

Changes in standing stock and vertical distribution of benthic foraminifera along a depth gradient (58-2750 m) in the southeastern Arabian Sea

Dharmendra Pratap Singh[#], Rajeev Saraswat^{*}, Amrata Kaithwar

Micropaleontology Laboratory, Geological Oceanography Division, National Institute of Oceanography, Goa, India

Corresponding Author: # dsingh@nio.org; * rsaraswat@nio.org

Abstract

Benthic foraminifera are a reliable proxy to reconstruct past oceanographic conditions. The ecological preferences of benthic foraminifera are usually studied from the core-top samples. The habitat of living benthic foraminifera, however, can be much deeper. Here, we document the vertical distribution of living benthic foraminifera from the Gulf of Mannar, Southeastern Arabian Sea, to find out the sediment depth that contains representative living assemblage and to understand the relationship between ecological parameters and foraminiferal abundance. Additionally, as the region has a well-developed oxygen minimum zone, we also assess the effect of dissolved oxygen, organic carbon (%C_{org}) and other associated parameters on living benthic foraminifera. The multi-core samples were collected along a longitudinal transect covering the shelf, and slope (58- 2750 m), during the post southwest monsoon season. We report that at stations where dissolved oxygen is low (≤ 1.5 ml/l), >85% of the total living benthic foraminiferal population is confined to the top 0-1 cm section of the sediment and the average living depth decreases up to 0.6 cm. However, in the well-oxygenated waters, especially in the lower slope region, a substantial fraction of the total living benthic foraminiferal population inhabits deeper sections of the sediments. The calcareous benthic foraminifera dominates the foraminiferal population both within and outside the oxygen minimum zone. The absolute abundance of agglutinated benthic foraminifera is more on the continental slope, as compared to the shelf. The infaunal and epifaunal calcareous and agglutinated foraminifera show a different trend. We report that while the bottom water dissolved oxygen and depth controls the absolute abundance of benthic foraminifera, both the %C_{org} and ambient temperature, affect the relative abundance of living calcareous and agglutinated benthic foraminifera in the Gulf of Mannar.

Introduction

Foraminifera are a hugely successful group of predominantly marine, single-celled microorganisms (Saraswat & 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 & 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 & Murray 1999), and others (Boltovskoy et al., 1991; Murray 2001; Murray 2006). 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 Shimmiel 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.

Physiographic Setting

The Gulf of Mannar is situated at the junction of the Arabian Sea and Bay of Bengal. It is a large semi-enclosed bay bound by the southeastern coast of India on its left and the northwest coast of Sri Lanka on the eastern side. The water depth ranges between 50 to 3000 m. The region is influenced by the seasonal reversal of monsoon winds. The seasonally reversing winds and associated physical forces result in strong upwelling (Wyrтки 1973; Shetye et al. 1991; Pankajakshan et al. 1997; Krishna 2009; Paul et al. 2009). The upwelling of cold, nutrient-rich deep water to the surface increases surface productivity (Banse 1987; PrasannaKumar 2002; Smitha et al. 2008; Jyothibabu et al. 2008). Upwelling begins at the southern tip of India during May–June and subsequently propagates northwards and into the Gulf of Mannar (Banse 1959). 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 using available oxygen, thus lowering the dissolved oxygen content of the seawater to drastically low levels. This area also receives a large amount of organic matter flux during southwest monsoon (Yapa 2012), leading to the development of OMZ.

A limited variation is observed in the sea surface temperature (27.97°C to 28.34°C) along the study transect. The bottom seawater temperature varies from 2.06°C to 25.96°C and decreases with increasing water depth. As expected, the largest difference between surface and bottom water temperature is at MC-60 (2750 m). The sea surface salinity varies from 34.45 psu to 35.03 psu. The maximum sea surface salinity is in the region closer to the coast. The bottom seawater salinity varies from 34.76 psu to 35.19 psu and continuously decreases with increasing water depth. The largest salinity difference between surface and bottom water is at MC-05 (510 m) and the lowest at MC-07 (152 m) water depth. Along the transect, bottom water dissolved oxygen decreases to ≤ 2 ml/l, between 152 m and 1250 m water depths, which is often considered as oxygen minimum zone in the Arabian Sea (Naqvi et al. 2003). The minimum dissolved oxygen (0.53 ml/l) is at 152 m, and the maximum (3.48 ml/l) is at 2750 m water depth.

Materials and Methodology

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) covering the oxygen minimum zone (water depth varying from 58 m to 2750 m) (Figure 1). 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 samples were collected in October 2014, after the end of the summer monsoon. Since it was a multi-disciplinary cruise, including people working on macro- and meiobenthos, geochemistry, sedimentology and palynology, only one tube was used for foraminiferal studies. 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 of Rose-Bengal dissolved in 1 l of 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. 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 labeled 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 1000 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. 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) 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)]

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.

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 analyzed by using coulometer (CM 5015 CO₂) and the total carbon was analyzed by using elemental analyzer (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, 2016) (Figure 2).

Results

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 3, Table 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 3).

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 4, Table 1). 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 4).

Absolute Abundance

The vertical foraminifera stock (sum of top 5 cm sediment) varied from 46 specimen/g sediment to 3480 specimen/g sediment (Figure 5, Table 1). 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. 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). 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). 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 $\geq 60\%$ 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.

Average living depth (ALD)

Average living depth was calculated at every station to understand the vertical living preference of fauna following Jorissen et al. (1995) equation. ALD_5 was calculated up to top five-centimeter sediment sections at all the stations. ALD_5 was shallower (0.6 cm) at intermediate depths (215 - 1550 m) and comparatively deeper (1.9 cm) at shallow and deeper depths. Benthic foraminifera in the upper slope region, mostly lived in the upper half centimeter of sediment (Figure 7).

Calcareous and agglutinated foraminifera

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 8). 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 8).

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 9). The contribution of living calcareous foraminifera to the vertical stock drastically decreases in sub-surface samples (average 14% in 1-2 cm section and $\leq 5\%$ in subsequent sections) (Figure 9). 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 10).

The living agglutinated benthic foraminifera are also relatively more abundant in core top (0-1 cm) section than sub-surface samples (Figure 10). 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 (Figure 10). 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 10).

Calcareous epifaunal and infaunal benthic foraminifera

The epifaunal calcareous foraminifera are dominant in the middle slope and relatively less abundant in both the shelf and outer slope region (Figure 11). 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 11). 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 11). 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 11).

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 12A). 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 12B). 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 12B).

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 13A). Surprisingly, even the infaunal agglutinated foraminifera are present only in the top 0-1 cm section at a majority of the stations (Figure 13 B). 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 13B). 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.

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 14). None of these and even other ambient parameters, however, seem to have a dominant significant effect on the absolute abundance of benthic foraminifera. The relative abundance of agglutinated benthic foraminifera is significantly positively correlated with %C_{org} and negatively correlated with bottom water temperature (Figure 14). 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 14). 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 14).

Discussion

Benthic foraminiferal abundance

As the dissolved oxygen decreases to ≤ 1 ml/l at 152 m water depth, 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 5). 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 4, 5). 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 4, Table 1). 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; Cauille 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 (Cauille 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 (Cauille 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 (Cauille 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 megafaunal population (Gooday et al., 2010).

