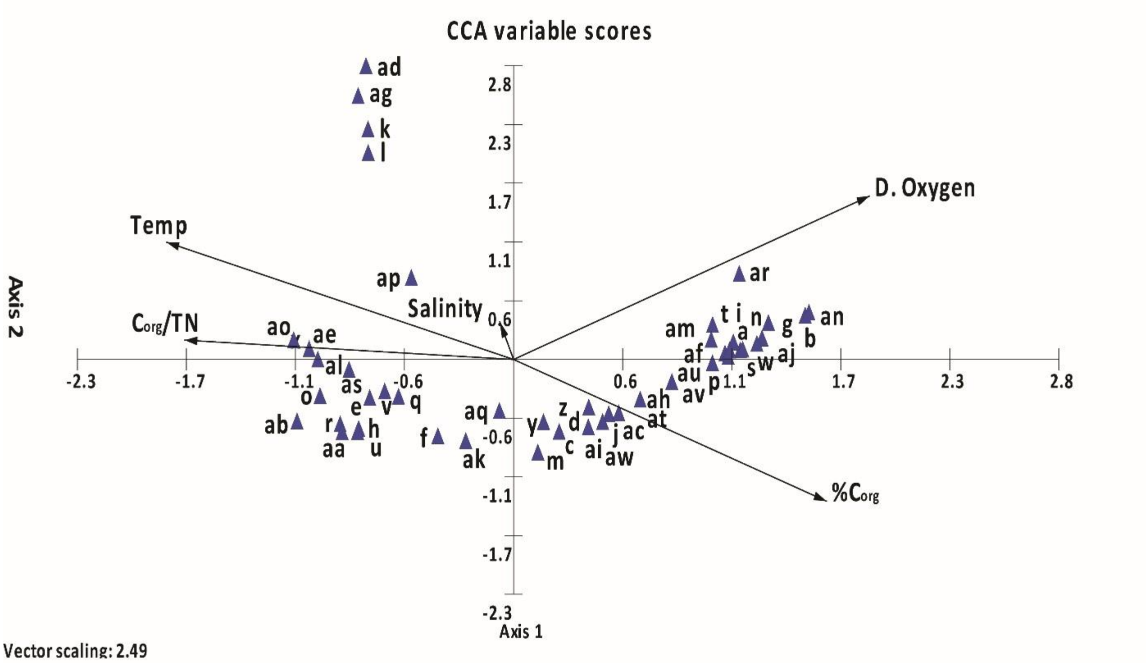

**Figure 7.6: Canonical Correspondence Analysis plot between the relative abundance of species in the core-top section and ambient ecological parameters. See Table 3 for abbreviation details.**

## Ecological preferences of living benthic foraminifera in core-top section

Total 49 species had ≥3% abundance in core top samples (0-1 cm). In the Canonical Correspondence Analysis (CCA), total 14 species had a negative relationship and 11 were positively correlated with the bottom water dissolved oxygen (Figure 7.6, 7.7a). The relationship of benthic foraminifera species with the organic matter was also evaluated, as ODZ and %$C_{org}$ are closely linked. A total of 13 species were positively correlated with %$C_{org}$ and 7 were negatively correlated (Figure 7.7b). With the bottom water temperature, salinity and %$C_{org}$/TN, the relationship, however, was opposite to that with %$C_{org}$. Considering the large number of species with positive/negative correlation, we evaluated the significance level of the relationship between species abundance and ecological parameters (p-value <0.05). From the p-value, we observed that only *Lagenammina longicolli* and *Gyroidina pilasensis* had significantly positive relationship and *Bolivina currai* and *Hopkinsinella glabra* had negative relationship with dissolved oxygen (Table 7.3). It is interesting to mention that none of the species had a significantly positive correlation with organic carbon. This is likely because %$C_{org}$ is in excess and not limiting in the Gulf of Mannar. However, *Cassidulina carinata*, *Cassidulina laevigata, Cancris sagra* and *Eponides umbonatus* are negatively correlated with %$C_{org}$ (Table 7.3).

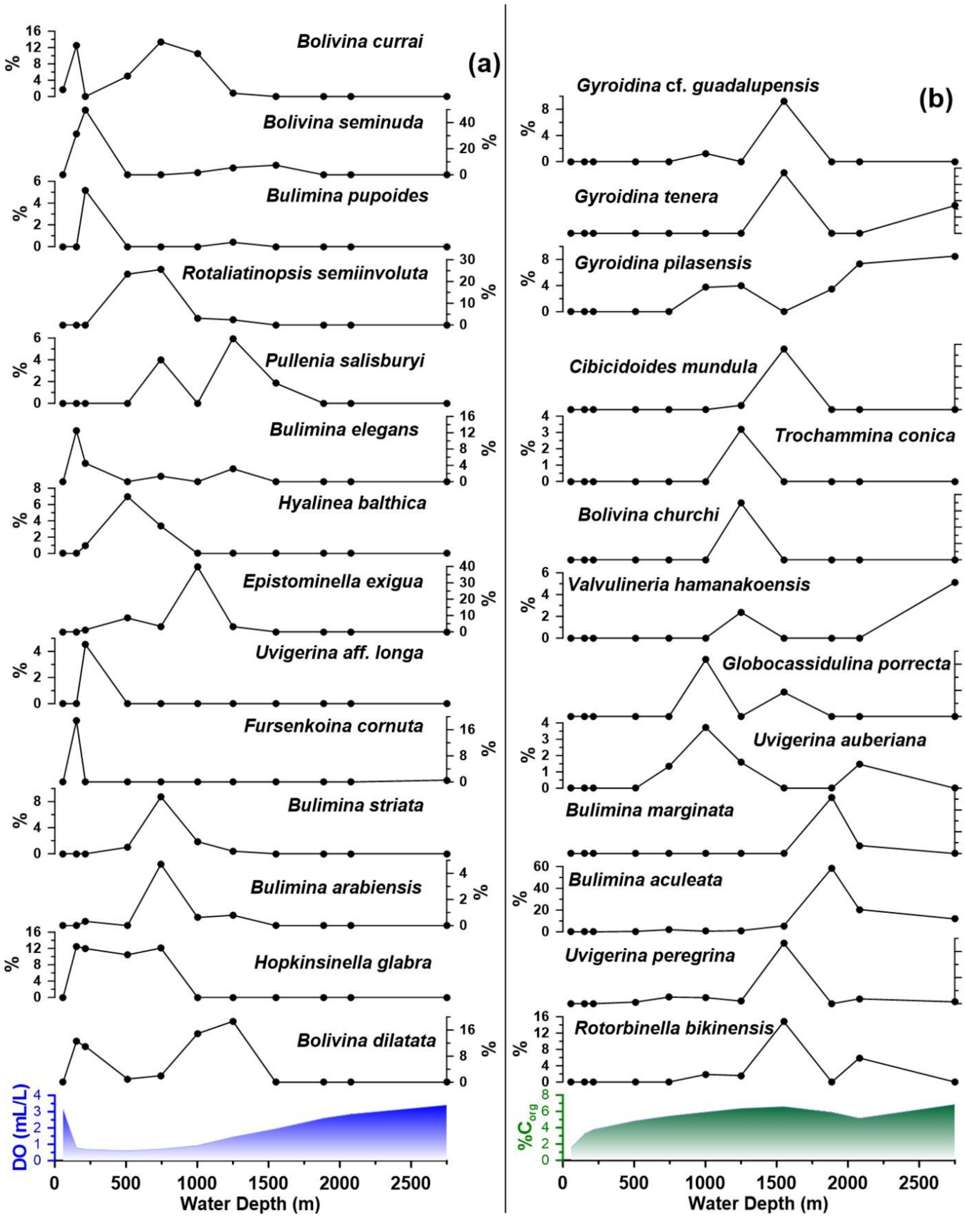

**Figure 7.7: The a) relative abundance (%) of benthic foraminifera showing negative relationship with bottom water dissolved oxygen, and b) positive relationship with organic carbon (%$C_{org}$), in the core-top section.**

*Lagenammina longicolli*, *Bolivina spinescens*, *Globocassidulina subglobosa*, *Cibicidoides wuellerstorfi* and *Gyroidina pilasensis* were negatively correlated with %$C_{org}$/TN, whereas *Fursenkoina cornuta* and *Bulimina elegans* were positively correlated. Beside this, species like *Cassidulina carinata*, *Cassidulina laevigata*, *Cancris sagra* and *Eponides umbonatus* showed a significant positive correlation with bottom water temperature and *Gyroidina pilasensis* was negatively correlated. In case of bottom water salinity, only *Bolivina seminuda* showed a significant positive correlation, while *Bulimina striata*, *Hyalinea balthica* and *Rotaliatinopsis semiinvoluta* showed a significant negative correlation with ambient salinity (Figure 7.6; Table 7.3).

## Living benthic foraminifera in 0-5 cm section and their ecological preferences

Total 43 species had ≥3% relative abundance in the top 5 cm section. Amongst all the abundant species, 10 showed positive and 12 species showed negative correlation with bottom water dissolved oxygen in the CCA plot (Figure 7.8, 7.9a). *Lagenammina longicolli* was significantly positively correlated, whereas *Hopkinsinella glabra* and *Bulimina elegans* were significantly negatively correlated with dissolved oxygen. Beside this, 14 species showed a positive and 6 species showed a negative relationship with %$C_{org}$ in sediments (Figure 7.9b). *Lagenammina longicolli*, *Cassidulinoides waltoni*, *Pseudoeponides equatoriana*, *Gyroidina pilasensis* showed a positive correlation, whereas *Cassidulina laevigata* and *Nonion glabrella* were negatively correlated with %$C_{org}$.

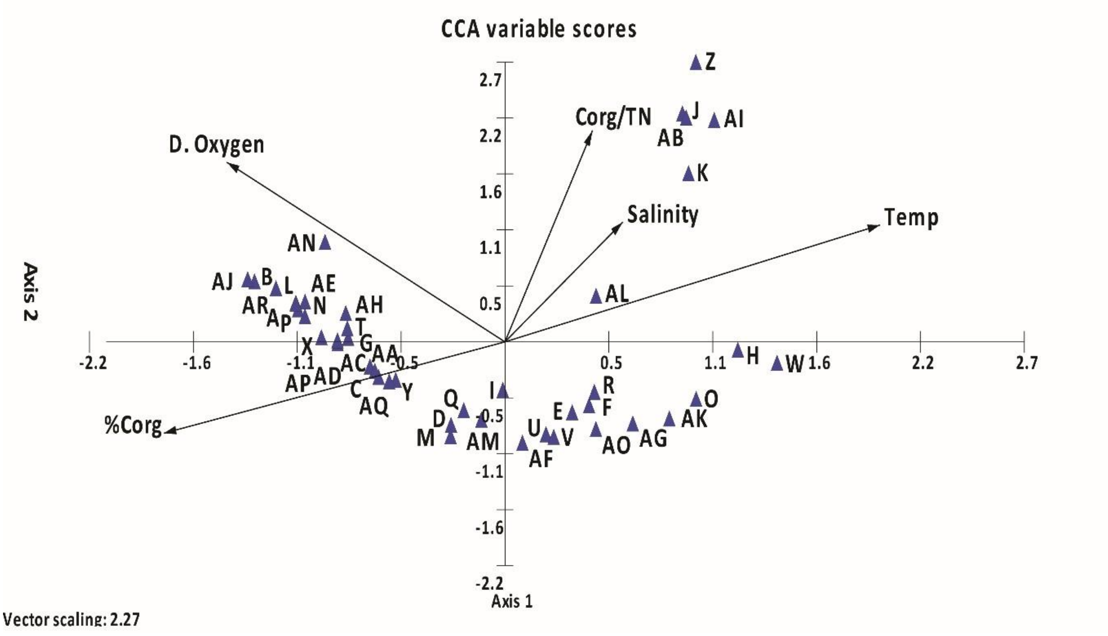

**Figure 7.8: Canonical Correspondence Analysis plot between the relative abundance of species in the top 5 cm section and ambient ecological parameters. See Table 4 for abbreviation. details.**

*Cassidulina carinata*, *Cassidulina laevigata, Cancris sagra*, *Eponides umbonatus*, *Nonion glabrella* were significantly positively correlated with %$C_{org}$/TN and none of the species were significantly negatively correlated. *Bolivina seminuda, Cassidulina carinata, Cassidulina laevigata, Eubuliminella exilis, Cancris sagra*, *Eponides umbonatus*, *Nonion glabrella* were significantly positively correlated, whereas *Gyroidina pilasensis* showed a significant negative relationship with bottom water temperature (Figure 7.8; Table 7.4). *Bolivina seminuda*, *Eubuliminella exilis* showed a significant positive and *Bolivina currai*, *Bulimina pseudoaffinis*, *Bulimina striata*, *Hyalinea balthica*, *Rotaliatinopsis semiinvoluta* showed a significant negative correlation with bottom water salinity (Figure 7.9; Table 7.4).

