

Assessing the ecological preferences of agglutinated benthic foraminiferal morphogroups from the western Bay of Bengal

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Abstract

Agglutinated benthic foraminiferal morphogroups have often been used as a proxy in paleoecological studies. The response of various agglutinated morphogroups may, however, vary regionally. Here we report the ecological preferences of agglutinated morphogroups from the fresh-water influx dominated western Bay of Bengal. The abundance of both living (rose-Bengal stained) as well as dead agglutinated benthic foraminifera and their morphogroups, has been studied in a total of 42 core-top samples from the depth range of 25 to 2540 m, covering the entire shelf and slope. Agglutinated foraminifera are divided into four morphogroups (A to D). Out of these, two morphogroups, namely B and C are sub-grouped into (B1-B4) and (C1-C2), respectively. We report exceptionally high agglutinated benthic foraminiferal abundance on the slope of the western Bay of Bengal. The depth and temperature affect the total abundance of agglutinated benthic foraminifera. Morphogroups A (tubular), B1 (globular), and B3 (planispiral/trichospiral, only dead) are positively correlated with water depth and negatively correlated with the ambient temperature, suggesting its preference for deeper waters. Both the dead and living assemblages of morphotype B2 as well as C1, are negatively correlated with dissolved oxygen (DO) and positively correlated with organic carbon (%C_{org}) suggesting its preference for depleted oxygen environment. The morphotype B4 prefers relatively deeper depths. The morphotype C2 (quinqueloculine/milioline forms) is positively correlated with DO, temperature, coarse fraction and organic carbon/nitrogen, and negatively correlated with %C_{org} and water depth, thus indicating that species belonging to this morphotype prefer shallow water, oxic, coarse-grained environment. The relative abundance of morphogroup D (dead) is negatively correlated with ambient salinity, thus suggesting its preference for hyposaline conditions in the shallow marine environment. The study suggests a clear ecological preference of a majority of the agglutinated morphotypes and morphogroups and thus their potential application in paleoecological interpretations.

Keywords: Agglutinated, benthic foraminifera, morphogroups, ecology, Bay of Bengal

Introduction

Ecology plays a vital role in the distribution and abundance of benthic foraminifera. Any or a combination of several ambient environmental parameters, especially dissolved oxygen, food availability, substrate, depth, salinity, pH and temperature, affect benthic foraminiferal abundance (Saraswat and Nigam, 2013). Species with preferred boundary conditions and therefore niche microhabitats, have been identified (Boltovskoy and Wright 1976; Corliss, 1985; Corliss and Chen, 1988; Jorissen et al., 1995; 1999; Gooday, 1986, Mackensen et al., 1995; Nigam et al., 2004; Saraswat et al., 2017). The delineation of species microhabitats helps in effectively explaining the abundance and distribution of living benthic foraminifera and their potential application in paleoclimatic studies. However, several workers advised to use assemblages, instead of individual species, as changes in assemblage parameters better defines a broad microhabitat. Additionally, application of individual species or assemblage based characteristics requires detailed identification of foraminifera and can create ambiguity. As a particular microhabitat also supports a specific morphology, benthic foraminifera were combined into morphogroups, and temporal changes in their collective abundance were suggested as an effective paleoclimatic proxy (Bandy 1960; Chamney 1976; Severin, 1983; Jones and Charnock, 1985; Nigam et al., 1992; Manasa et al., 2016). Further, morphogroups are independent of species-level taxonomy and can help to avoid the ambiguity in taxonomic differences that would otherwise arise (Severin, 1983; Preece et al., 1999). Jones and Charnock (1985) delineated agglutinated benthic foraminiferal morphogroups based on inferred feeding habitat and life positions. Several authors used this scheme of agglutinated benthic foraminiferal morphogroups at different stratigraphic levels from the Devonian to Holocene (Nagy, 1992; Nagy et al., 1995; Kaminski et al., 1995; Preece et al., 1999; Van Den Akker et al., 2000; Jones et al., 2005; Kaminski et al., 2005; Kender et al., 2008a, b; Reolid et al., 2008; Cetean et al., 2011; Setoyama et al., 2011; Holcová and Slavík, 2013; Kaminski and Ortiz, 2014; Setoyama et al., 2017). However, agglutinated morphogroup classification of Jones and Charnock (1985) and even subsequent workers (Jones, 1986; Violanti, 2000; Murray et al., 2011), is based on the modern agglutinated foraminiferal distribution mainly from the temperate and polar environments. There is a need for morphogroup studies from cold and tropical/subtropical environments, especially for regions with low dissolved oxygen and high productivity, as such information will help in paleoecological studies (Murray et al., 2011). We present the modern ecological preferences of agglutinated benthic foraminiferal morphogroups, as defined by Jones and Charnock (1985) and later modified by Murray et al. (2011), from a unique, freshwater influx dominated tropical environment.