In the Gulf of Mannar, more than 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. ALD₅ 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 ALD₅ 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; Cauille 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 14). 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. 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 11). 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 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) in the Gulf of Mannar. 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 region. 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 in the Gulf of Mannar region 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. Based on this work, it is clear that not all the living benthic foraminifera are confined to the core-top section in the Gulf of Mannar, and therefore one has to be careful in using benthic foraminiferal characteristics for paleoceanographic studies.

Acknowledgements

Authors are thankful to Dr. Rajiv Nigam and Dr. B. Nagender Nath, CSIR-National Institute of Oceanography, Goa for the support and encouragement. The funding from Council of Scientific and Industrial Research, New Delhi to RS (Young Scientist Project) and GEOSINKS project is thankfully acknowledged. Authors are also thankful to the Department of Science and Technology, India for a financial grant to a project sanctioned under the 'Climate Change and Coastal Vulnerability Programme. The authors also thank Dr. C. Prakash Babu, CSIR-National Institute of Oceanography, Goa for the help in total and inorganic carbon analysis.

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Legend to Figures:

- Figure 1: Location of multicore samples collected from the Gulf of Mannar. The bathymetry is marked in shaded contours.
- Figure 2: Annual average bottom water salinity (psu) (A), temperature (°C) (B), dissolved oxygen (ml/l) (C) and surface chlorophyll (mg/m³) (D) in the southeastern Arabian Sea.
- Figure 3: 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 4: The organic carbon (%C_{org}) in core top (0-1 cm) and sub-surface (1-2 cm) samples, at the sampling stations.
- Figure 5: 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.
- Figure 6: 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.
- Figure 7: The average living depth (ALD₅) of vertical foraminifera stock at different stations.
- Figure 8: 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.
- Figure 9: 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.
- Figure 10: 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.
- Figure 11: 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.
- Figure 12: 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.

Figure 13: 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.

Figure 14: 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.

Legend to Tables:

Table 1: The details of stations, ambient physico-chemical parameters and total benthic foraminiferal characteristics in top 5 cm of the sediments.