### Benthic foraminifera within ODZ (core-top, 0-1 cm)

A total 14 species (*Bolivina dilatata*, *Hopkinsinella glabra, Bulimina arabiensis, Bulimina striata*, *Fursenkoina cornuta, Uvigerina* aff. *longa, Epistominella exigua, Hyalinea balthica, Bulimina elgans, Pullenia salisburyi, Rotaliatinopsis semiinvoluta, Bolivina seminuda, Bolivina currai and Bulimina pupoides*) (Figure 7.7a) were negatively correlated with bottom water dissolved oxygen. Out of these, two species, namely *Bolivina currai* and *Hopkinsinella glabra* showed a significant negative correlation with dissolved oxygen, based on p-value. These species were abundant at ODZ depths, especially lower to mid-ODZ depths. These highly abundant benthic foraminifera species of ODZ, belong to the angular asymmetrical morpho-group, a widely accepted morphological adaptation in the ODZ conditions. Surprisingly, a few rounded symmetrical forms like *Epistominella exigua*, *Hyalinea balthica*, as well as the rounded symmetrical forms with comparatively bigger aperture, like *Rotaliatinopsis semiinvoluta* and *Pullenia salisburyi*, are also abundant in the ODZ. These findings suggest that except angular asymmetrical forms, the rounded forms with bigger aperture can also adapt and thrive well in the ODZ.

### Benthic Foraminifera within ODZ (0-5 cm section)

In the top 5 cm section, 12 species (*Bolivina dilatata, Hopkinsinella glabra, Bulimina striata, Epistominella exigua, Hyalinea balthica, Bulimina elgans, Bulimina pseudoaffinis, Rotaliatinopsis semiinvoluta, Bolivina seminuda, Bolivina currai, Melonis chathamensis* and *Eubuliminella exilis*) (Figure 7.9a) were negatively correlated with bottom water dissolved oxygen.

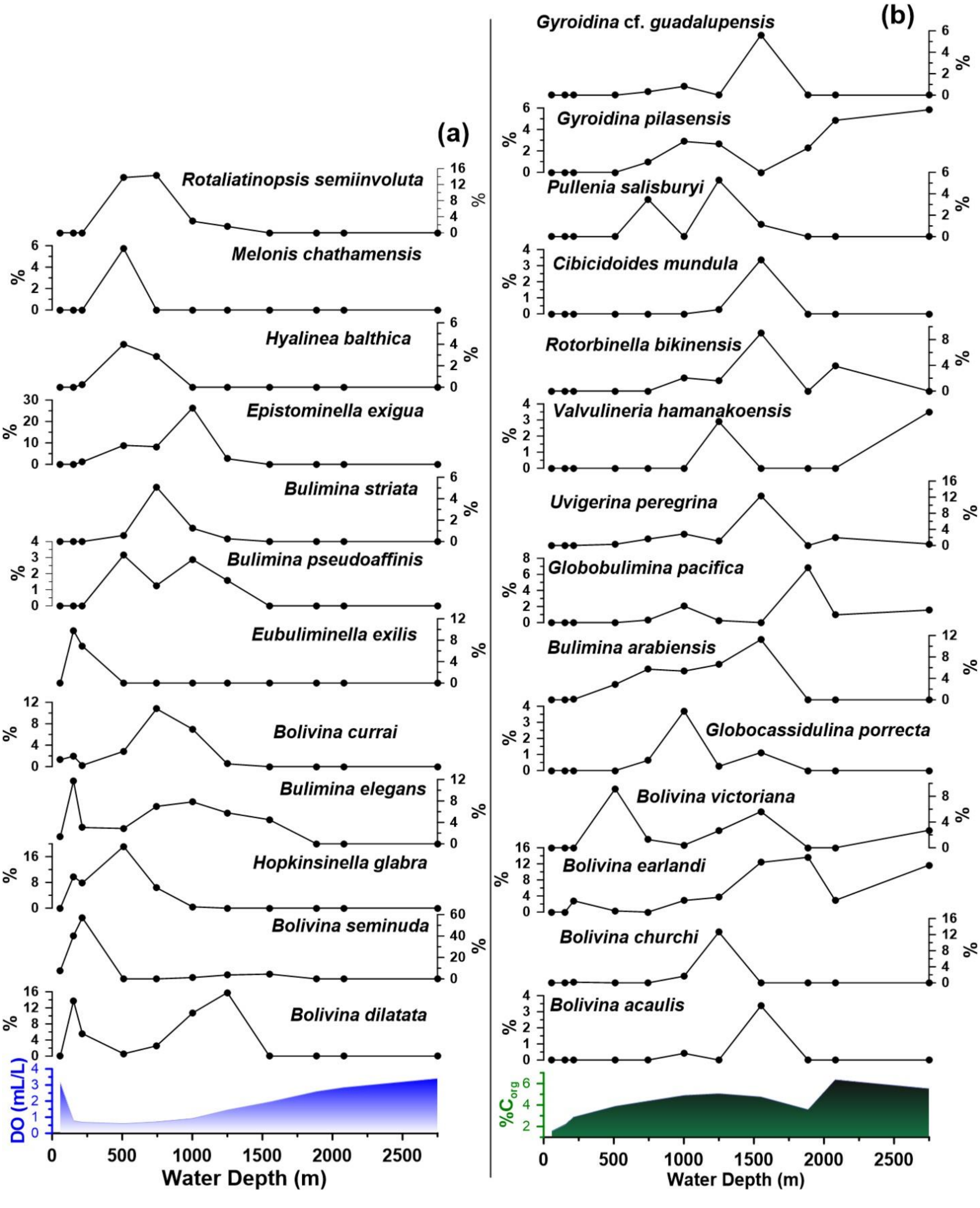

**Figure 7.9: The a) relative abundance (%) of benthic foraminifera showing negative relationship with bottom water dissolved oxygen, and b) positive relationship with organic carbon (%$C_{org}$) in the top 5 cm section.**

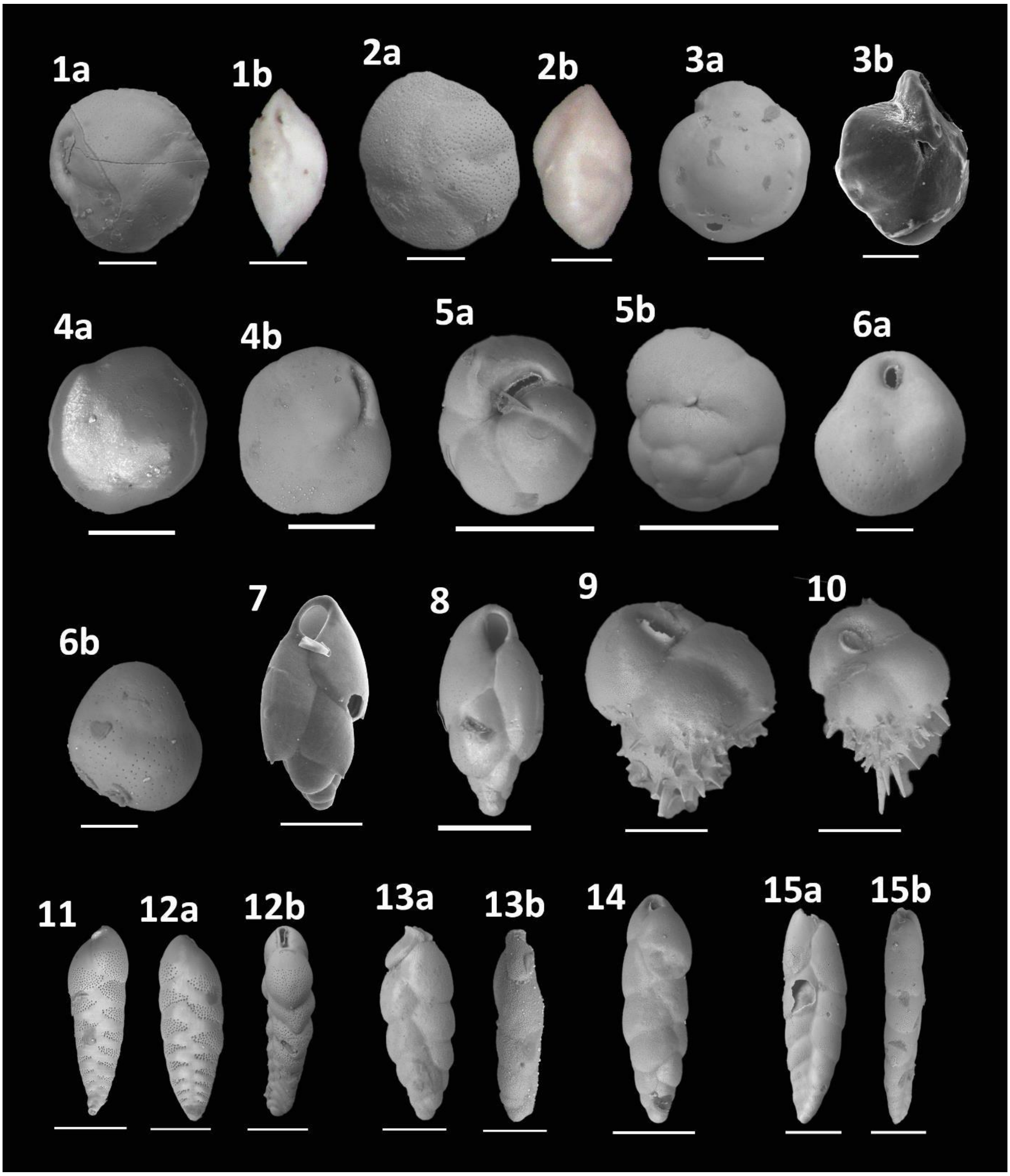

**Plate 1: 1. *Cassidulina laevigata* (a-side view; b- lateral view), 2. *Cassidulina carinata* (a-side view; b- lateral view, 3. *Eponides umbonatus* (a-side view; b- lateral view, 4. *Epistominella exigua* (a-side view; b- apertural view), 5. *Rotaliatinopsis semiinvoluta* (a- apertural view; b- side view;), 6. *Globocassidulina subglobosa* (a-side view; b- lateral view), 7. *Bulimina arabiensis,* 8. *Bulimina elegans,* 9 and 10. *Bulimina aculeata,* 11 and 12. *Bolivina seminuda* (a-side view; b- lateral view), 13. *Hopkinsinella glabra* (a-side view; b- lateral view), 14. *Eubuliminella exilis,* 15. *Bolivina earlandi* (a-side view; b- lateral view). Scale= 100 µm.**

*Hopkinsinella glabra* and *Bulimina elegans* were significantly negatively correlated with the ambient dissolved oxygen. Interestingly, it is evident that the species that showed affinity for intense ODZ condition in core top section, does not necessarily show a similar preference in 0-5 cm section. The difference in the representative species in the core-top and 0-5 cm section suggests vertical migration of species is important phenomena in the ODZ and the species representing vertical movement, should be carefully considered for paleo-reconstruction.

## Discussion

Benthic foraminifera are relatively abundant in the ODZ. We also found higher abundance of benthic foraminifera in the intermediate depths where organic matter was more, and dissolved oxygen was deficient. The quality and quantity of organic matter in the sediments is considered as one of the major factors modulating abundance and diversity of living benthic foraminifera (Jorissen et al., 1995; 2007; Jannink et al., 1998; Schumacher et al., 2007). Benthic foraminifera thrive well in high %$C_{org}$ environments (Bhaumik et al., 2014; Den Dulk et al., 2000; Gooday and Turley, 1990; Jorissen et al., 1992; 1995; Kaminski et al., 1995; McCorkle et al., 1997; Nomaki et al., 2008). The high %$C_{org}$ sediments are often oxygen deficient. In the Gulf of Mannar, the sediments have excess organic matter. The excess organic matter facilitates such high abundance of living benthic foraminifera, despite of the low dissolved oxygen. The low dissolved oxygen in organic matter rich sediments, however, allows only a few selected benthic foraminiferal species to thrive (Sen Gupta and Machain-Castillo, 1993; Van Der Zwaan et al., 1999). Interestingly, this low dissolved oxygen severely affects the predators, thus imparting a positive influence on the survival and growth of benthic fauna in $C_{org}$ rich sediments (Jorissen et al., 1995). As evident, the higher %$C_{org}$ at the intermediate depths of the southeastern Arabian Sea also facilitates prolific abundance of benthic foraminifera. Although in core- top sections, we did not find any species with significant positive correlation with %$C_{org}$, in 0-5 cm section *Lagenammina longicolli, Cassidulina laevigata, Pseudoeponides equatoriana, Gyroidina pilasensis* showed a significant positive correlation with %$C_{org}$. Our findings are partially in-line with previous reports from the eastern Arabian Sea where bottom water dissolved oxygen was reported as the prime factor controlling the species composition (Caulle et al., 2015).

In the Gulf of Mannar, *Bolivina seminuda*, *Bolivina dilatata*, *Eubuliminella exilis, Bulimina elegans, Bulimina aculeata and Hopkinsinella glabra* are highly abundant in waters with low dissolved oxygen. Several attempts have been made to identify the key benthic foraminiferal species from the world ocean ODZ, including parts of the Arabian Sea (Hermelin and Shimmield, 1990; Jannink et al., 1998; Gooday et al., 2000; Schumacher et al., 2007; Larkin and Gooday, 2008; Enge et al., 2014; Erbacher and Nelskamp, 2006; Gooday et al., 2009; Jannink et al., 1998; Caulle et al., 2014; 2015; Mazumder and Nigam, 2014). Earlier, several of these species, including *Bolivina seminuda*, *Bolivina dilatata* and *Eubuliminella exilis* were reported to be abundant in the upper part of ODZ in the northeastern Arabian Sea (Jannink et al., 1998; Erbacher and Nelskamp, 2006; Schumacher et al., 2007; Larkin and Gooday, 2008; Gooday et al., 2009; Caulle et al., 2014; Enge et al., 2014). We report a difference in the depth preference of these species in the ODZ of the southeastern Arabian Sea. *Bolivina dilatata* was abundant throughout the ODZ and *Bulimina elegans* as well as *Hopkinsinella glabra* were abundant in the middle and lower part of the ODZ in the southeastern Arabian Sea, with much higher abundance at deeper ODZ depths. We report that *Bulimina currai*, *Bulimina elegans* and *Hopkinsinella glabra* are the most significant species to reconstruct past ODZ from the southeastern Arabian Sea. Besides this, out of the several other dominant species within and below the ODZ of the northern Arabian Sea (*Rotaliatinopsis semiinvoluta*, *Uvigerina peregrina*, *Bulimina aculeata* and *Epistominella exigua*) (Schumacher et al., 2007; Caulle et al., 2014), we only found *Rotaliatinopsis semiinvoluta* and *Epistominella exigua* being negatively correlated with dissolved oxygen in the southeastern Arabian Sea. *Bolivina*, *Bulimina* and *Uvigerina* were also reported to be abundant genera in the eastern Arabian Sea ODZ (Mazumder and Nigam, 2014).