Study Area

The study area (17°N - 19°N and 83°E - 85°E) lies in the western Bay of Bengal, between the Mahanadi and Godavari rivers and often termed as Mahanadi basin (Fig. 1). The Bay of Bengal is the second largest hydrologic system in the world and offers ample opportunity for high-resolution paleoclimatic reconstruction. The direction and intensity of the sea surface circulation in the western Bay of Bengal changes seasonally, in response to the Indian summer (southwest) and winter (northeast) monsoon (Wyrski, 1971). A majority of the Indian rivers drain into the western Bay of Bengal. The suspended sediment discharge into the bay is estimated to be 1.4×10^9 tons compared to about 200×10^6 tons in the Arabian Sea (Madhupratap et al., 2003). The total river runoff during the summer monsoon amounts to $943.206 \times 10^9 \text{ m}^3$, while that during winter monsoon is $103.767 \times 10^9 \text{ m}^3$ (Varkey et al., 1996). The fresh-water discharge stratifies and changes the surface water circulation and salinity in the northern Bay of Bengal (Gomes et al., 2000; Levitus et al., 1994; Benschila et al., 2014). Although the riverine flux brings in nutrients, they are thought to be lost to the deeper regions because of its narrow shelf (Qasim, 1977; Sen Gupta et al., 1977; Sarma, 2002). The productivity is not comparable to the Arabian Sea, due to strong stratification, cloud cover and turbidity (Madhupratap et al., 1996; 2003). The high productivity in the northern Bay of Bengal is due to the eddies that bring up the nutrients in the otherwise stratified waters (Prasanna kumar et al., 2004). The high productivity depletes the dissolved oxygen thus forming an oxygen minimum zone (OMZ) at intermediate depths of 600~800 m, but no anoxic zone (Bristow et al., 2017). The dissolved oxygen concentration ranges from as high as 73.5 μM to as low as $>5.0 \mu\text{M}$ (Wyrski, 1971; Sardesai et al., 2007; Sarma et al., 2013). The coastal Bay of Bengal has also been reported to have depleted oxygen levels due to nutrient enrichment and stratification through river discharge (Sarma et al., 2013).

Materials and Methods

A total of 42 surface sediment samples (29 multicore and 13 spade core) collected from the western Bay of Bengal were used. The surface sediment samples were collected on board RV *Sindhu Sadhana* (SK 308) during January 2014 and *Sindhu Sankalp* (SSK 35) during June 2012. The sediment samples were collected from a depth range of 25 m to 2540 m covering the entire shelf to the slope of the Mahanadi basin. One-half of the top 0-1 cm section of each sample was stained with ethanol rose-Bengal solution onboard, to identify the living specimens. After 3-4 weeks, the ethanol from the rose-Bengal stained sediment samples was flushed with filtered sea water. The treated sediments were freeze dried. The dried sediment samples were wet sieved by using a 63 μm sieve. The $>63 \mu\text{m}$ fraction (coarse fraction, CF) was oven dried. A representative aliquot of CF was taken for foraminiferal picking by coning and quartering. A minimum of 300 specimens were picked from each sample.

However, a maximum of 0.1 g CF was used to pick all available specimens, if a sufficient number of specimens were not available.

Counting of Agglutinated Benthic Foraminiferal Morphogroups

All agglutinated benthic foraminifera were divided into four major morphogroups (A-D) following Jones and Charnock (1985) and Murray et al. (2011). Morphogroups B and C were sub-grouped into morphotypes B1-B4 and C1-C2. The elongated tubular forms are categorized as morphogroup A. Morphogroup B includes globular, coiled/flattened, planispiral/trichospiral, and irregular to conical unilocular and multilocular forms. All the elongated forms of varying sizes were placed in morphogroup C. Morphogroup C was sub-divided into two morphotypes, namely C1 and C2. The morphotype C1 includes the elongated forms comprising of all uniserial, biserial and triserial forms. The morphotype C2 comprises of the milioline forms of the elongated type. Morphogroup D includes lenticular to planoconvex and low trochospiral forms, mainly consisting of trochamminids. Unlike in the Murray et al. (2011) study, the tubular forms were not subdivided and instead counted and placed in morphogroup A. Here we would like to note that it is difficult to obtain reliable counts of tubular forms because they readily fragment leading to overrepresentation (Murray et al., 2011). Additionally, the relative and absolute abundance of both the agglutinated morphogroups and calcareous-agglutinated benthic foraminifera were calculated.