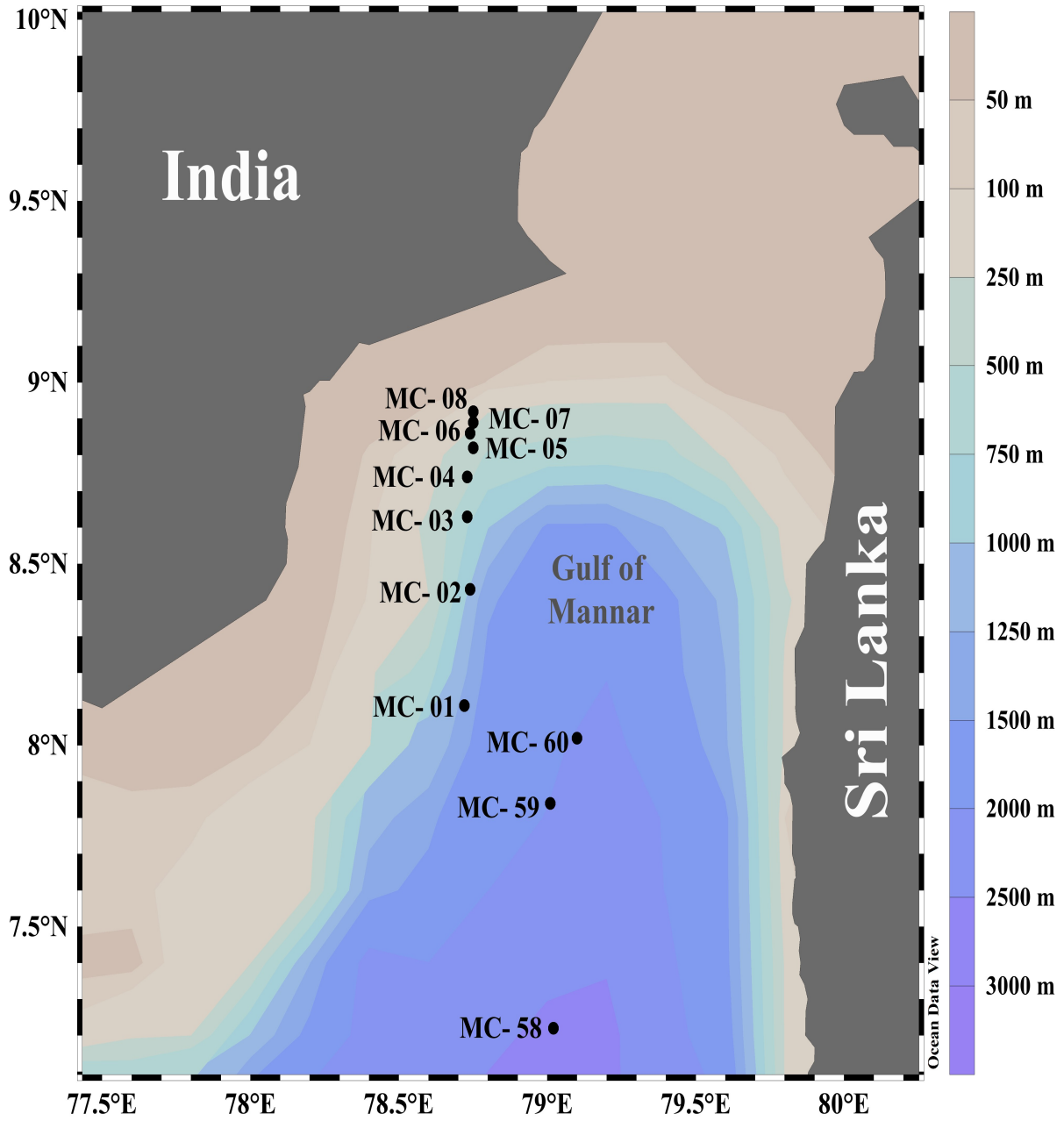


Figure 1

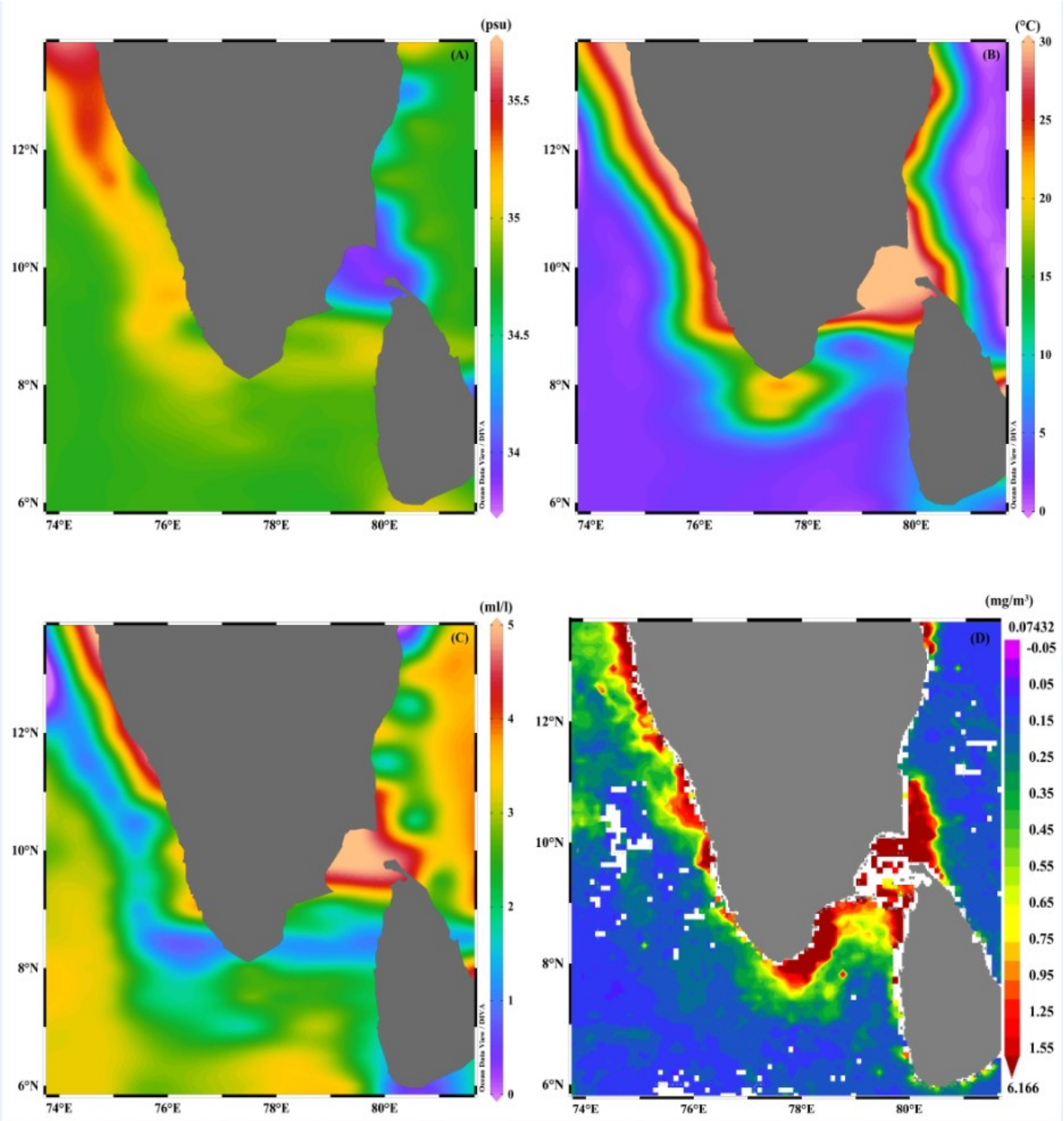


Figure 2

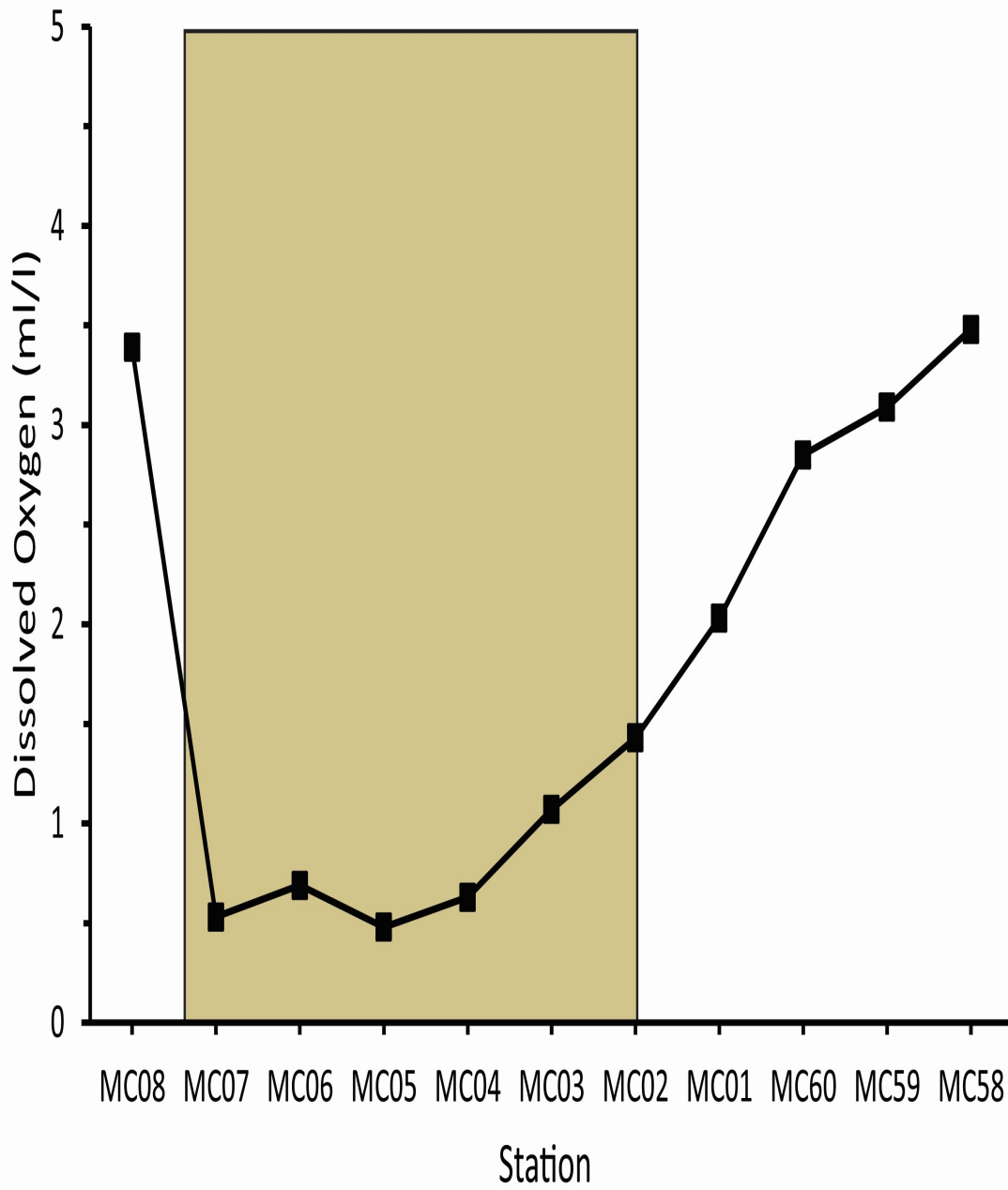