Recently, a detailed description of living benthic foraminifera from the continental shelf to slope and further deeper region of the central-western Bay of Bengal ODZ was published (Suokhrie et al., 2020). The central-western Bay of Bengal receives a huge riverine influx. We compared the living benthic foraminifera dominant in the southeastern Arabian Sea ODZ with that from the central-western Bay of Bengal ODZ. Amongst the fourteen species abundant in the surface sediments and the top 5 cm section of the southeastern Arabian Sea ODZ, only three (*Eubuliminella exilis*, *Hopkinsinella glabra*, *Rotaliatinopsis semiinvoluta*) were also found in the central Bay of Bengal ODZ (Suokhrie et al., 2020). Incidentally, two of these species, namely *Eubuliminella exilis* and

*Rotaliatinopsis semiinvoluta* are abundant in the ODZ of the central-western Bay of Bengal, northern Arabian Sea as well as the southeastern Arabian Sea.

Within the ODZs, denitrification also strongly modulates living benthic foraminifera. The denitrification has been widely reported from the northern Arabian Sea ODZ (Naqvi et al., 2006). The prevalence of denitrification leads to a unique assemblage, as a few benthic foraminifera (*Globobulimina pseudospinescens*, *Nonionella* cf. *stella* and *Stainforthia*, *Bolivina seminuda, B. plicata, B. subaenariensis, B. argentea, Buliminella tenuata, Virgulinella fragilis, Globobulimina turgida*) are capable of denitrification (Risgaard-Petersen et al., 2006; Piña-Ochoa et al., 2010; Bernhard et al., 2012a; 2012b; Glock et al., 2013). Although, several species abundant in the southeastern Arabian Sea ODZ (*Bolivina seminuda*, *Bolivina dilatata*, *Eubuliminella exilis, Rotaliatinopsis semiinvoluta* and *Epistominella exigua*), are also present in the northern Arabian Sea, only a few of them (*Bolivina seminuda*) have so far been reported to denitrify. The denitrification has not been reported from the southeastern Arabian Sea, so far (S.W.A. Naqvi, personal communication). Despite of the no report of denitrification from the southeastern Arabian Sea, the presence of several common species in the southeastern and northern Arabian Sea, especially of a species (*B. seminuda*) reported to denitrify, is intriguing. However, a point to be kept in mind here, is that the species reported to denitrify can also respire with oxygen, suggesting that denitrification is an auxiliary metabolism and such foraminifera are facultative anaerobes (Piña-Ochoa et al., 2010). Therefore, it is likely that the abundance of *B. seminuda* at a few depths of the southeastern Arabian Sea ODZ, is not associated with denitrification. Detailed studies on water column and surface sediments of the south-eastern Arabian Sea, during different seasons, will help to confirm the presence of denitrification and its influence on living benthic foraminifera in the southeastern Arabian Sea.

### Depth zonation of living benthic foraminifera within the ODZ

A clear demarcation is observed in the depth preference of living benthic foraminifera, within the southeastern Arabian Sea ODZ. *Bolivina seminuda*, *Bolivina dilatata, Eubuliminella exilis, Bulimina elegans* and *Hopkinsinella glabra* were the most abundant at shallow ODZ depth (Station MC06 and MC07). Earlier, *Bolivina dilatata* and *Eubuliminella exilis* were reported to be the most abundant species in the upper part of ODZ (~500 m water depth and 0.1 mL/L dissolved oxygen) from the northeastern Arabian

Sea (Jannink et al., 1998; Caulle et al., 2014). The shallow ODZ stations in the southeastern Arabian Sea had low dissolved oxygen (0.5-0.7 mL/L; 22-31 µM) and moderate %$C_{org}$ (2.1-2.8%). *Uvigerina* ex *gr. Uvigerina semiornata* and *Bolivina* aff. *Bolivina dilatata* were reported at similar depth and %$C_{org}$, in the northeastern Arabian Sea (Schumacher et al., 2007). We do not find *Uvigerina* in abundance at shallow depths; this could be because of the difference in size fraction used for picking living benthic foraminifera in two studies. We used the widely recommended >63 µm fraction (Murray, 2006) to pick living benthic foraminifera from all the sections. However, in the study from the southeastern Arabian Sea, the fractions >150 µm and 125-150 µm were used to pick living benthic foraminifera, except for the top 1 cm section, for which 63 µm fraction was used (Caulle et al., 2014).

*Bolivina dilatata* was present throughout the ODZ in the southeastern Arabian Sea, with comparatively higher abundance in lower ODZ depths. *Bolivina dilatata* is one of the dominant benthic foraminifera in the oxygen deficient waters of several regions, including the Adriatic Sea (Barmawidjaja et al., 1992), eastern south Atlantic Ocean (Schmiedl et al., 1997) and the Arabian Sea (Jannink et al., 1998; Caulle et al., 2014, 2015). Jannink et al. (1998) reported it only from the upper ODZ but Caulle et al. (2015) found it in the lower part of the ODZ.

*Eubuliminella exilis* (also referred as *Bulimina exilis*) was only present at two shallow ODZ stations (MC06 and 07) along the transect. *Eubuliminella exilis* is commonly referred to as the low oxygen high organic matter favouring species (Jannink et al., 1998; Caulle et al., 2014; 2015). In the southeastern Arabian Sea, however, *E. exilis* is mainly associated with low oxygen rather than higher organic matter. *Eubuliminella exilis* prefers unaltered/labile organic matter (Caralp, 1989; Jorissen et al., 1998). We do not have qualitative data of organic matter as this could be a limiting factor for *E. exilis* abundance in the southeastern Arabian Sea. *Bulimina elegans*, was found throughout the ODZ which suggests its preference for low dissolved oxygen conditions.

Abundance of *Bolivina seminuda* has previously been reported from the deeper ODZ depths (1000-1500 m) of the northern Arabian Sea (Jannink et al., 1998; Caulle et al., 2014). In the southeastern Arabian Sea transect, we found abundant presence of *Bolivina seminuda*, with a very high abundance (~50%) at upper ODZ depths. The abundant presence of *B. seminuda* throughout the Arabian Sea ODZ, indicates its preference for oxygen deficient environment, as well as its capability of denitrification (Piña-Ochoa et al., 2010). *Hopkinsinella glabra* as an indicator of ODZ in the region is the first report from the Indian Ocean. Although *Hopkinsinella glabra* was earlier reported from the northern Indian Ocean (Gandhi et al., 2002), it was not associated with oxygen deficient environment. In the culture experiments, *Hopkinsinella glabra* was reported to prefer fresh food (Ernst et al., 2005). It was also reported as an opportunistic species (Jorissen et al., 1992) which moves upward and is mainly confined to the sediment water interface (Ernst et al., 2006; Langlet et al., 2013).

Based on the distribution of benthic foraminifera in the southeastern Arabian Sea and its ecological preferences, we delineate specific benthic foraminifera assemblage characteristic of different dissolved oxygen concentration as well as associated parameters. The assemblages are delineated considering the abundance of species in core-top as well as 0-5 cm section (Table 7.5, Plate 1). Assemblage (Ass.) 1, comprising of *Cassidulina laevigata, Cassidulina carinata* and *Eponides umbonatus* represents shallow depth oxygen rich warm water environment with low organic matter availability and saltier condition. Assemblage 2 includes *Bolivina seminuda*, *Hopkinsinella glabra* and *Eubuliminella exilis* and represents shallow water intense suboxic condition with moderate organic matter availability. The assemblage 3 represented by *Rotaliatinopsis semiinvoluta, Hopkinsinella glabra* and *Epistominella exigua* indicates similar kind of suboxic environment but with comparatively high %$C_{org}$ and lower bottom water temperature. Assemblage 4 includes *Bulimina arabiensis, Bulimina elegans* and *Bolivina earlandi* and represents comparatively higher dissolved oxygen condition (1-2 mL/L, 45-90 µM) with high organic carbon at deeper water depths (˜1000-1500 m). Assemblage 5 comprising of *Bolivina earlandi, Bulimina aculeata* and *Globocassidulina subglobosa* includes deep-water benthic foraminifera where bottom water is oxygen rich (>2.0 mL/L or >90 µM) along with high food availability with the lowest bottom water temperature and salinity.

## Living benthic foraminifera at depths deeper than ODZ

All living benthic foraminifera dominant in the ODZ, were completely absent in the 0-5 cm section at depths deeper than ODZ. The sediments at depths deeper than intermediate ODZ, were rich in organic matter with well oxygenated waters, an unusual complex oceanographic condition. *Bulimina aculeata, Bolivina earlandi, Cassidulionoides waltoni, Pseudoeponides equatoriana, Globocassidulina subglobosa* are the most abundant species in the region deeper than ODZ. These species have earlier been reported from the well oxygenated and low %$C_{org}$ environment. *Bulimina aculeata* and *Globocassidulina subglobosa* are previously reported from well oxygenated waters of the northern Arabian Sea (Jannink et al., 1998; Caulle et al., 2014). The abundant presence of these species in the organic matter rich sediments of the southeastern Arabian Sea, however, indicates that these species favour higher dissolved oxygen and are not strongly influenced by %$C_{org}$.

### Diversity at different depths

The increased diversity within the ODZ of the southeastern Arabian Sea is intriguing. The stressed environments usually support a few opportunistic fauna, thus reducing the diversity. The low dissolved oxygen is suggested as a severe stress for benthic foraminifera (Jorissen et al., 1995). Therefore, benthic foraminiferal diversity should decrease within the ODZ. The increased diversity in the ODZ, thus suggests a combination of several possibilities. The low diversity on the continental shelf is attributed to the coarse-grained sediments and low %$C_{org}$. The grain size and %$C_{org}$ are often linked, as fine-grained sediments provide increased surface area for the organic matter to adhere, thus leading to its better preservation, and vice versa (Burdige, 2007). The lack of food availability in coarse grained sediments acts as a deterrent for proliferation of benthic foraminiferal diversity as well as population. The coarse-grained texture, also implies high energy condition, another adverse factor for benthic foraminifera to thrive. The predatory pressure is also comparatively high in the shallow water shelf environment, as macro and mega-benthic population is more here (Ingole et al., 2010). Thus, the coarse-grained texture, high energy environment coupled with very low %$C_{org}$ reduces the foraminiferal diversity on the continental shelf in the southeastern Arabian Sea.

Although the dissolved oxygen concentration decreases on the slope, the availability of plenty of organic matter, coupled with decreased predatory pressure leads to proliferation of diverse benthic foraminiferal species within ODZ (den Dulk et al., 2000; Levin, 2003; Enge et al., 2016). The strong seasonality in the southeastern Arabian Sea, leading to change in type of organic matter flux to the sediments during different seasons (Jyothibabu et al., 2014), coupled with comparatively higher dissolved oxygen concentration, may also drive the increased diversity. The food preference of living benthic foraminifera varies with species. The availability of different organic matter flux, thus supports various species, increasing the diversity. Additional sampling at the same stations during different seasons, will further confirm the influence of seasonal organic matter flux on benthic foraminifera diversity in the Gulf of Mannar. The decreased diversity at deeper, well oxygenated depths, despite of the availability of plenty of organic matter with fine grained sediments, is attributed to the increased predatory pressure as well as low temperature. Interestingly, the richness and evenness is also higher within the ODZ. The higher richness and evenness suggests abundant presence of several species, again pointing towards the strong seasonality including the availability of different types of food, supporting diverse species. The living benthic foraminiferal diversity indices in the southeastern Arabian Sea are opposite to that of macrobenthic community across a depth transect covering the ODZ in the eastern Arabian Sea (Ingole et al., 2010). The difference in diversity and abundance suggests that the low dissolved oxygen is a severe limiting ecological factor for macrobenthic community, whereas several benthic foraminifera are well adapted to low dissolved oxygen. The low predatory pressure due to decreased macrobenthic population (Ingole et al., 2010), allows sustenance of abundant benthic foraminiferal population.

### Comparison of abundance and diversity in the Southeastern Arabian Sea with other ODZs

The abundance of living benthic foraminifera (in >63 µm fraction) increases many folds at ODZ depths in the southeastern Arabian Sea, with an exceptionally high value at MC06 (215 m) in the core-top section. A similar increase in the abundance within ODZ was also reported from other parts of the Arabian Sea, including off Pakistan (Caulle et al., 2014; Schumacher et al., 2007), off Oman (Gooday et al., 2000) and off Mumbai (Caulle et al., 2015) (>63 µm). This trend of increased abundance within ODZ was not so prominent in other size fractions (>150 and 63-150 µm). In the top 5 cm section also, the increase in living benthic foraminiferal abundance was not so prominent. A similar abundance pattern with only a marginal increase in benthic foraminiferal abundance in ODZ has also been reported from other parts of the Arabian Sea (Caulle et al., 2014; 2015; Gooday et al., 2000; Schumacher et al., 2007).