Environmental and geochemical parameters

The salinity and pH at the sediment-water interface were measured onboard from the water collected in the multicores. The seasonal bottom temperature and annual dissolved oxygen (DO) data was downloaded from the 'World Ocean Atlas 2013' by using 'Ocean Data View software' (Schlitzer, 2017). A part of the dry sediment was powdered and homogenized in a mortar pestle for total carbon (TC), total nitrogen (TN) and inorganic carbon (TIC) measurement. The TC and TN were measured by using a CNS analyzer, and TIC was measured on UIC CM 5015 CO₂ Coulometer. The organic carbon (C_{org}) was calculated by subtracting TIC from TC. The principal components analysis (PCA) was done by using STATISTICA 6.0 software, to understand the relationship between environmental and geochemical parameters with agglutinated benthic foraminifera morphogroups. The marked correlations are significant at $p < 0.05$.

Results

Physico-chemical parameters

The annual average bottom water DO is high at shallower stations and dysoxic at intermediate depths (Fig. 2). It varies from 0.3 ml/l to 4.2 ml/l with the highest concentration at stations MC 40 (29 m) and

MC 68 (29 m). The lowest DO is at station MC 42 (280 m), MC 52 (225 m), and MC 65 (260 m). The seasonal ambient temperature decreases with increasing water depth. The highest temperature is at station SC 35 (31 m) and lowest at station MC 59 (2240 m). The salinity is minimum at shallower depths and maximum at intermediate and deeper depths. The salinity varies from 32.2 to 34.9 psu and is the highest at station SC 25 (106 m), SC 26 (122 m), SC 28 (100 m) and SC 33 (114 m). The lowest salinity is at station MC 40 (29 m). The bottom water pH (varying from 7.5 to 8.1) is low at intermediate and deeper depths, as compared to the shallower depths. The maximum pH is at station MC 39 (55 m), MC 40 (29 m), MC 49 (30 m), MC 51 (73 m) and MC 68 (29 m). The minimum pH is at station MC 42 (280 m) and MC 43 (520 m).

Coarse fraction (CF%), inorganic carbon (TIC), organic carbon (C_{org}) and organic carbon/nitrogen (C_{org}/N)

The coarse fraction (CF%) ranged from 0.3% to 88%. The maximum CF% is at station SC 23 (34 m) and the minimum is at station MC 60 (2073 m). The total inorganic carbon (TIC) co-varies with pH and is the lowest (0.03%) at station MC 56 (2098 m) and highest (3.6%) at shallower station MC 66 (105 m). The organic carbon (%C_{org}) is the highest (2.1%) at station MC 42 (280 m) and the lowest (0.1%) at station SC 23 (34 m) and SC 35 (31 m). The C_{org}/N is maximum (13.8) at station SC 26 (122 m) and minimum (7.4) at station MC 58 (2386 m) (Fig. 3).

Agglutinated and Calcareous benthic foraminifera

The relative abundance of dead agglutinated and calcareous benthic foraminifera varies from 1% to 98% and 2% to 99%, respectively (Fig. 4A). The relative abundance of agglutinated benthic foraminifera is >90% at deeper stations (MC 48, MC 56, MC 57, MC 59, MC 60). Contrary to this, calcareous benthic foraminifera are >95% in the inner shelf (stations MC 40, MC 42, MC 49, MC 60, SC 23, SC 24, SC 30, SC 31 and SC 34). The relative abundance of calcareous benthic foraminifera decreases with depth, and that of agglutinated benthic foraminifera increases with increasing water depth. The living population of both the agglutinated and calcareous benthic foraminifera also have a robust relationship with depth (Fig. 4B). The highest relative abundance of living agglutinated benthic foraminifera is 90% at station MC 56 (2098 m water depth). The lowest (10%) relative abundance of calcareous benthic foraminifera is also at the same station. Stations MC 50 and SC 26 (58 m and 122 m water depth) had the maximum (100%) calcareous benthic foraminifera and are devoid of any agglutinated forms.