Figure 3

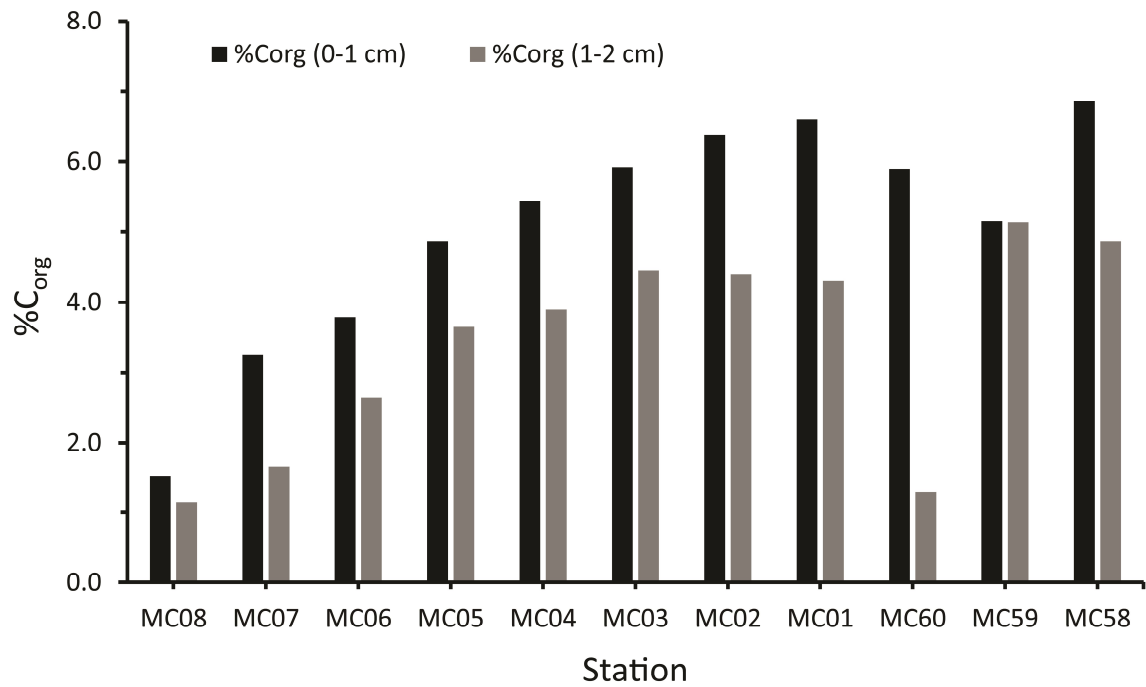


Figure 4

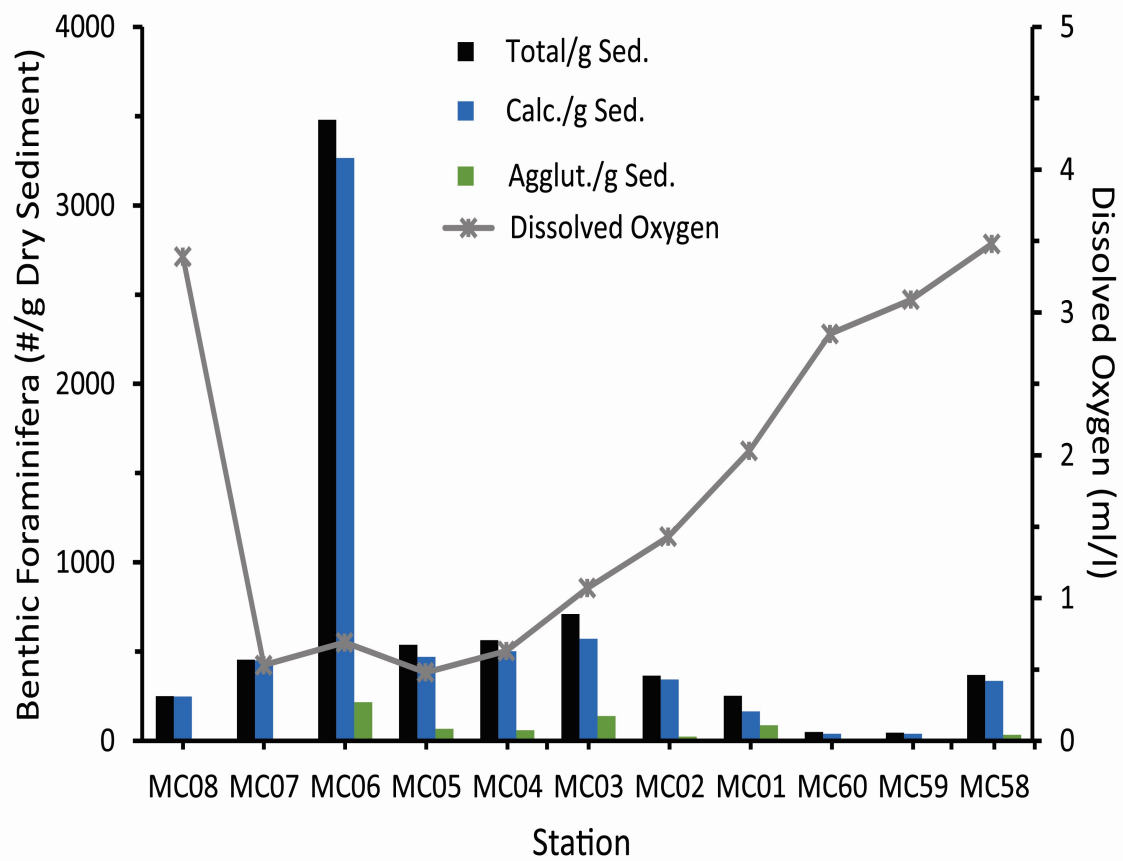


Figure 5

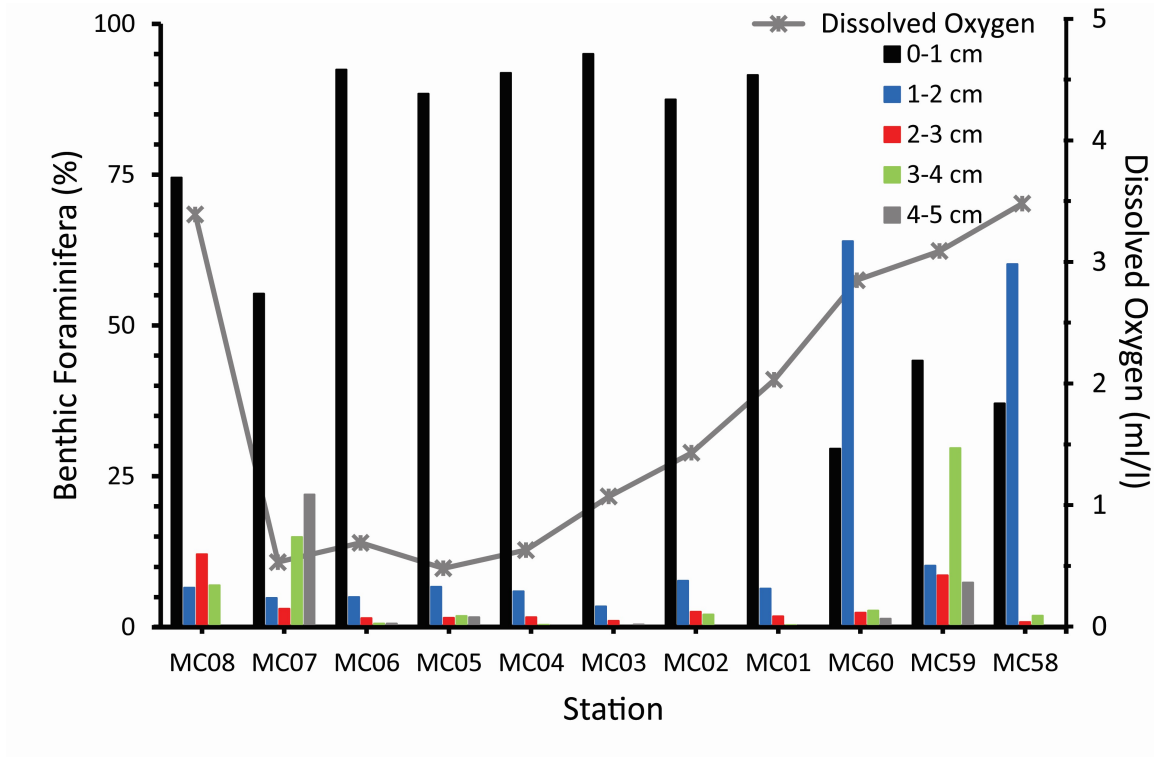