Shannon index (H) is often used to represent diversity (number of species present at a station and its relative abundance). In the southeastern Arabian Sea, Shannon index (H) varies between ~1.7-3.0. The lower values (~1.7) were at shallow water depths (58 and 152 m) and below ODZ at 1887 m. The lower diversity on the continental shelf is attributed to the coarse-grained texture, very low organic matter and heavy predatory pressure, as well as high energy condition. The low diversity in both the core-top as well as the 0-5 cm section at 1887 m is attributed to the low organic carbon at this station, as compared to other immediate stations. At, rest of the stations, Shannon index (H) varies between ˜2.0-3.0 in both the core-top as well as the 0-5 cm section. A similar range of Shannon index (H) was reported previously from the different parts of the Arabian Sea (Caulle et al., 2014; 2015; Schumacher et al., 2007) except off Oman, where diversity decreased to 0.9 at 412 m with dissolved oxygen concentration being 0.13 mL/L. A comparable low H value (<1) was also found in Santa Barbara Basin (Bernhard et al., 1997; Gooday et al., 2000) where bottom waters were nearly anoxic. This demonstrates that the extremely low dissolved oxygen or anoxic conditions decrease benthic foraminiferal diversity. As the bottom water dissolved oxygen does not decrease to anoxic levels in the Gulf of Mannar, benthic foraminiferal diversity is not severely affected.

## Conclusions

Living (rose Bengal stained) benthic foraminifera from the southeastern Arabian Sea have been documented. The increased abundance of benthic foraminifera in the core-top (0-1 cm) as well as 0-5 cm section at the intermediate depths, with oxygen deficient waters is attributed to availability of higher organic matter/food availability. The species abundance is mainly controlled by the bottom water dissolved oxygen in the region. The abundant presence of *Bolivina currai* and *Hopkinsinella glabra* in the core-top sections is correlated with the dissolved oxygen. However, in the top 5 cm section, *Hopkinsinella glabra* and *Bulimina elegans* are significantly affected by the low dissolved oxygen. The significant negative relationship of *Hopkinsinella glabra* with the ambient dissolved oxygen, in both the top 0-1 cm section as well as the top 5 cm section, suggests it to be a good indicator of low dissolved oxygen environment in the southeastern Arabian Sea. Besides this, we also report five assemblages of living benthic foraminifera representing different bottom water conditions. Assemblage 1, dominated by *Cassidulina laevigata, Cassidulina carinata* and *Eponides umbonatus* indicates shallow depth, hypersaline oxygen rich warm water environment with low organic matter availability. Assemblage 2 includes *Bolivina seminuda, Hopkinsinella glabra* and *Eubuliminella exilis* and represents shallow water intense suboxic condition with moderate organic matter availability. The assemblage 3 includes *Rotaliatinopsis semiinvoluta*, *Hopkinsinella glabra* and *Epistominella exigua* and indicates similar kind of suboxic environment but with comparatively high %$C_{org}$ and lower bottom water temperature. Assemblage 4 mainly comprise of rectilinear infaunal species, dominated by *Bulimina arabiensis*, *Bulimina elegans* and *Bolivina earlandi* and represents comparatively higher dissolved oxygen condition (1-2 mL/L; 45-90 µM) with high organic carbon at deeper water depths (˜1000-1500 m). Assemblage 5 comprising of *Bolivina earlandi, Bulimina aculeata* and *Globocassidulina subglobosa* includes deep-water benthic foraminifera where bottom water is oxygen rich (>2.0 mL/L or >90 µM) along with high food availability with the lowest bottom water temperature and salinity. These representative benthic foraminiferal assemblages will help in reconstructing paleoceanographic conditions from the southeastern Arabian Sea.

**Table 7.1: The check-list of the living benthic foraminifera reported from the southeastern Arabian Sea. The details of the type species are also included. [Note: For the references cited in this table, please refer to the Loeblich and Tappan (1988) and online resources.]**

| Species | Original Description | Identification Source |
|---|---|---|
| *Adercotryma glomeratum* | *Lituola glomerata* Brady, 1878 | Zheng and Fu, 2001, Pl. 44, Fig. 8. |
| *Ammodiscus gullmarensis* | *Ammodiscus gullmarensis* Höglund, 1948 | Lei and Li, 2016, Pg. 9, Fig. 5 |
| *Ammoglobigerina globigeriniformis* | *Lituola nautiloidea* var. *globigeriniformis* Parker & Jones, 1865 | Zheng and Fu, 2001, Pl. 61, Figs. 1-3. |
| *Anturina haynesi* | *Anturina haynesi* Jones, 1984 | Loeblich and Tappan, 1988, Pl. 462, Fig. 1. |
| *Baggina diversa* | *Baggina diversa* McCulloch, 1981 | McCulloch, 1981, Pl. 51, Fig. 12, 13. |
| *Bolivina acaulis* | *Bolivina acaulis* Egger, 1893 | Ellis and Messina Foraminifera Catalogue, Fig. 73620. |
| *Bolivina advena* | *Bolivina advena* Cushman, 1925 | Ellis and Messina Foraminifera Catalogue, Fig. 1545. |
| *Bolivina* aff. *mera* | *Bolivina plicatella* var. *mera* Cushman & Ponton, 1932 | Ellis and Messina Foraminifera Catalogue, Fig. 1867. |
| *Bolivina churchi* | *Bolivina churchi* Kleinpell & Tipton, 1980 | Ellis and Messina Foraminifera Catalogue, Fig. 65532. |
| *Bolivina compacta* | *Bolivina robusta* var. *compacta* Sidebottom, 1905 | Ellis and Messina Foraminifera Catalogue, Fig. 1912. |
| *Bolivina cuneatum* | *Bolivina (Loxostoma) cuneatum* Hofker, 1951 | Ellis and Messina Foraminifera Catalogue, Fig. 41079. |
| *Bolivina currai* | *Bolivina currai* Sellier de Civrieux, 1976 | Ellis and Messina Foraminifera Catalogue, Fig. 68144. |
| *Bolivina dilatata* | *Bolivina dilatata* Reuss, 1850 | Ellis and Messina Foraminifera Catalogue, Fig. 1664. |
| *Bolivina earlandi* | *Bolivina earlandi* Parr, 1950 | Ellis and Messina Foraminifera Catalogue, Fig. 38250. |
| *Bolivina jacksonensis* | *Bolivina jacksonensis* Cushman & Applin, 1926 | Ellis and Messina Foraminifera Catalogue, Fig. 1750. |
| *Bolivina lowmani* | *Bolivina lowmani* Sellier, 1976 | Ellis and Messina Foraminifera Catalogue, Fig. 68151. |
| *Bolivina robusta* | *Bulimina (Bolivina) robusta* Brady, 1881 | Barkar, 1960, Pl. 53, Figs. 7-9. |
| *Bolivina seminuda* | *Bolivina seminuda* Cushman, 1911 | Ellis and Messina Foraminifera Catalogue, Fig. 1932. |
| *Bolivina spinescens* | *Bolivina spinescens* Cushman, 1911 | Ellis and Messina Foraminifera Catalogue, Fig. 1950. |
| *Bolivina striatula* | *Bolivina striatula* Cushman, 1922 | Ellis and Messina Foraminifera Catalogue, Fig. 1957. |
| *Bolivina subspathulata* | *Bolivina subspathulata* Boomgaart, 1949 | Ellis and Messina Foraminifera Catalogue, Fig. 37544. |

| | | |
|---|---|---|
| *Bolivina victoriana* | *Bolivina victoriana* Cushman, 1936 | Ellis and Messina Foraminifera Catalogue, Fig. 2029. |
| *Bolivina zanzibarica* | *Bolivina zanzibarica* Cushman, 1936 | Ellis and Messina Foraminifera Catalogue, Fig. 2033. |
| *Buccella differens* | *Buccella differens* McCulloch, 1981 | McCulloch, 1981, Pl. 58, Fig. 8. |
| *Bulimina aculeata* | *Bulimina aculeata* d'Orbigny, 1826 | Barkar, 1960, Pl. 51, Figs. 7-9. |
| *Bulimina alazanensis* | *Bulimina alazanensis* Cushman, 1927 | Ellis and Messina Foraminifera Catalogue, Fig. 2156. |
| *Bulimina arabiensis* | *Bulimina arabiensis* Bharti & Singh, 2013 | Bharti and Singh, 2013, Fig. 3. |
| *Bulimina elegans* | *Bulimina elegans* d'Orbigny, 1826 | Ellis and Messina Foraminifera Catalogue, Fig. 2243. |
| *Bulimina marginata* | *Bulimina marginata* d'Orbigny, 1826 | Ellis and Messina Foraminifera Catalogue, Fig. 2317. |
| *Bulimina marginospinata* | *Bulimina marginospinata* Cushman & Parker, 1938 | Ellis and Messina Foraminifera Catalogue, Fig. 2322. |
| *Bulimina pseudoaffinis* | *Bulimina psuedoaffinis* Kleinpell, 1938 | Martin, 1952, Pl. 23, Fig. 4. |
| *Bulimina pupoides* | *Bulimina pupoides* d'Orbigny, 1846 | Ellis and Messina Foraminifera Catalogue, Fig. 76935. |
| *Bulimina spinosa* | *Bulimina spinosa* Seguenza, 1862 | Ellis and Messina Foraminifera Catalogue, Fig. 2462. |
| *Bulimina striata* | *Bulimina striata* d'Orbigny in Guérin-Méneville, 1832 | Ellis and Messina Foraminifera Catalogue, Fig. 24405. |
| *Cancris* cf. *penangensis* | *Cancris* cf. *penangensis* McCulloch, 1977 | McCulloch, 1977, Pg. 344, Pl. 135, Fig. 110. |
| *Cancris sagra* | *Rotalina (Rotalina) sagra* d'Orbigny, 1839 | Loeblich and Tappan, 1988, Pl. 591, Fig. 4. |
| *Cancris* sp. | *Cancris* sp. | Loeblich and Tappan, 1988, Pl. 591. |
| *Cassidulina* aff. *minuta* | *Cassidulina* aff. *minuta* Cushman, 1933 | Ellis and Messina Foraminifera Catalogue, Fig. 2803. |
| *Cassidulina angulosa* | *Cassidulina angulosa* Cushman, 1933 | Ellis and Messina Foraminifera Catalogue, Fig. 2724. |
| *Cassidulina carinata* | *Cassidulina laevigata* var. *carinata* Silvestri, 1896 | Ellis and Messina Foraminifera Catalogue, Fig. 2786. |
| *Cassidulina laevigata* | *Cassidulina laevigata* d'Orbigny, 1826 | Ellis and Messina Foraminifera Catalogue, Fig. 2782. |
| *Cassidulinoides waltoni* | *Cassidulionoides waltoni* Uchio 1960 | McCulloch, 1977, Pl. 166, Fig. 8, 12. |
| *Cibicidoides mundula* | *Truncatulina mundula* Brady, Parker & Jones, 1888 | Loeblich and Tappan, 1955, Pl. 4, Fig. 4. |
| *Cibicidoides wuellerstorfi* | *Anomalina wuellerstorfi* Schwager, 1866 | Jones, 1994, Pl. 93, Fig. 9. |
| *Crespinella umbonifera* | *Operculina umbonifera* Howchin & Parr, 1938 | Loeblich and Tappan, 1988, Pl. 632, Figs. 9-13. |
| *Eggerelloides scaber* | *Bulimina scabra* Williamson, 1858 | Mendes et al., 2013, Pl. 1, Fig. 1. |
| *Epistominella exigua* | *Pulvinulina exigua* Brady, 1884 | Barker, 1960, Pl. 107, Figs. 13, 14. |
| *Epistominella pulchella* | *Epistominella pulchella* Husezima & Maruhasi, 1944 | Ellis and Messina Foraminifera Catalogue, Fig. 39933. |
| *Epistominella* sp. | *Epistominella* sp. | Loeblich and Tappan, 1988, Pl. 627. |
| *Epistominella umbonifera* | *Pulvinulinella umbonifera* Cushman, 1933 | Ellis and Messina Foraminifera Catalogue, Fig. 18042. |
| *Eponides umbonatus* | *Rotalina umbonata* Reuss, 1851 | Barker, 1960, Pl. 105, Fig. 2. |
| *Eubuliminella exilis* | *Bulimina elegans* var. *exilis* Brady, 1884 | Jones, 1994**,** Pl.50, Figs. 5, 6. |
| *Fissurina caudimarginata* | *Fissurina aligeria* subsp. *caudimarginata* McCulloch, 1977 | McCulloch, 1977, Pl. 58, Fig. 28. |
| *Fissurina crassiporosa* | *Fissurina crassiporosa* McCulloch, 1977 | McCulloch, 1977, Pl.56, Fig. 22. |
| *Fursenkoina cornuta* | *Virgulina cornuta* Cushman, 1913 | Matoba, 1982, Pl. 2, Fig. 8. |
| *Fursenkoina obliqua* | *Fursenkoina obliqua* Saidova 1975 | Ellis and Messina Foraminifera Catalogue, Fig. 80524. |
| *Globobulimina pacifica* | *Globobulimina pacifica* (Cushman, 1927) | Barker, 1960, Pl. 50, Figs. 7-10. |
| *Globocassidulina porrecta* | *Cassidulina crassa* var. *porrecta* Heron- | Ellis and Messina Foraminifera Catalogue, Fig. 2754. |