The absolute abundance of both the living and dead agglutinated and calcareous benthic foraminifera was also calculated (Fig. 5A-D). The lowest abundance of dead agglutinated benthic

foraminifera is on the inner shelf and increases with depth (Fig. 5A). The absolute abundance of dead calcareous benthic foraminifera is, however, opposite to that of the dead agglutinated foraminifera and decreases with water depth (Fig. 5B). The living agglutinated benthic foraminiferal abundance also increases with depth (Fig. 5C). The absolute abundance of living calcareous benthic foraminifera is, however, the highest on the upper slope and decreases at further deeper stations (Fig. 5D).

Morphogroup A

Both the dead and living morphogroup A forms comprised of tubular/branching agglutinated benthic foraminifera and show a positive affinity with depth (Fig. 6A, 6B). The relative abundance of dead and living morphogroup A varies from 0% to 21% and 0% to 19%, respectively. The highest relative abundance of the dead (21%) and living (19%) morphogroup A is at MC 58 (2386 m water depth) and MC 59 (2240 m water depth). Morphogroup A is completely absent in the shallow marine to continental shelf, and its maximum abundance is on the lower slope.

Morphogroup B

Morphogroup B is subdivided into 4 morphotypes. B1 contains all the globular forms and the relative abundance of its dead and living forms varies from 0% to ~9% and 0% to ~19%, respectively (Fig. 7A, 7B). The maximum relative abundance (~9%) of fossil morphotype B1 is at station MC 57 (2489 m water depth) and that of living (~19%) is at station MC 47 (2030 m water depth). The relative abundance of morphotype B1 increases with increasing depth, and it is absent in the continental shelf.

The morphotype B2 is abundant on the upper slope, unlike other morphogroups. The highest relative abundance of dead (58%) and living (43%) morphotype B2 is at station MC 52 (225 m water depth) and station MC 64 (500 m water depth), respectively (Fig. 7C, 7D). The relative abundance varies from 0% to 58% (fossil) and 0% to 43% (living). The dead and living forms of morphotype B2 are absent at all the stations in the continental shelf, except MC 68 (29 m water depth). The relative abundance of morphotype B2 is very low on the lower slope as well, as compared to that in the upper slope.

Among the morphogroup B, morphotype B3 is most abundant at a majority of the stations. The relative abundance of both the dead as well as living morphotype B3 varies from 0% to 100% (Fig. 7E, 7F). The maximum relative abundance of living morphotype B3 is at station SC 23 (34 m), SC 24 (55 m), SC 25 (106 m), SC 27, SC 28 (100 m), SC 30 (36 m), SC 33 (114 m) and SC 35 (31 m). The maximum abundance of dead morphotype B3 is at station SC 23. The relative abundance of morphotype B3 is high on the shelf and upper slope and low on the lower slope.

Both the dead and living agglutinated benthic foraminifera belonging to morphotype B4 are rarely present in the northwestern Bay of Bengal, except at a few stations. The maximum (100%) relative abundance of dead morphotype B4 is at station SC 31 (33 m water depth) and that of living (13%) is at station SC 32 (55 m water depth) (Fig. 7G, 7H).

Morphogroup C

The relative abundance of morphotype C1 is higher than that of C2. The C1 is also the most abundant among all the morphotypes (Fig. 8A, 8B). The relative abundance of morphotype C1 varies from 0% to 100% (dead) and 0% to 89% (living). The maximum relative abundance of dead morphotype C1 is at station MC 66 (105 m) and that of living is at station MC 44 (763 m). The relative abundance of morphotype C1 is opposite to that of B3. The relative abundance of morphotype C2 is very different than the others and varies from 0% to 44% (dead) and 0% to 36% (living) (Fig. 8C, 6D). The highest relative abundance of dead morphotype C1 is at station SC 35 (31 m) and that of living is at station MC 40 (29 m). A prominent peak in the inner shelf points towards its affinity to the shallow environment.