Figure 6

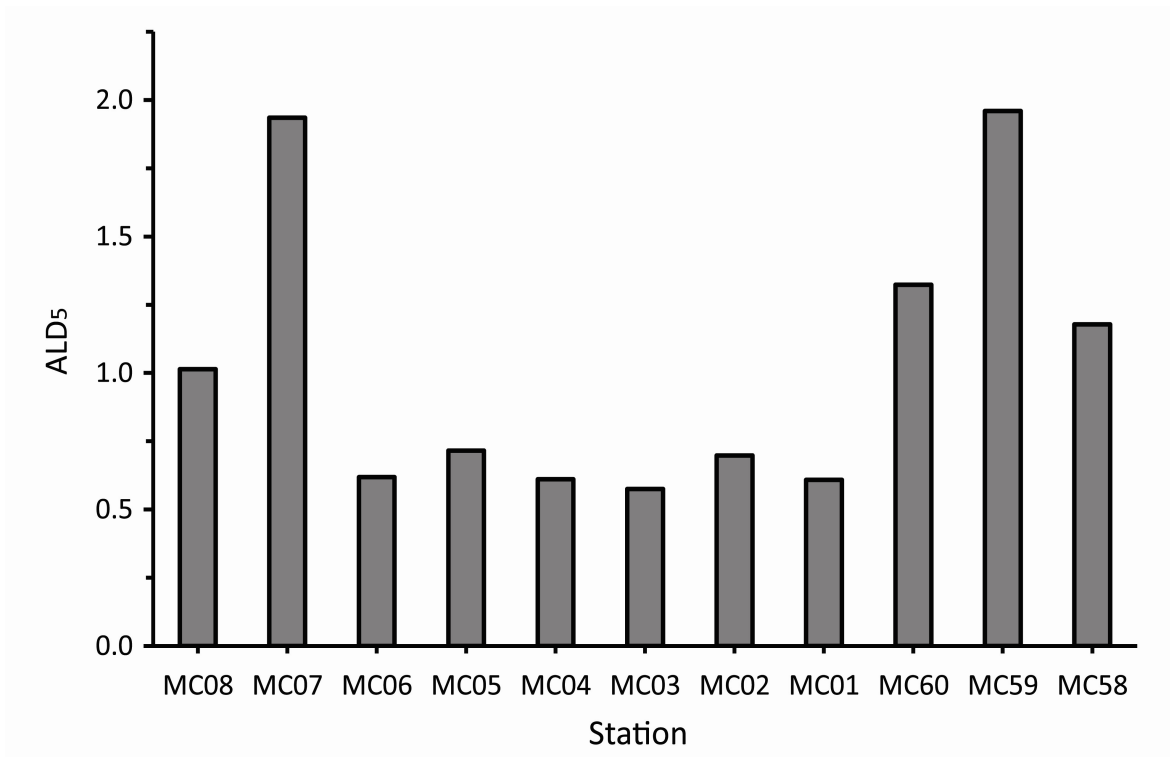


Figure 7

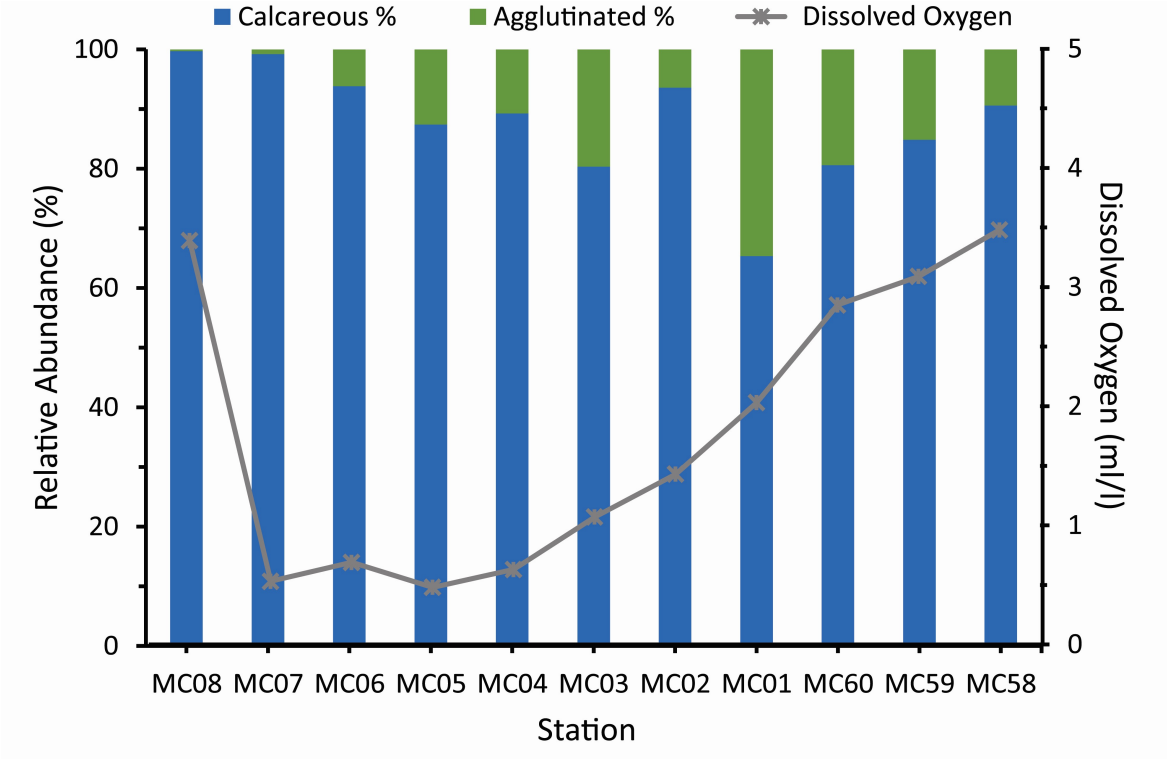


Figure 8