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|---|---|---|
| | Allen & Earland, 1932 | |
| *Globocassidulina subglobosa* | *Cassidulina subglobosa* Brady, 1881 | Loeblich and Tappan 1988, Pl. 557, Figs. 18-23. |
| *Gyroidina* cf. *guadalupensis* | *Gyroidina cf. guadalupensis* McCulloch, 1977 | McCulloch, 1977, P1. 140, Figs. 8, 12. |
| *Gyroidina io* | *Gyroidina io* Resig, 1958 | Ellis and Messina Foraminifera Catalogue, Fig. 47407. |
| *Gyroidina pilasensis* | *Gyroidina pilasensis* McCulloch, 1977 | McCulloch, 1977, P1. 140, Figs. 1, 2. |
| *Gyroidina quinqueloba* | *Gyroidina quinqueloba* Uchio, 1960 | Ellis and Messina Foraminifera Catalogue, Fig. 54104. |
| *Gyroidina tenera* | *Truncatulina tenera* Brady, 1884 | McCulloch, 1977, P1. 141, Fig. 13. |
| *Hansenisca soldanii* | *Gyroidina soldanii* (d'Orbigny, 1826) | Ellis and Messina Foraminifera Catalogue, Fig. 9058. |
| *Hanzawaia concentrica* | *Cibicides concentricus* Cushman, 1918 | Ellis and Messina Foraminifera Catalogue, Fig. 22756. |
| *Haplophragmoides evolutum* | *Haplophragmoides columbiense* var. *evolutum* Cushman & Mcculloch, 1939 | Ellis and Messina Foraminifera Catalogue, Fig. 77360. |
| *Hoeglundina heterolucida* | *Hoeglundina heterolucida* McCulloch, 1981 | McCulloch, 1981, Pl. 57, Fig. 7. |
| *Hopkinsina atlantica* | *Hopkinsina pacifica* var. *atlantica* Cushman, 1944 | Ellis and Messina Foraminifera Catalogue, Fig. 32481. |
| *Hopkinsinella glabra* | *Uvigerina auberiana* var. *glabra* Millett, 1903 | Ellis and Messina Foraminifera Catalogue, Fig. 23035. |
| *Hyalinea balthica* | *Nautilus balthicus* Schröter, 1783 | Ellis and Messina Foraminifera Catalogue, Fig. 37878. |
| *Hyalinonetrion elongata* | *Miliola elongata* Ehrenberg, 1844 | Loeblich and Tappan, 1988, Pl. 455, Figs. 6-8. |
| *Lagena oceanica* | *Lagena oceanica* Albani 1974 | Ellis and Messina Foraminifera Catalogue, Fig. 61865. |
| *Lagenammina longicollis* | *Lagenammina longicolli* Wiesner, 1931 | Zheng and Fu, 2001, Pl. 6, Fig. 11. |
| *Lagenosolenia eucerviculata* | *Lagenosolenia eucerviculata* McCulloch, 1977 | McCulloch, 1977, Pl. 60, Fig. 5-7. |
| *Lenticulina tortugaensis* | *Robulus tortugaensis* McCulloch, 1981 | McCulloch, 1981, Pl. 27, Fig. 1. |
| *Melonis chathamensis* | *Melonis chathamensis* McCulloch, 1977 | McCulloch, 1977, Pl.180, Fig. 5. |
| *Melonis pompilioides* | *Nautilus pompilioides* Fichtel & Moll, 1798 | Khare, 1992, Pg. 171, Pl. 16, Fig. 1. |
| *Melonis* sp. | *Melonis* sp. | Loeblich and Tappan, 1988, Pl. 696. |
| *Neouvigerina ampullacea* | *Uvigerina asperula* var. *ampullacea* Brady, 1884 | Ellis and Messina Foraminifera Catalogue, Fig. 23031. |
| *Neouvigerina porrecta* | *Uvigerina porrecta* Brady, 1879 | Ellis and Messina Foraminifera Catalogue, Fig. 23214. |
| *Nonion glabrella* | *Nonion glabrella* Cushman, 1930 | Ellis and Messina Foraminifera Catalogue, Fig. 13968. |
| *Nonion granosum* | *Nonionina granosa* d'Orbigny, 1846 | Cushman, 1939, Pl. 2, Fig. 17. |
| *Nonion* sp. | *Nonion* sp. | Loeblich and Tappan, 1988, Pl. 690. |
| *Nonionella limbato-striata* | *Nonionella limbato-striata* Cushman, 1931 | Ellis and Messina Foraminifera Catalogue, Fig. 14046. |
| *Nonionella simplex* | *Ziesenhenneia simplex* McCulloch, 1977 | McCulloch, 1977, Pl. 160, Figs. 12, 14. |
| *Nonionellina labradorica* | *Nonionina labradorica* Dawson, 1860 | Loeblich and Tappan, 1988, Pl. 689, Figs. 8-17. |
| *Oridorsalis umbonatus* | *Rotalina umbonata* Reuss, 1851 | Jones, 1994, Pl. 95, P1. 11. |
| *Osangularia bengalensis* | *Anomalina bengalensis* Schwager, 1866 | Loeblich and Tappan, 1988, Pl. 708, Figs. 1-5. |
| *Portatrochammina eltaninae* | *Portatrochammina eltaninae* Echols, 1971 | Loeblich and Tappan, 1988, Pl. 129, Figs. 4-6. |
| *Pseudoeponides equatoriana* | *Rotalia equatoriana* LeRoy, 1941 | Bhatia and Kumar, 1976, Pl. 2, Fig. 8. |
| *Pullenia bulloides* | *Nonionina bulloides* d'Orbigny, 1846 | Barker, 1960, Pl. 84, Figs. 12, 13. |
| *Pullenia salisburyi* | *Pullenia salisburyi* Stewart & Stewart, | Yassini and Jones, 1995, Pg. 249, Figs. 936-939. |

| | | |
|---|---|---|
| | 1930 | |
| *Pullenia* sp. | *Pullenia* sp. | Loeblich and Tappan, 1988, Pl. 696. |
| *Pyropiloides elongatus* | *Pyropiloides elongatus* Zheng, 1979 | Loeblich and Tappan, 1988, Pl. 689, Figs. 8-17. |
| *Reophax rostrata* | *Reophax rostrata* Höglund, 1947 | Zheng and Fu, 2001, Pl. 22, Figs. 1-7. |
| *Rosalina columbiensis* | *Discorbis columbiensis* Cushman, 1925 | Ellis and Messina Foraminifera Catalogue, Fig. 59055. |
| *Rotaliatinopsis semiinvoluta* | *Pulleniatina semiinvoluta* Germeraad, 1946 | Loeblich and Tappan, 1988, Pl. 714, Figs. 7-11. |
| *Rotalidium annectens* | *Rotalia beccarii* var. *annectens* Parker & Jones, 1865 | Khare, 1992, Pg. 181-182, P1. 17, Fig. 51. |
| *Rotorbinella bikiniensis* | *Rotorbinella bikinensis* McCulloch, 1977 | McCulloch, 1977, Pl. 115, Figs. 14-15. |
| *Rutherfordoides rotundiformis* | *Rutherfordoides rotundiformis* McCulloch, 1977 | McCulloch, 1977, Pl. 105, Figs. 6-10. |
| *Saccammina huanghaiensis* | *Saccammina huanghaiensis* Zheng & Fu, 2001 | Zheng and Fu, 2001, Pl. 5, Figs. 22- 25 |
| *Saccorhiza ramosa* | *Hyperammina ramosa* Brady, 1879 | Zheng and Fu, 2001, Pl. 9, Figs. 9-12. |
| *Trochammina conica* | *Trochammina conica* Earland, 1934 | Zheng and Fu, 2001, Pl. 115, Fig. 7. |
| *Uvigerina* aff. *longa* | *Uvigerina longa* Cushman & Bermúdez, 1937 | Ellis and Messina Foraminifera Catalogue, Fig. 23159. |
| *Uvigerina* aff. *mediterranea* | *Uvigerina mediterranea* Hofker, 1932 | Ellis and Messina Foraminifera Catalogue, Fig. 29802. |
| *Uvigerina auberiana* | *Uvigerina auberiana* d'Orbigny, 1839 | Ellis and Messina Foraminifera Catalogue, Fig. 23033. |
| *Uvigerina canariensis* | *Uvigerina canariensis* d'Orbigny, 1839 | Ellis and Messina Foraminifera Catalogue, Fig. 23067. |
| *Uvigerina multicostata* | *Uvigerina multicostata* Leroy, 1939 | Ellis and Messina Foraminifera Catalogue, Fig. 31290. |
| *Uvigerina peregrina* | *Uvigerina peregrina* Cushman, 1923 | Ellis and Messina Foraminifera Catalogue, Fig. 23190. |
| *Valvulineria hamanakoensis* | *Anomalina hamanakoensis* Ishiwada, 1958 | Matoba, 1970, Pl. 4, Figs. 12, 13. |
| *Valvulineria minuta* | *Valvulineria minuta* Parker, 1954 | Ellis and Messina Foraminifera Catalogue, Fig. 43951. |

**Table 7.2: Depth habitat of the dominant living benthic foraminifera in the south-eastern Arabian Sea. The epifaunal forms were found in the top 0-1 cm, shallow-infaunal in top 1-3 cm and deep-infaunal in 3-5 cm of the sediments.**

| **Species** | **Living Habitat** | | |
|---|---|---|---|
| | **Epifaunal (0-1 cm)** | **Shallow-infaunal (1-3 cm)** | **Deep-infaunal (3-5 cm)** |
| *Baggina diversa* | 🟥 | | |
| *Bolivina acaulis* | | 🟧 | |
| *Bolivina churchi* | 🟪 | 🟪 | |
| *Bolivina currai* | 🟪 | 🟪 | |
| *Bolivina dilatata* | 🟪 | 🟪 | |
| *Bolivina earlandi* | 🟪 | 🟪 | |
| *Bolivina seminude* | 🟪 | 🟪 | |
| *Bolivina Victoriana* | ⬛ | ⬛ | ⬛ |

| | | | |
|---|---|---|---|
| *Bulimina aculeate* | 🟪 | 🟪 | |
| *Bulimina arabiensis* | ⬛ | ⬛ | ⬛ |
| *Bulimina elegans* | ⬛ | ⬛ | ⬛ |
| *Bulimina marginata* | | 🟥 | 🟥 |
| *Bulimina marginospinata* | 🩷 | | |
| *Bulimina pseudoaffinis* | 🟪 | 🟪 | |
| *Bulimina pupoides* | 🩷 | | |
| *Bulimina striata* | 🩷 | | |
| *Cancris* cf. *penangensis* | 🩷 | | |
| *Cancris sagra* | 🟪 | 🟪 | |
| *Cassidulina carinata* | 🩷 | | |
| *Cassidulina laevigata* | ⬛ | ⬛ | ⬛ |
| *Cassidulionoides waltoni* | 🟪 | 🟪 | |
| *Cibicidoides mundula* | 🩷 | | |
| *Cibicidoides wuellerstorfi* | 🩷 | | |
| *Epistominella exigua* | ⬛ | ⬛ | ⬛ |
| *Eponides umbonatus* | 🩷 | | |
| *Eubuliminella exilis* | | 🟥 | 🟥 |
| *Fursenkoina cornuta* | 🟦 | | 🟦 |
| *Globobulimina pacifica* | | 🟥 | 🟥 |
| *Globocassidulina porrecta* | 🟪 | 🟪 | |
| *Globocassidulina subglobosa* | 🟪 | 🟪 | |
| *Gyroidina* cf. *guadalupensis* | 🩷 | | |
| *Gyroidina pilasensis* | 🟪 | 🟪 | |
| *Gyroidina tenera* | 🩷 | | |
| *Gyroidinoides soldanii* | 🩷 | | |
| *Hopkinsinella glabra* | ⬛ | ⬛ | ⬛ |
| *Hyalinea balthica* | 🟪 | 🟪 | |
| *Lagenammina longicolli* | 🩷 | | |
| *Melonis chathamensis* | 🩷 | | |
| *Neouvigerina porrecta* | 🩷 | | |
| *Nonion glabrella* | 🟪 | 🟪 | |
| *Nonion* sp. | | 🟥 | 🟥 |
| *Nonionella limbato-striata* | 🟪 | 🟪 | |
| *Pseudoeponides equatoriana* | ⬛ | ⬛ | ⬛ |

| | | | |
|---|---|---|---|
| *Pullenia bulloides* | 🟪 | 🟪 | |
| *Pullenia salisburyi* | 🟪 | 🟪 | |
| *Rotaliatinopsis semiinvoluta* | 🟪 | 🟪 | |
| *Rotorbinella bikinensis* | 🟪 | 🟪 | |
| *Saccammina huanghaiensis* | 🟥 | | |
| *Trochammina conica* | 🟥 | | |
| *Uvigerina* aff. *Longa* | 🟪 | 🟪 | |
| *Uvigerina auberiana* | 🟪 | 🟪 | |
| *Uvigerina peregrine* | 🟪 | 🟪 | |
| *Valvulineria hamanakoensis* | 🟪 | 🟪 | |