Morphogroup D

Morphogroup D comprises of only the trochamminids with low trochospiral forms and lenticular shape. The relative abundance of dead morphogroup D is the highest (25%) at station MC 40 (29 m) and of living (30%) at station MC 39 (55 m water depth) (Fig. 9A, 9B). Both the dead and living morphogroup D are absent at several stations. The trochamminids also depict the same trend as that of morphogroup C2 and are concentrated in the shallow water depths.

Principal Component Analysis (PCA) and correlation

Principal component analysis was carried out to assess the relationship between physico-chemical parameters and the relative abundance of agglutinated benthic foraminifera and their morphogroups. As water depth, per se, is not a factor, PCA was run with and without depth as the independent variable. The PCA plot was nearly same in both the cases. We retained and discuss the PCA plot with water depth as the independent variable. The three axes, axis 1 (Eigen value 3.45), axis 2 (Eigen value 1.67) and axis 3 (Eigen value 0.89) account for 49.42%, 23.87% and 12.82% of the total variation in the data, respectively, thus making a total of 86.12% (Fig. 10). On the biplot, the length of the arrow indicates the intensity of the ecological parameter. The morphogroups are projected orthogonally on the ecological arrows to understand the relationship between the parameters and the morphogroups. The angle between the ecological arrows suggests the correlation.

The water depth, followed by ambient temperature are the most dominant ecological parameters that significantly affect the relative abundance of calcareous and agglutinated benthic foraminifera. The relative abundance of both the living and dead calcareous benthic foraminifera is negatively correlated with depth and positively correlated with temperature. The calcareous benthic foraminiferal abundance is also positively correlated with the CF% and C_{org}/N . On the other hand, the relative abundance of agglutinated benthic foraminifera is positively correlated with depth and negatively correlated with ambient temperature. Both the CF% and C_{org}/N are negatively correlated with agglutinated abundance. Interestingly, only the dead population of agglutinated and calcareous benthic foraminifera correlates significantly with the C_{org}/N . The depth and temperature, along with CF%, % C_{org} , C_{org}/N are significantly correlated with several of the agglutinated morphogroups.

A significant negative correlation with salinity is observed only for a couple of morphogroups (C2 living, D dead). Both the dead and living population of morphotypes B2 and C2 is also significantly negatively correlated with DO. Morphotypes B2 (both living and dead population), B3 (only dead) and C1 (only living) are significantly positively correlated, and C2 (both living and dead population) is negatively correlated with % C_{org} . The ambient temperature significantly negatively correlates with both the living and dead populations of morphogroups A and B1, the dead population of B3 and living population of C1. The dead population of morphotype C2 is positively correlated with ambient temperature. The living population of morphotype B3 is positively correlated with only one (C_{org}/N) of the ambient parameters. On the other hand, the dead population of morphotype C2 is significantly correlated with all but one (salinity) ambient parameters. Morphotype B4 falls at the center of the plot and is not significantly correlated with any of the studied ambient parameters.

Discussion

In the western Bay of Bengal, agglutinated benthic foraminifera are abundant on the continental slope and in deeper areas. The excessive abundance of agglutinated benthic foraminifera on the slope of western Bay of Bengal, with a few stations being almost completely devoid of calcareous foraminifera, is exceptional and rare in the tropical waters of the Indian Ocean. The relative abundance of agglutinated benthic foraminifera is positively correlated with depth (0.92 and 0.90 for dead and living, respectively) and negatively with temperature (-0.77 and -0.78 for dead and living, respectively). The ambient temperature decreases with increasing depth. The carbonate saturation decreases with decreasing temperature. Therefore, the abundant presence of agglutinated benthic foraminifera in the slope region is attributed to shallower calcium carbonate compensation depth and corrosive bottom waters, as also reported from the Baffin Bay (Schröder-Adams et al., 2011). In general, agglutinated benthic foraminifera are abundant in carbonate under-saturated marine environments (Sabbatini et al.,

2007), and their abundance increases with depth (Schröder-Adams et al., 2008). The agglutinated benthic foraminifera are abundant on the continental slope and deeper regions with an increase in species diversity with depth (Murray 2006, Murray et al., 2011). A reduction in organic carbon with the increasing depth results in an upsurge in species diversity (Murray et al., 2011). The living agglutinated benthic foraminifera are also abundant in the oxygen-depleted waters of the California Borderland basins (Kaminski et al., 1995) and in the eastern Arabian Sea (Gooday et al., 2000; Taylor and Gooday, 2014; Caille et al., 2014; 2015). Agglutinated forms are also present in the marginal marine to shelf regions of the western Bay of Bengal (Almeida and Setty, 1972; Rao and Rao, 1974; Rao et al., 1979). Calcareous benthic foraminifera dominate sediments shallower than 4500 m water depth in the southeast Indian Ocean, with only a few stations having abundant agglutinated foraminifera (Corliss, 1979).