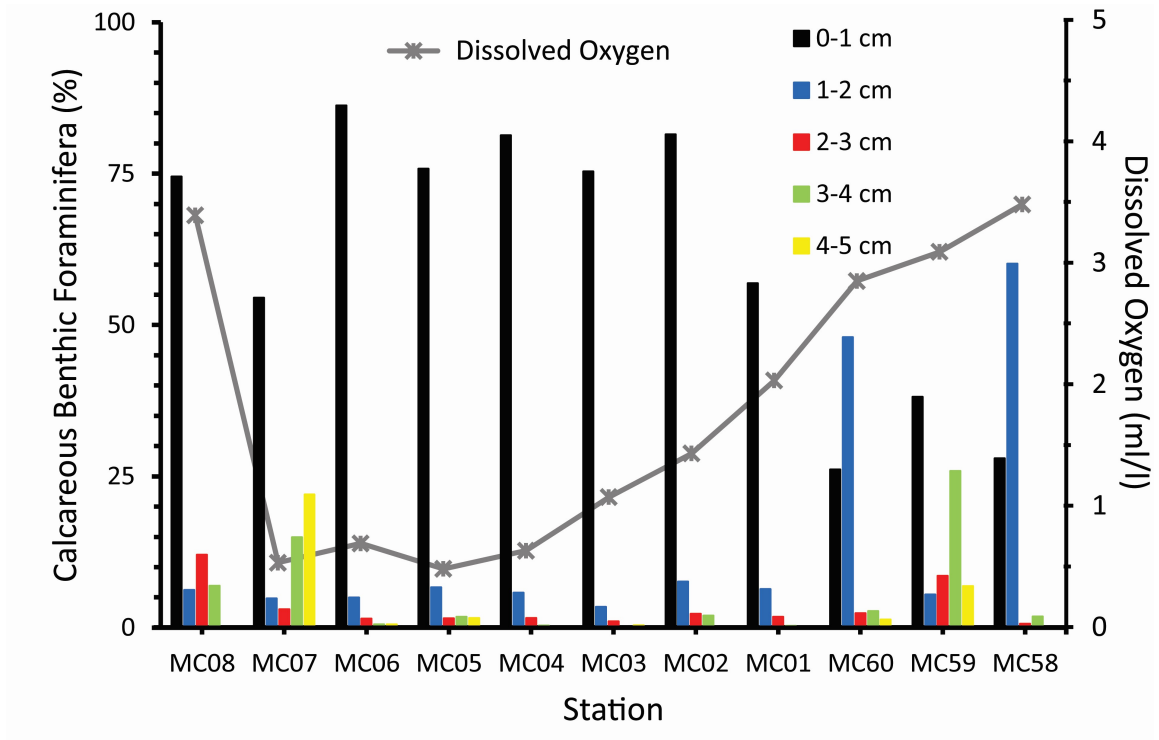


Figure 9

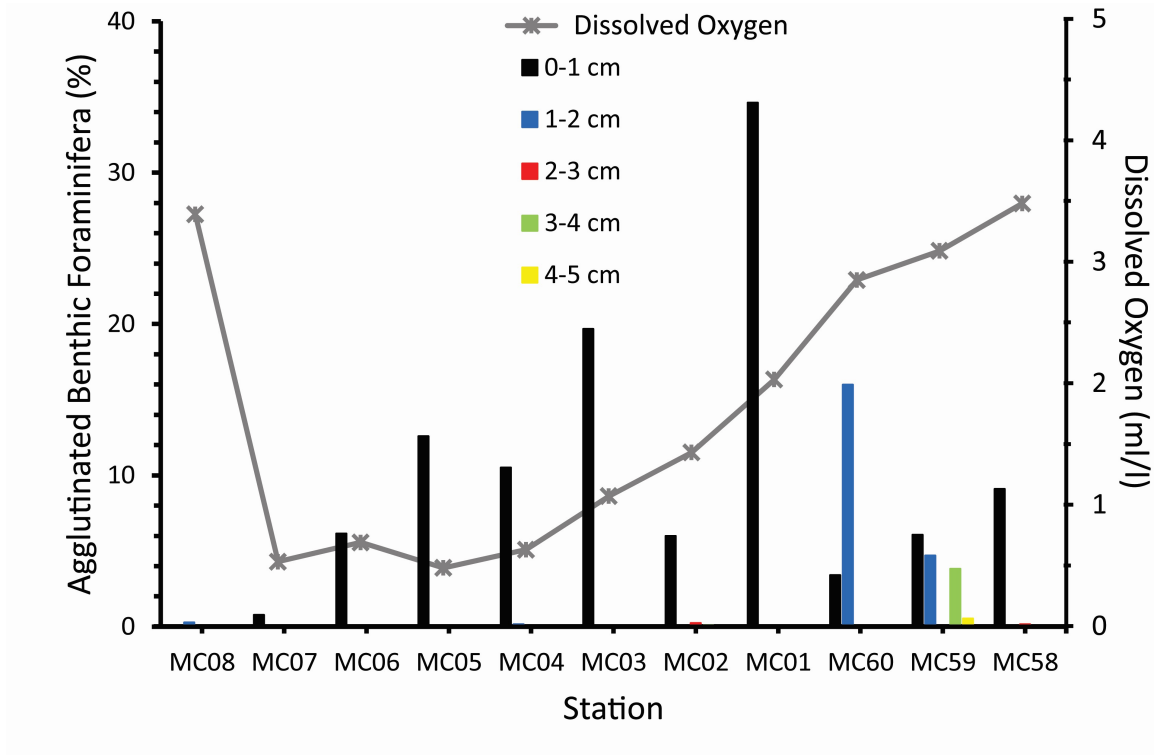


Figure 10

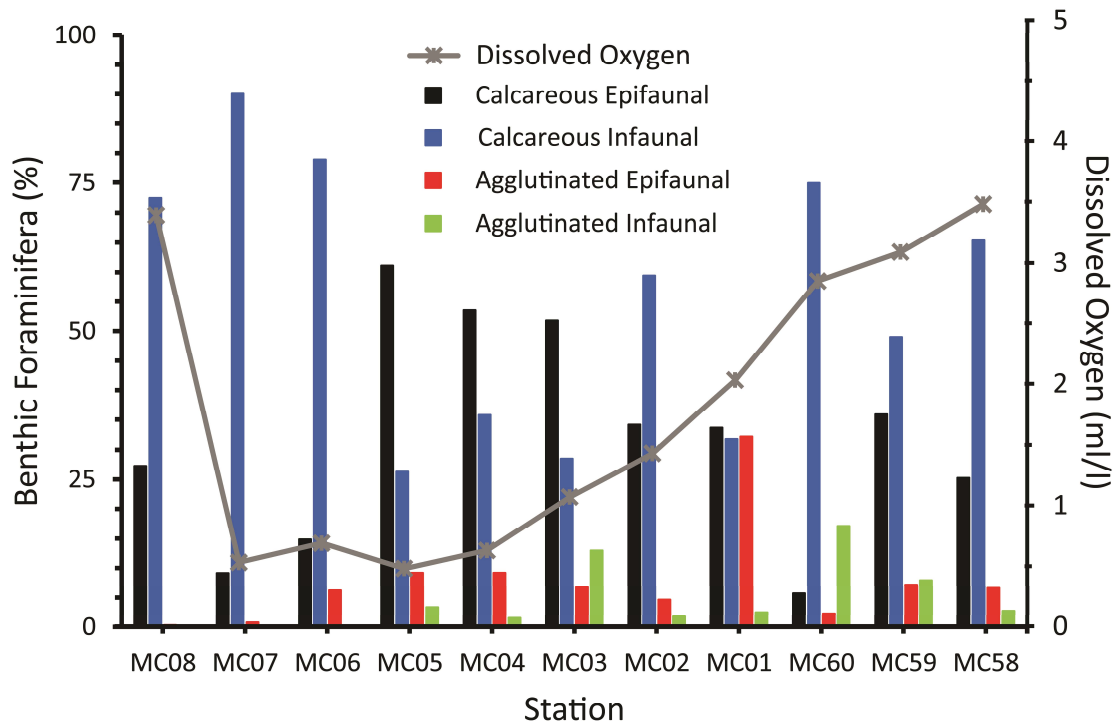