**Table 7.3: The species with significant correlation with the ecological parameter (p=/<=0.05) in the core top section (0-1 cm). The numbers marked in red, indicate the significant correlation.**

| Species | Abbr. | DO | C$_{org}$ | Species | Abbr. | DO | C$_{org}$ |
|---|---|---|---|---|---|---|---|
| ***Lagenammina Longicolli*** | a | .6904 | .4306 | ***Uvigerina peregrina*** | Z | .0357 | .3747 |
| | | p=.019 | p=.186 | | | p=.917 | p=.256 |
| ***Saccammina Huanghaiensis*** | b | .5665 | .3719 | ***Uvigerina* aff. *longa*** | Aa | -.3179 | -.2602 |
| | | p=.069 | p=.260 | | | p=.341 | p=.440 |
| ***Trochammina conica*** | c | -.0874 | .2687 | ***Fursenkoina cornuta*** | Ab | -.2759 | -.3597 |
| | | p=.798 | p=.424 | | | p=.412 | p=.277 |
| ***Bolivina churchi*** | d | -.0874 | .2687 | ***Baggina diversa*** | Ac | .0642 | .3144 |
| | | p=.798 | p=.424 | | | p=.851 | p=.346 |
| ***Bolivina currai*** | e | -.6320 | -.1626 | ***Cancris sagra*** | Ad | .4312 | -.7223 |
| | | p=.037 | p=.633 | | | p=.186 | p=.012 |
| ***Bolivina dilatata*** | f | -.5591 | .0106 | ***Cancris* cf. *penangensis*** | Ae | -.4322 | -.0167 |
| | | p=.074 | p=.975 | | | p=.184 | p=.961 |
| ***Bolivina earlandi*** | g | .4792 | .3447 | ***Valvulineria hamanakoensis*** | Af | .4399 | .4648 |
| | | p=.136 | p=.299 | | | p=.176 | p=.150 |
| ***Bolivina seminude*** | h | -.4648 | -.3730 | ***Eponides umbonatus*** | Ag | .3908 | -.7306 |
| | | p=.150 | p=.259 | | | p=.235 | p=.011 |
| ***Bolivina spinescens*** | i | .4807 | .1654 | ***Rotorbinella bikinensis*** | Ah | .1546 | .3661 |
| | | p=.134 | p=.627 | | | p=.650 | p=.268 |
| ***Bolivina zanzibarica*** | j | .0642 | .3144 | ***Cibicidoides mundula*** | Ai | .0583 | .3352 |
| | | p=.851 | p=.346 | | | p=.865 | p=.314 |
| ***Cassidulina carinata*** | k | .3701 | -.7346 | ***Cibicidoides wuellerstorfi*** | Aj | .4997 | .1729 |
| | | p=.263 | p=.010 | | | p=.118 | p=.611 |
| ***Cassidulina laevigata*** | l | .3406 | -.7636 | ***Epistominella exigua*** | Ak | -.3713 | .1896 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| | | p=.305 | p=.006 | | | p=.261 | p=.577 |
| ***Globocassidulina Porrecta*** | m | -.2108 | .2955 | ***Hyalinea balthica*** | Al | -.5113 | -.0373 |
| | | p=.534 | p=.378 | | | p=.108 | p=.913 |
| ***Globocassidulina Subglobosa*** | n | .5556 | .1777 | ***Pseudoeponides equatoriana*** | Am | .5932 | .4287 |
| | | p=.076 | p=.601 | | | p=.054 | p=.188 |
| ***Hopkinsinella glabra*** | o | -.7507 | -.3667 | ***Nonionella limbato-striata*** | An | .5070 | .3677 |
| | | p=.008 | p=.267 | | | p=.111 | p=.266 |
| ***Bulimina aculeate*** | p | .4719 | .2919 | ***Melonis chathamensis*** | Ao | -.3451 | -.0398 |
| | | p=.143 | p=.384 | | | p=.299 | p=.908 |
| ***Bulimina arabiensis*** | q | -.3875 | .1290 | ***Pullenia bulloides*** | Ap | .0406 | -.4072 |
| | | p=.239 | p=.705 | | | p=.906 | p=.214 |
| ***Bulimina elegans*** | r | -.4545 | -.3819 | ***Pullenia salisburyi*** | Aq | -.2427 | .3646 |
| | | p=.160 | p=.246 | | | p=.472 | p=.270 |
| ***Bulimina marginata*** | s | .3105 | .1738 | ***Gyroidinoides soldanii*** | Ar | .5881 | .2333 |
| | | p=.353 | p=.609 | | | p=.057 | p=.490 |
| ***Bulimina Marginospinata*** | t | .4309 | .3407 | ***Rotaliatinopsis semiinvoluta*** | As | -.5277 | .0682 |
| | | p=.186 | p=.305 | | | p=.095 | p=.842 |
| ***Bulimina pupoides*** | u | -.3261 | -.2407 | ***Gyroidina quinqueloba*** | At | .0642 | .3144 |
| | | p=.328 | p=.476 | | | p=.851 | p=.346 |
| ***Bulimina striata*** | v | -.4126 | .1228 | ***Gyroidina pilasensis*** | Au | .6074 | .5275 |
| | | p=.207 | p=.719 | | | p=.047 | p=.095 |
| ***Globobulimina pacifica*** | w | .4228 | .2551 | ***Gyroidina tenera*** | Av | .2812 | .4570 |
| | | p=.195 | p=.449 | | | p=.402 | p=.158 |
| ***Neouvigerina porrecta*** | x | -.3451 | -.0398 | ***Gyroidina cf. guadalupensis*** | Aw | .0311 | .3395 |
| | | p=.299 | p=.908 | | | p=.928 | p=.307 |
| ***Uvigerina auberiana*** | y | -.2480 | .3047 | | | | |
| | | p=.462 | p=.362 | | | | |

**Table 7.4: The species with significant correlation with the ecological parameter (p=/<=0.05) in the 0-5 cm section. The numbers marked in red, indicate the significant correlation.**

| **Species** | **Abbr.** | **DO** | **$C_{org}$** | **Species** | **Abbr.** | **DO** | **$C_{org}$** |
|---|---|---|---|---|---|---|---|
| ***Lagenammina longicolli*** | A | .6987 | .6717 | ***Eubuliminella exilis*** | W | -.4419 | -.5622 |
| | | p=.017 | p=.024 | | | p=.174 | p=.072 |
| ***Saccammina Huanghaiensis*** | B | .5646 | .4051 | ***Globobulimina pacifica*** | X | .3366 | .1820 |
| | | p=.070 | p=.216 | | | p=.312 | p=.592 |
| ***Bolivina acaulis*** | C | .0341 | .1666 | ***Uvigerina peregrina*** | Y | .0205 | .3085 |
| | | p=.921 | p=.624 | | | p=.952 | p=.356 |
| ***Bolivina churchi*** | D | -.1246 | .2332 | ***Cancris sagra*** | Z | .4312 | -.5902 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| | | p=.715 | p=.490 | | | p=.186 | p=.056 |
| ***Bolivina currai*** | E | -.5327 | .0035 | ***Valvulineria hamanakoensis*** | AA | .3529 | .4019 |
| | | p=.092 | p=.992 | | | p=.287 | p=.220 |
| ***Bolivina dilatata*** | F | -.5329 | -.1222 | ***Eponides umbonatus*** | AB | .3780 | -.5973 |
| | | p=.091 | p=.720 | | | p=.252 | p=.052 |
| ***Bolivina earlandi*** | G | .5225 | .3998 | ***Rotorbinella bikinensis*** | AC | .1338 | .4291 |
| | | p=.099 | p=.223 | | | p=.695 | p=.188 |
| ***Bolivina seminude*** | H | -.4157 | -.5821 | ***Cibicidoides mundula*** | AD | .0577 | .1618 |
| | | p=.203 | p=.060 | | | p=.866 | p=.635 |
| ***Bolivina Victoriana*** | I | -.2181 | .1894 | ***Cibicidoides wuellerstorfi*** | AE | .5016 | .5720 |
| | | p=.520 | p=.577 | | | p=.116 | p=.066 |
| ***Cassidulina carinata*** | J | .3923 | -.5953 | ***Epistominella exigua*** | AF | -.4791 | .1798 |
| | | p=.233 | p=.053 | | | p=.136 | p=.597 |
| ***Cassidulina laevigata*** | K | .2972 | -.6709 | ***Hyalinea balthica*** | AG | -.5055 | -.0300 |
| | | p=.375 | p=.024 | | | p=.113 | p=.930 |
| ***Cassidulionoides Waltoni*** | L | .5943 | .6304 | ***Pseudoeponides equatoriana*** | AH | .5997 | .6626 |
| | | p=.054 | p=.038 | | | p=.051 | p=.026 |
| ***Globocassidulina Porrecta*** | M | -.2883 | .2434 | ***Nonion glabrella*** | AI | .3557 | -.6995 |
| | | p=.390 | p=.471 | | | p=.283 | p=.017 |
| ***Globocassidulina Subglobosa*** | N | .5209 | .5612 | ***Nonionella limbato-striata*** | AJ | .5070 | .3193 |
| | | p=.100 | p=.072 | | | p=.111 | p=.338 |
| ***Hopkinsinella glabra*** | O | -.6748 | -.3525 | ***Melonis chathamensis*** | AK | -.3451 | -.0560 |
| | | p=.023 | p=.288 | | | p=.299 | p=.870 |
| ***Bulimina aculeate*** | P | .4672 | .2462 | ***Pullenia bulloides*** | AL | .0068 | -.3943 |
| | | p=.147 | p=.466 | | | p=.984 | p=.230 |
| ***Bulimina arabiensis*** | Q | -.3128 | .3214 | ***Pullenia salisburyi*** | AM | -.2478 | .2471 |
| | | p=.349 | p=.335 | | | p=.463 | p=.464 |
| ***Bulimina elegans*** | R | -.7251 | -.2766 | ***Gyroidinoides soldanii*** | AN | .5964 | .1960 |
| | | p=.012 | p=.410 | | | p=.053 | p=.563 |
| ***Bulimina marginata*** | T | .2367 | .0334 | ***Rotaliatinopsis semiinvoluta*** | AO | -.5462 | .0461 |
| | | p=.483 | p=.922 | | | p=.082 | p=.893 |
| ***Bulimina pseudoaffinis*** | U | -.5720 | .1795 | ***Gyroidina pilasensis*** | AP | .5636 | .7685 |
| | | p=.066 | p=.597 | | | p=.071 | p=.006 |
| ***Bulimina striata*** | V | -.4190 | .1026 | ***Gyroidina*** **cf.** ***guadalupensis*** | AQ | .0104 | .1747 |
| | | p=.200 | p=.764 | | | p=.976 | p=.607 |
| | | | | ***Nonion*** **sp.** | AR | .5708 | .3432 |
| | | | | | | p=.067 | p=.302 |

**Table 7.5: Living benthic foraminifera assemblages' indicator of different bottom water dissolved oxygen concentration and other associated ecological parameters.**

| | **Species composition** | **Depth (m)** | **%$C_{org}$** | **DO (mL/L)** | **Temp. (°C)** | **Salinity (psu)** | **%$C_{org}$/TN** |
|---|---|---|---|---|---|---|---|
| **Assemblage 1** | ***Cassidulina laevigata, Cassidulina carinata* and *Eponides Umbonatus*** | Continental Shelf (58) | 1.52-1.57 | 3.39 (151 µM) | 25.96 | 35.18 | 14.6-15.1 |
| **Assemblage 2** | ***Bolivina seminuda, Hopkinsinella glabra* and *Eubuliminella Exilis*** | Upper Continental Slope (152-215) | 2.17-3.78 | 0.53-0.69 (24-31 µM) | 13.61-16.28 | 35.02-35.06 | 8.4-16.4 |
| **Assemblage 3** | ***Rotaliatinopsis semiinvoluta, Hopkinsinella glabra* and *Epistominella Exigua*** | Middle Continental Slope (510-745) | 3.90-5.43 | 0.48-0.63 (21-28 µM) | 8.26-9.94 | 34.98-35.04 | 7.2-12.1 |
| **Assemblage 4** | ***Bulimina arabiensis, Bulimina elegans* and *Bolivina earlandi*** | Lower Continental Slope (1002-1550) | 4.78-6.60 | 1.07-2.03 (48-91 µM) | 4.09-6.56 | 34.85-34.95 | 6.6-13.2 |
| **Assemblage 5** | ***Bolivina earlandi, Bulimina aculeata* and *Globocassidulina Subglobosa*** | Deeper Region (1887-2750) | 4.02-6.86 | 2.85-3.84 (127-171 µM) | 2.06-3.01 | 34.75-34.79 | 7.3-11.0 |

# Chapter-8: Pore density and diameter of *Bolivina seminuda*: A robust proxy for dissolved oxygen

The dissolved oxygen is the second most abundant dissolved gas after nitrogen in the seawater. The dissolved oxygen concentration increases with increase in the salinity and decreases with the rising temperature (Gupta, 1994). The restricted circulation, water column stratification and high productivity, creates oxygen deficient zones in several parts of the world oceans. The persistent oxygen-depleted waters of the deep sea environment create a zone in which benthic foraminifera increase in abundance but develop a low diversity assemblage. Many eurytolerant species including calcareous and agglutinated benthic foraminifera of diverse taxa are able to survive in modern depleted oxygen zones as well in higher oxygen waters. Many of these benthic species easily tend to migrate to lower or higher oxygen levels and related high organic matter zones. Benthic foraminifera generally need very low oxygen to respire (Lee and Muller, 1973). To survive in low dissolved oxygen concentration, foraminifera have developed different kind of mechanisms as nitrate respiration, sequestration of chloroplasts, bacterial symbionts, ultra-structural adaptation or dormancy. The difference in dissolved oxygen concentration affects both the diversity as well as morphology of benthic foraminifera. The low oxygen indicators (e.g. *Bolivina*, *Bulimina*, *Cassidulina*) are usually, flat elongated tapered forms, mostly infaunal with highly porous test, as compared to oxic condition indicators (e.g. *Cibicides*, *Cibicidoides*), which are epifaunal planoconvex, biconvex, rounded trochospiral, and spherical in shape (Gary et al., 1989; Kaiho, 1994).

The dissolved oxygen concentration in the seawater is likely to deplete further, in view of the global warming and eutrophication. To find the solution for harmful impact of global warming or other anthropogenic activities on marine life in near future, it is important to understand the factors affecting the dissolved oxygen concentration. The dissolved oxygen concentration during different boundary conditions in the past can help to understand the dynamics of the oxygen deficient zones. Recently, foraminiferal pore pattern is proposed as proxy to study the bottom water oxygenation (Richirt et al., 2019). Pores are formed at an early stage of chamber formation, and thus play a major role in calcification of the organism. The pores in benthic foraminifera facilitate gas exchange between the surroundings and organism as well as maintain the oxygen uptake. The higher porosity of dysoxic benthic forms is attributed to the difficulty in secreting calcium carbonate and in providing higher mitochondrial oxygen uptake (SenGupta and Machain-Castillo, 1993). A comparison of pore density in living (rose-Bengal stained) specimens of shallow infaunal *Bolivina pacifica*, and deep-infaunal species *Fursenkoina mexicana*, and *Chilostomella oolina* isolated from surface sediment samples collected from the oxygen deficient zone off Namibia and Pakistan, suggests that pore density depends on dissolved oxygen, as well as nitrate concentration and temperature (Kuhnt et al., 2013). Further, the response of benthic foraminifera to dissolved oxygen is species specific. The pore diameter also varies with dissolved oxygen concentration.

Here, an attempt is made to understand the effect of dissolved oxygen on the pore diameter and density of living benthic foraminifera isolated from the surface sediments collected along a depth transect covering the oxygen deficient zone in the Gulf of Mannar. A total 391 Scanning Electron Microscope images have been taken to understand the variation in pore size from shallow to deep water depths in the Gulf of Mannar (Figure 8.1).

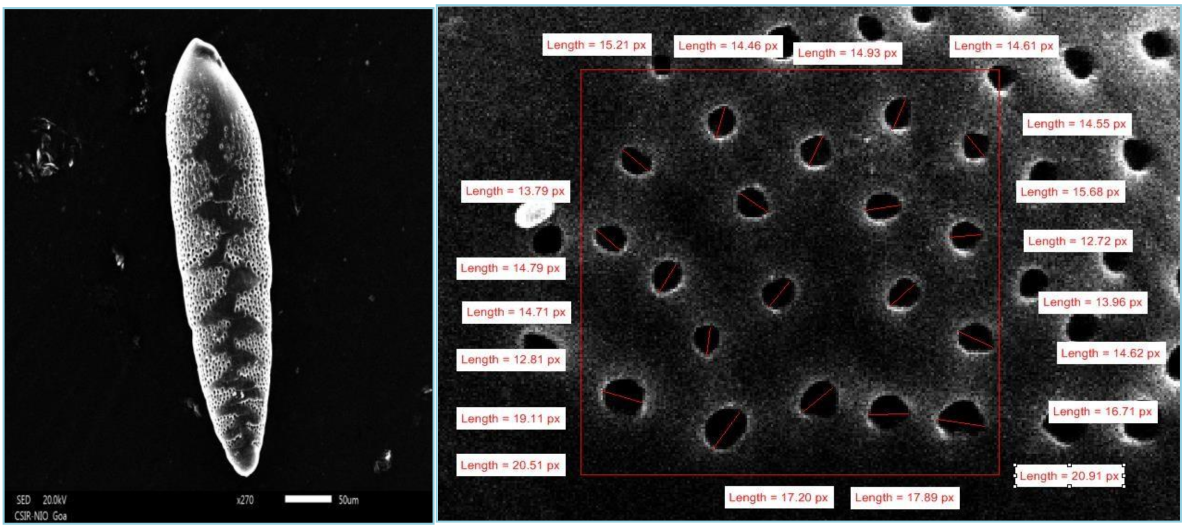

**Figure 8.1. Scanning Electron Micrograph of *Bolivina seminuda* (A) and measurements of pore-size and counting of pores/grid (180×180) by using NIS-Element BR 4.10.00 software (B).**

## Results

The living (rose-Bengal stained) *Bolivina seminuda* was available at four stations (SSD004 MC04, MC05, MC06 and MC07). All 5 sections (top 5 cm) of SSD004 MC06 only, had living *Bolivina seminuda*. In all these sections, 25 specimens each, were picked for detailed pore size study. At other stations, *B. seminuda* was mainly found in the top (0-1 cm) section. The pore density [number of pores in unit area (100 µm$^2$) of the last formed chamber of the specimen] as well as the diameter of all available pores in the selected unit grid, was measured. The dissolved oxygen was measured onboard at the time of collection of samples, as well as downloaded from the World Ocean Atlas. The results for the core tops (0-1) of all the stations and the depth sections of SSD004 MC06 are discussed separately.

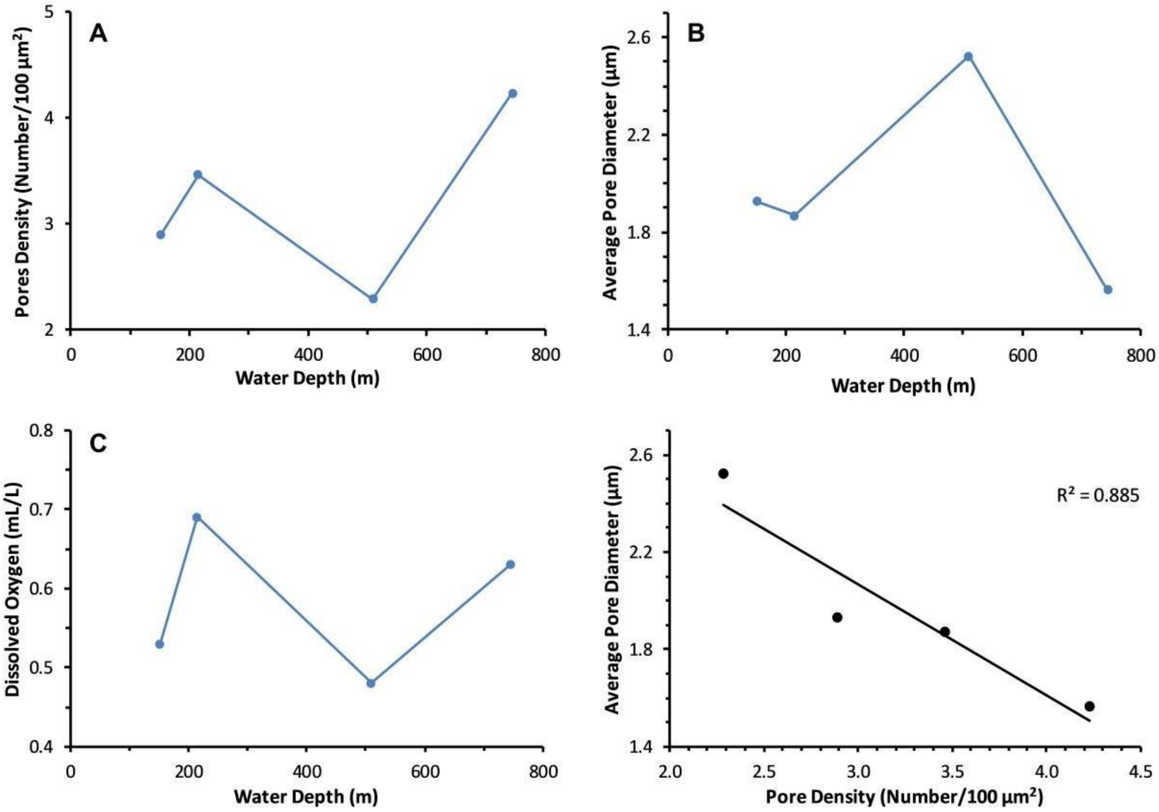

**Figure 8.2: Pore density (A) and average pore diameter (B) of the living specimens of *Bolivina seminuda* in the core top (0-1 cm) section of the four stations (MC04-MC08) in the oxygen deficient zone of the Gulf of Mannar. The change in dissolved oxygen concentration at these four stations (C). Inverse relationship between the pore density and diameter of the living specimens of *B. seminuda* in the core top section (D).**

### Pore morphology in core tops

The pore openings were generally well defined and clearly distinguishable from the smooth surrounding calcite surface. A large variation was observed in both the pore density (Figure 2A) and average pore diameter (Figure 8.2B) of the living specimens of

*Bolivina seminuda* in the core top (0-1 cm) section of the four stations (MC04-MC08) in the oxygen deficient zone of the Gulf of Mannar. The average pore density varied from a minimum of 2.29/100 µm$^2$ to the maximum of 4.23/100 µm$^2$. Similarly, the pore diameter also varied from 1.56 to 2.52 µm. Neither the pore density nor diameter showed a systematic trend with depth. The average pore density in the core top sections, however, followed a trend similar to that of the ambient dissolved oxygen (Figure 8.2C). Incidentally, the pore diameter was significantly inversely related ($R^2$ = 0.885) to the pore density in the core top sections (Figure 8.2D).

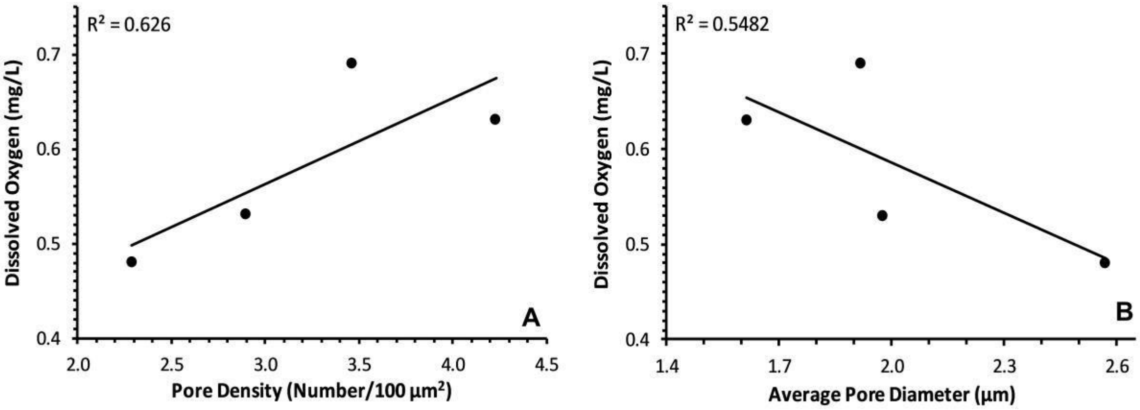

**Figure 8.3: Relationship between the dissolved oxygen and the pore density (A) as well as the average pore diameter (B) of the living specimens of *Bolivina seminuda* in the core top (0-1 cm) section of the four stations (MC04 - MC08) in the oxygen deficient zone of the Gulf of Mannar.**

Both the pore density and pore diameter show a significant relationship with the ambient dissolved oxygen. The pore density increased with the increasing dissolved oxygen concentration ($R^2$ = 0.63). However, the pore diameter of *B. seminuda* in the core top sections decreased with increasing dissolved oxygen ($R^2$ = 0.55) (Figure 8.3).

### Pore morphology in depth sections (SSD004 MC06)

A clear variation in pore diameter from core top (0-1 cm) to deeper sediments (4-5 cm) was observed. The pore diameter increased with depth (Figure 8.4A). The smallest pore size 1.87 µm, was in the core top section and the largest pore size (2.22 µm) was in the deepest section at MC06 station, within the oxygen deficient zone. The pore density was normalized to 100 µm$^2$.

The pore-density does not have any distinct trend with depth in the sediment. The average number of pores only slightly decreased with depth in the top 5 cm section of

MC06 (Figure 8.4B). The decrease in pore density was, however, insignificant. Interestingly, the pore density was nearly consistent in all the sections from the core top (0-01 cm) to the deepest section (4-5 cm).