Figure 11

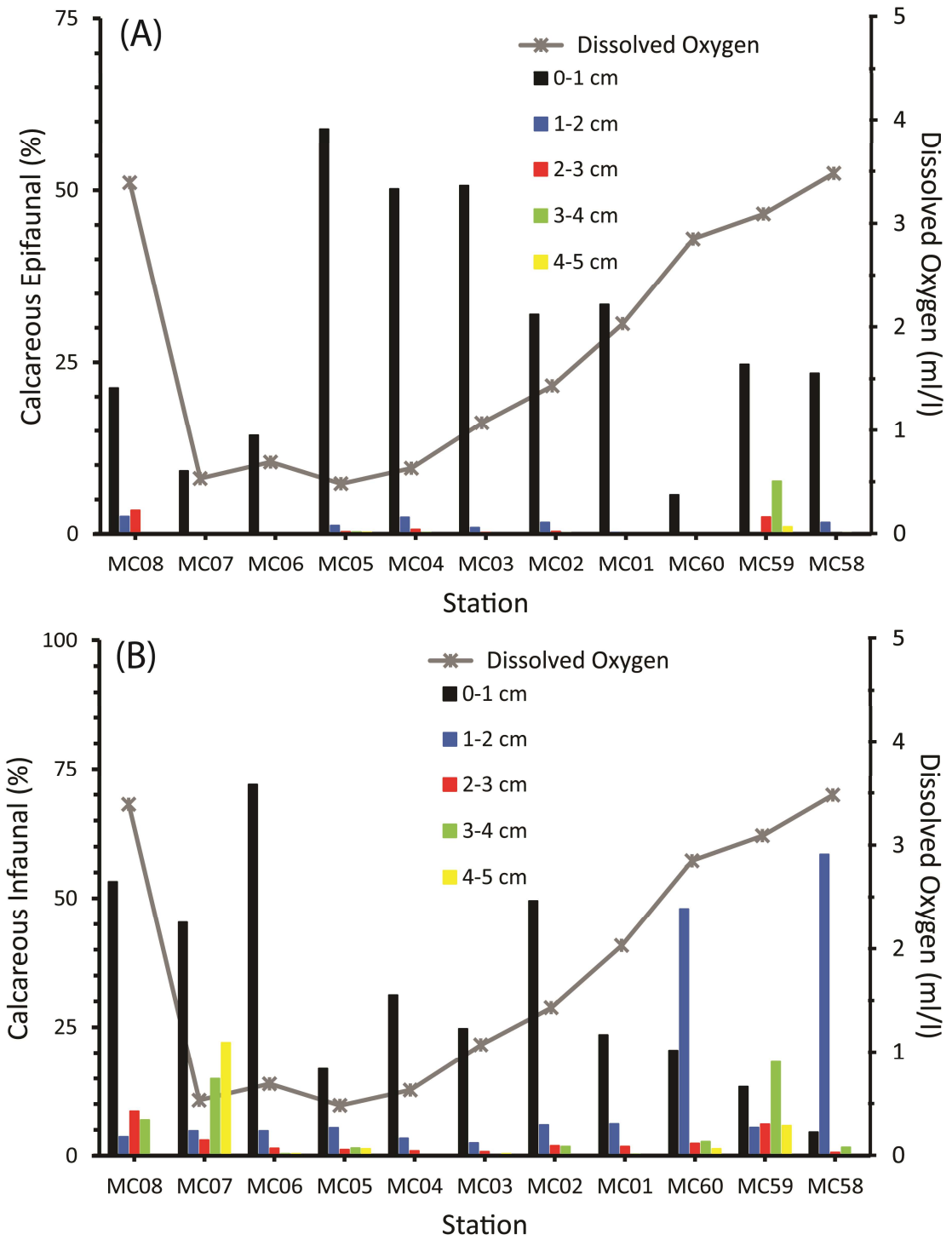


Figure 12

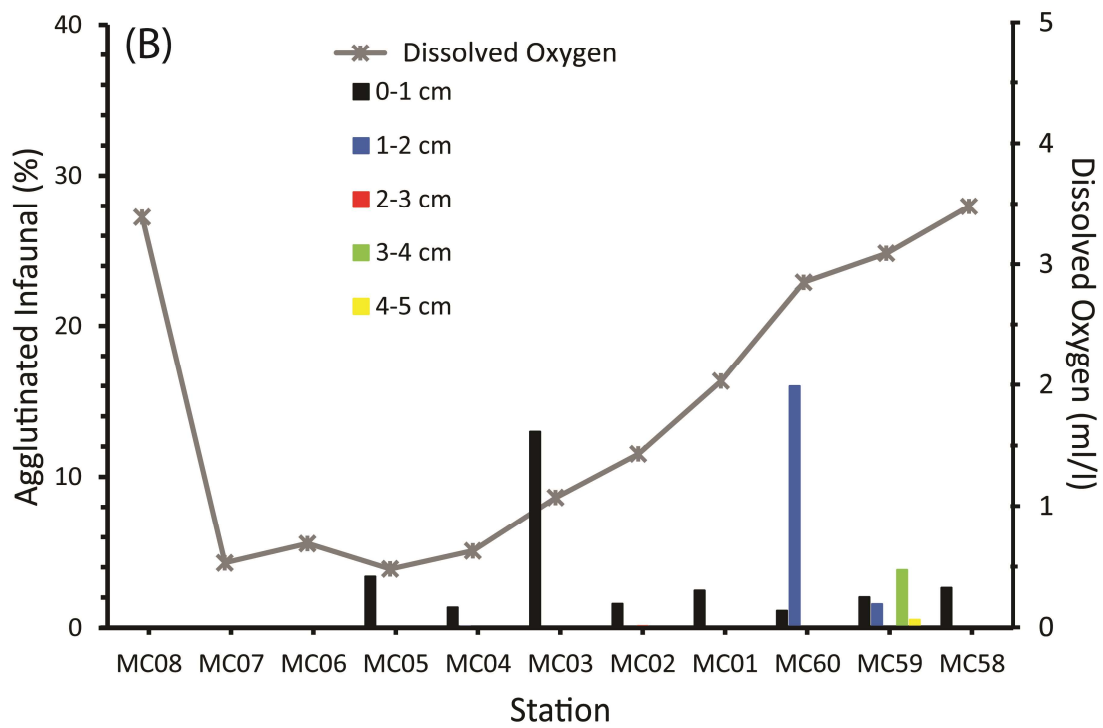
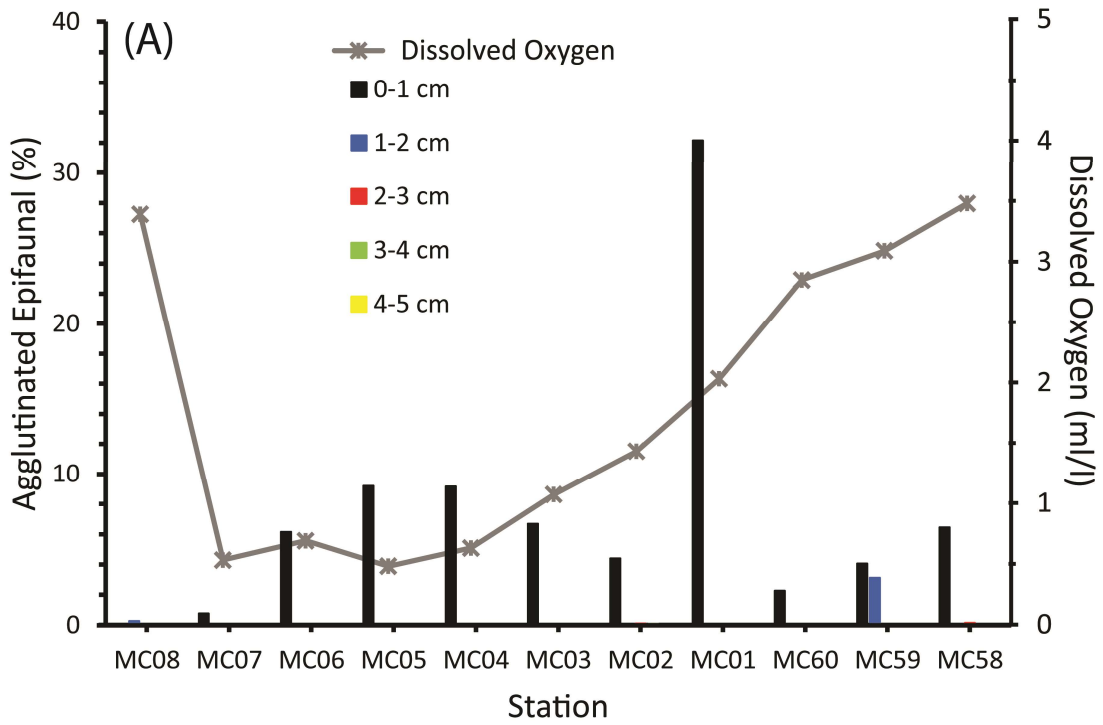