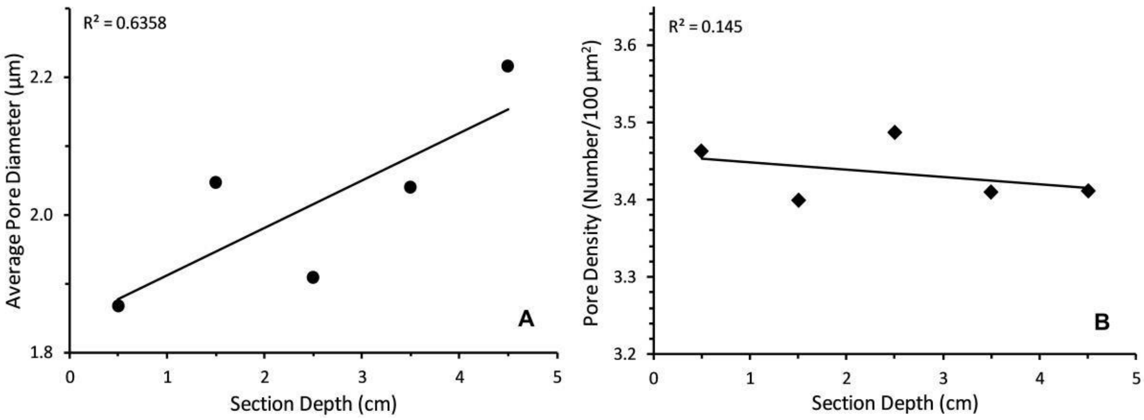

**Figure 8.4: Average pore diameter (A) and pore density (B) in the last chamber of living *Bolivina seminuda* in the top 5 cm sections of station SSD004 MC06.**

## Discussion

The dominant species of oxygen deficient waters are mainly opportunistic, as they are adapted to and utilize the sudden organic matter pulse, common in such environment. Mainly hyaline species (e.g. *Bolivina*, *Sugurunda*, *Bulimina*, *Globobulimina*, *Uvigerina*, *Epistominella and Cassidulina*) constitute the typical bathyal oxygen deficient water assemblage (Gupta and Machain-Castillo, 1993). Many workers reported that *Bolivina* survives under intense hypoxic conditions (<0.3 mL/L) in the modern ocean. Therefore, *Bolivina seminuda* was selected to study the pore-pattern. The rectilinear species generally dominate the oxygen deficient waters, and are normally present in high oxygen environments also. Additionally, a majority of the low oxygen tolerant species are very small. Therefore, for efficient study of species distribution pattern, it is necessary to use >63 µm coarse fraction in oxygen deficient environment. The living specimens were picked from >63 µm coarse fraction. It is always good to focus on the last formed chamber to study the pore size pattern because it contains the largest volume of the protoplasm. Additionally, the last formed chamber has a comparatively thinner wall. In a majority of foraminifera, with every new chamber formation, there is a secretion of calcite layer over the entire test. Although the old pores remain open, the original characteristics of pores are not clear due to secondary layer formation. Main characteristics of the low oxygen tolerant species include bigger pores, small, thin-walled and mostly infaunal habitat. Being small, their oxygen demand is also very low and it is easy for such species to adjust in low oxygen water, by modulating the pore size and density. The bigger and more number of pores per unit area, with increasing depth in the sediments, clearly indicates that *Bolivina seminuda* adapts to low dissolved oxygen by modulating the pore size and density.

Although, the factors controlling pore pattern are still not clear, it is speculated that the pores in benthic foraminifera play an important role in gas exchange between the surroundings/environments and organism. Thus the gas exchange intensity can be estimated by the pore size and density (Petersen et al., 2016). Not only pore density and pore size but test wall thickness also defines the gas exchange intensity. The thin-walled species dominate the oxygen depleted environment (Richirt et al., 2019). *Bolivina seminuda* is also a thin walled species. In a majority of the previously studies done to understand pore pattern, only pore density was estimated. Recently, it has been suggested that it is mandatory to study both the pore density and size for reliable results. The increase in pore size with decreasing oxygen availability is confirmed in the living specimens of *Bolivina seminuda* in the surface sediments of the Gulf of Mannar. The increased pore density at higher dissolved oxygen availability is intriguing. Additionally, the pore density is inversely related with the pore diameter. This inverse relationship is expected as a lesser number of bigger pores can be accommodated in the same area, as compared to the large number of small pores. From the linear relationship between the dissolved oxygen concentration and the pore density, it is evident that *B. seminuda* prefers more number of smaller pores under favourable conditions. The lesser number of bigger pores per unit area, is an adaptation under unfavourable low dissolved oxygen environment. Similar inferences are also drawn from the variation in pore density and diameter with the depth in sediments. Although the pore density only slightly decreased with depth, the pore diameter significantly increases at deeper sections. Therefore, it is evident that with decreasing dissolved oxygen with depth, *B. seminuda* adapts by increasing the pore size with a imperceptible change in pore density.

Two constraints mainly control foraminiferal porosity, namely metabolic constraints and mechanical constraints. Foraminifera need a minimal respiration rate in order to ensure a nominal metabolism (metabolic constraints) and test mechanical resistance integrity (mechanical constraints). Laboratory culture studies have also confirmed that benthic foraminifera increase the pore diameter under low oxygen conditions (Kitazato and

Tsuchiya, 1999). The gas exchange intensity in foraminifera increases with increase in pore size and density and thus is one of the adaptations under hypoxia. Incidentally, test robustness is inversely related to porosity. Therefore, in order to make the test robust, foraminifers increase the pore size without increasing the pore density (Richirt et al., 2019). The quantitative studies on foraminiferal pore pattern clearly demonstrated that the bigger pores under increased physical stress result in the increased test robustness (Wetmore, 1987). Therefore, the lower pore density and bigger pore size in *Bolivina seminuda* in the Gulf of Mannar, is an adaptation to survive under low dissolved condition while maintaining the test robustness.

## Conclusions

*Bolivina seminuda* is a typical low dissolved oxygen water infaunal species in the modern ocean. *Bolivina seminuda* are very small, thin-walled and abundant in oxygen deficient zones of the Gulf of Mannar. Their small size and thinner test makes them adaptable to low oxygen waters as it can survive in very less amount of oxygen concentrations. The presence of larger pores at deeper sections suggest that *Bolivina seminuda* tend to maintain good metabolic activity when food is available as it is safe from mechanical stress in deeper sections. The pore density and diameter of *B. seminuda* can be used as reliable proxy to reconstruct changes in the intensity and extent of the low dissolved oxygen zones in the past.

# Chapter-9: Inferences and Future Scope

The dissolved oxygen concentration in the seawater is vital for the living organisms. The warming and nutrient input is likely to reduce the dissolved oxygen in the seawater in future. Therefore, it is important to understand the effect of dissolved oxygen on marine organisms. Benthic foraminifera are amongst the dominant microorganisms inhabiting the ocean sediments from the coast to the deepest point. Being very slow crawlers, benthic foraminifera are likely to be affected by the decreasing dissolve oxygen concentration. This thesis work included both the laboratory culturing and field studies to understand the effect of dissolved oxygen and associated parameters on benthic foraminifera.

From the laboratory culture experiment, a non-linear response of marginal marine benthic foraminiferal community to different levels of oxygen concentration has been assessed. The pattern is attributed to the combined effect of the presence of macrobenthic community as well as the dominance of epifaunal benthic foraminifera in the population. The dominance of epifaunal *Pararotalia nipponica* at all the oxygen concentrations, is attributed to its very high abundance in the original community as well as resilience to a wide range of oxygen levels. It is inferred that the decreasing dissolved oxygen concentration will cause a poor preservation of calcareous benthic foraminifer shells due to a concomitant drop in pH.

The organic matter flux significantly modulates the dissolved oxygen concentration. From the experiment to understand the effect of different amount of organic matter on benthic foraminifera, it is inferred that the high amount of phytodetritus (200 cells/mL) is responsible for the maximum growth in *Rosalina globularis* as this concentration represent the diatom flux during the summer monsoon in the field area. A good growth was also recorded in test-size of *Rosalina globularis* fed with pre-monsoon phytodetritus (50-100 cells/mL). Specimens which were fed 25 cells/mL (post-monsoon phytodetritus) were smaller than other specimens. The growth of unfed specimens of *Rosalina globularis* confirms the previous studies that unfed foraminifers can also survive for longer duration in the absence of phytodetritus and this response is species specific. The survival of *Rosalina globularis* specimens without additional food provides clues about how a few species could survive during low productivity in the sea. It is highly likely that the unfed *Rosalina* *globularis* fed on algae or bacteria present in sea water. 127 From the relationship between temperature and *Rosalina globularis*, with the simultaneous change in phytodetritus, it can be concluded that *Rosalina globularis* prefers higher temperature range (27ºC-32ºC) for their growth. But in long term they prefer lower temperature range (25ºC-30ºC) as the mortality rate is higher at higher temperature. Therefore, it is clear that *Rosalina globularis*, a shallow water benthic species, prefers high productivity regions for their growth. As the mortality is higher at high temperature, summer monsoon is perfect season for their optimum growth, as during this time, phytodetritus flux is high and the temperature is also comparatively low. Although *Rosalina globularis* can survive in less phytodetritus flux, long term food scarcity could lead to smaller test size of *Rosalina globularis*.

The effect of ambient conditions, especially dissolved oxygen and organic matter on the vertical habitat of living benthic foraminifera has been documented from the Gulf of Mannar, western Bay of Bengal and eastern Arabian Sea. The top 0-1 cm section of the sediment contains >85% of the total living benthic foraminifera at stations within the oxygen minimum zone. The low oxygen in the upper slope region affect the vertical living of foraminifera as the average living depth in this region reduced more than a centimeter, as compared to both the shallow and deeper stations. At stations with high dissolved oxygen, especially in the lower slope, a substantial fraction of the total living benthic foraminiferal population inhabits deeper sections of the sediments. Therefore, it is evident that vertical distribution of benthic foraminifera depends on bottom water oxygen concentration and organic matter quantity. The calcareous benthic foraminifera dominate the foraminiferal population both within and outside the oxygen minimum zone, suggesting their higher adaptability in all types of marine environments. The relative abundance of agglutinated benthic foraminifera is higher in the continental slope as compared to the shelf. All the agglutinated foraminifera are confined to the top 0-1 cm of the sediments in the shelf and upper slope.

Additionally, the species level distribution of the living (rose Bengal stained) benthic foraminifera from the southeastern Arabian Sea has also been documented. The abundant presence of *Bolivina currai* and *Hopkinsinella glabra* in the core-top sections is correlated with the dissolved oxygen. However, in the top 5 cm section, *Hopkinsinella glabra* and *Bulimina elegans* are significantly affected by the low dissolved oxygen. The significant negative relationship of *Hopkinsinella glabra* with the ambient dissolved oxygen, in both the top 0-1 cm section as well as the top 5 cm section, suggests it to be a 128 good indicator of low dissolved oxygen environment in the southeastern Arabian Sea. Besides this, five assemblages of living benthic foraminifera representing different bottom water conditions have also been reported. Assemblage 1, dominated by *Cassidulina laevigata, Cassidulina carinata* and *Eponides umbonatus* indicates shallow depth, hypersaline oxygen rich warm water environment with low organic matter availability. Assemblage 2 includes *Bolivina seminuda, Hopkinsinella glabra* and *Eubuliminella exilis* and represents shallow water intense suboxic condition with moderate organic matter availability. The assemblage 3 includes *Rotaliatinopsis semiinvoluta, Hopkinsinella glabra* and *Epistominella exigua* and indicates similar kind of suboxic environment but with comparatively high %Corg and lower bottom water temperature. Assemblage 4 mainly comprise of rectilinear infaunal species, dominated by *Bulimina arabiensis, Bulimina elegans* and *Bolivina earlandi* and represents comparatively well oxygenated water (1-2 mL/L; 45-90 µM) with abundant organic carbon at deeper depths (˜1000-1500 m). Assemblage 5 comprising of *Bolivina earlandi, Bulimina aculeata* and *Globocassidulina subglobosa* includes deep-water benthic foraminifera where bottom water is oxygen rich (>2.0 mL/L or >90 µM) along with high food availability with the lowest bottom water temperature and salinity. These representative benthic foraminiferal assemblages will help in reconstructing paleoceanographic conditions from the southeastern Arabian Sea.

The detailed morphological response of a species has been assessed to develop site specific proxy to reconstruct dissolved oxygen in the past. *Bolivina seminuda* is thin-walled benthic foraminifera abundant in the oxygen deficient zones of the Gulf of Mannar. The presence of larger pores at deeper sections suggest that *Bolivina seminuda* tend to maintain good metabolic activity when food is available as it is safe from mechanical stress in deeper sections. The pore density and diameter of *B. seminuda* can be used as reliable proxy to reconstruct changes in the intensity and extent of the low dissolved oxygen zones in the past.

The northern Indian Ocean has a wide range of dissolved oxygen concentration and thus is a suitable location to understand the response of marine organisms to dissolved oxygen. More studies on vertical distribution of living benthic foraminifera should be conducted from regions with different dissolved oxygen concentration. Efforts should also be made to understand the effect of seasonal changes in the organic matter flux and dissolved oxygen on living benthic foraminifera.

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# Publications

## Papers

1. **A. Kaithwar**, D.P. Singh, R. Saraswat, 2020. A highly diverse living benthic foraminiferal assemblage in the oxygen-deficient zone of the southeastern Arabian Sea. *Biodiversity and Conservation*, v. 29, pp. 3925-3958.
2. S.R. Kurtarkar, R. Saraswat, **A. Kaithwar**, R. Nigam, 2019. How will benthic foraminifera respond to warming and changes in productivity: A laboratory culture study on Cymbaloporetta plana. *Acta Geologica Sinica*, v. 93, pp. 175-182
3. S.R. Kurtarkar, Linshy V.N., **A. Kaithwar**, R. Saraswat, R. Nigam 2017. Experimental studies on benthic foraminifera: an update on the changing trends and challenges over the past decade. In P.K. Kathal, R. Nigam and A. Talib (Editors), *Micropaleontology and its Applications*, Scientific Publishers (India), pp 311-330.
4. D.P. Singh, R. Saraswat, **A. Kaithwar** 2017. Changes in standing stock and vertical distribution of benthic foraminifera along a depth gradient (58-2750). *Marine Biodiversity*, v. 48, pp. 73-88

## Abstracts (Oral Presentation)

1. 'Abundant presence of foraminifera in the Arabian Sea oxygen minimum zone'. In ESA-USSEE Joint Meeting (Ecological Society of America), August 14, 2019, USA.
2. 'Dissolved oxygen modulates pore density and diameter in infaunal benthic foraminifera *Bolivina seminuda*'. In International Conference on Paleoclimate Changes, July 2020, Vellore Institute of Technology, Vellore.
3. 'Effect of varying temperature and food availability on *Rosalinina globularis*'. In National Seminar on Recent Advances in Geosciences Research in India, July, 1-2, 2021, Delhi University, Delhi.