Figure 13

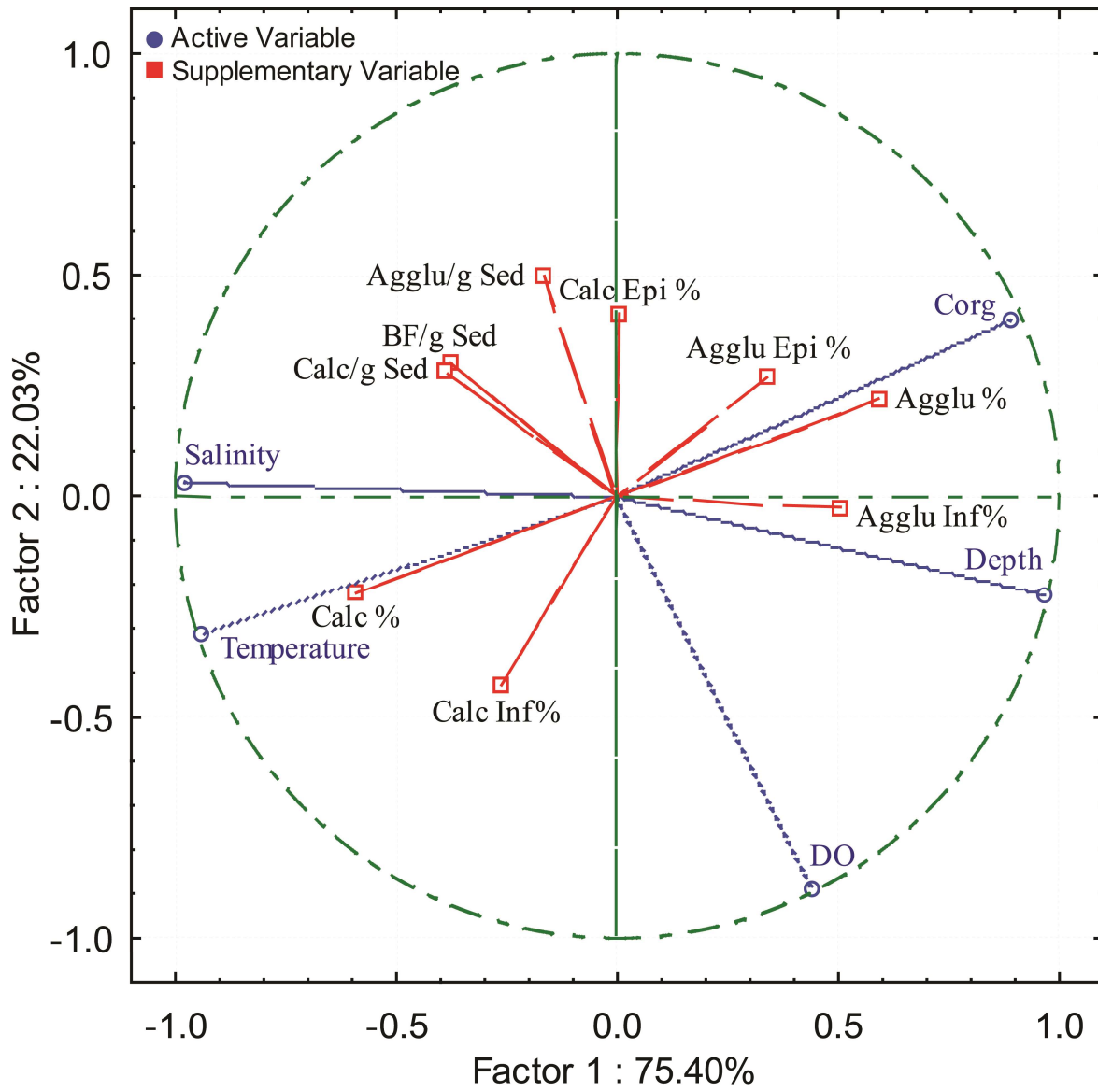


Figure 14

Table 1

Station	Depth (m)	Lat. (°N)	Long. (°E)	Bottom Sal (psu)	Bottom Temp. (°C)	Bottom DO (ml/l)	% Corg (0- 1 cm)	% Corg (1-2 cm)	Total Living Benthic (#)	Total Living Calc (#)	Total Living Agglut (#)	Calc Round (#)	Calc Angul (#)	Agglu Round (#)	Agglu Angul (#)
MC-08	58	8.92	78.75	35.19	25.96	3.39	1.52	1.14	40	39	1	13	26	1	0
MC-07	152	8.89	78.75	35.03	16.28	0.53	3.25	1.66	586	579	7	82	497	7	0
MC-06	215	8.86	78.74	35.07	13.61	0.69	3.77	2.65	1389	1354	35	161	1193	29	4
MC-05	510	8.82	78.75	35.04	9.94	0.48	4.87	3.65	485	444	41	229	215	30	11
MC-04	745	8.74	78.73	34.99	8.26	0.63	5.44	3.89	459	423	36	227	196	28	8
MC-03	1002	8.63	78.73	34.95	6.56	1.07	5.92	4.46	321	274	47	142	132	16	31
MC-02	1250	8.43	78.74	34.92	5.50	1.43	6.38	4.40	374	355	19	109	246	13	6
MC-01	1550	8.11	78.72	34.86	4.09	2.03	6.60	4.30	109	81	28	28	53	26	2
MC-60	1887	8.02	79.10	34.79	3.01	2.85	5.90	1.29	45	41	4	5	36	2	2
MC-59	2080	7.84	79.01	34.78	2.62	3.09	5.16	5.14	181	155	26	75	80	14	12
MC-58	2750	7.22	79.02	34.75	2.06	3.48	6.86	4.87	438	346	92	225	121	65	27