pH and its relation with agglutinated benthic foraminifera

The pH has not been included in the PCA plot as the data was available only for 28 stations. The bottom water pH ranged from as low as 7.5 to a maximum of 8.1. Such low pH has so far not been reported from this depth from the tropical waters, specifically the Bay of Bengal. Usually, such low pH is only confined to temperate regions (Nagy and Alve, 1987) or marshy environments. The calcareous tests start to dissolve below 7.5 pH (Nigam et al., 2008; Kurtarkar et al., 2011; Saraswat et al., 2015). Therefore, the strong positive correlation between the abundance of agglutinated benthic foraminifera and water depth in the western Bay of Bengal is mainly attributed to the dissolution of calcareous tests in carbonate under-saturated waters. The present study reveals two striking patterns in the abundance and distribution of both dead and living agglutinated benthic foraminifera and its morphogroups. The first one is in the deeper region with <7.7 pH and the second one is in the shallow marginal marine to continental shelf environment. The huge fresh water and sediment influx in the shallow regions is detrimental to calcareous foraminifera (Dias et al., 2010; Kurtarkar et al., 2011; Saraswat et al., 2015). However, the reason for the increased abundance of agglutinated benthic foraminifera in the deeper regions is different. The non-availability of fresh food in the deep sea compels the agglutinated fauna to depend more on refractory material unlike the calcareous fauna (Gooday, 2003; Koho et al., 2008). The microbial respiration during organic carbon consumption reduces dissolved oxygen and substantially lowers the pH (Hald and Steinsund, 1996). The pore water CO₂ concentration increases due to the enhanced recycling of organic matter, further lowering the pH. This in turn demands more energy to form carbonate shells (Gooday et al., 2010; Caille et al., 2015). The deep-sea carbon dioxide sequestration may also be responsible for high agglutinated benthic foraminiferal abundance in the western Bay of Bengal as only agglutinated forms could survive long-

term high pCO₂ and further lowering of pH by almost >1 unit (Bernhard et al., 2009). The surface water pH in the western Bay of Bengal has decreased during the last several decades due to the increased nitrate and sulfate aerosol loading (Sarma et al., 2015). The low pH with a mean of 7.75 has also been reported from the mixed layer in the Bangladesh margin (Rashid et al., 2013). The pH with a combination of depth and smaller grain size restricts the foraminiferal distribution and abundance (Arnal, 1961). The calcium carbonate concentration in the western Bay of Bengal, in general, is quite low (~10%) (Siddiquie, 1967). The excessive sedimentation (dilution) and dissolution restrict the calcareous benthic foraminiferal abundance to a minimum in the Bay of Bengal (Cullen and Prell, 1984). For the same reason, the foraminiferal lysocline is at ~2000 m water depth in the Bay of Bengal (Cullen and Prell, 1984; Rao et al., 2013).

Morphogroups A, B1, B3 and C1

The morphogroups A, B1, B3 and C1 have a significant relationship with almost all the ecological parameters. The morphogroups A (tubular), B1 (globular), and B3 (planispiral/trochospiral, dead population) are positively correlated with water depth, suggesting its preference for deeper waters. The deeper water preference of these morphogroups is further confirmed by a significant negative correlation with the ambient temperature. These morphogroups are considered to be epifaunal and surficial, respectively. The species belonging to morphogroup A require higher organic flux. The %C_{org} is comparatively more in slope (Fig. 3B), thus confirming the abundance of morphogroup A in deeper environments. The abundance of morphotype B1 is controlled by limited food supply. As the organic flux decreases with increasing depth, the members of morphotype B1 collect the food from sinking organic carbon (Jones, 2011). Likewise, morphotype B3 (planispiral/trochospiral, dead population) is also positively correlated with depth suggesting its preference for the deeper environment (Altenbach et al., 1988). In the western Bay of Bengal, however, only a few morphogroups are significantly correlated with water depth (Table 1). Earlier, morphogroups A and B1 were reported from the bathyal zone and abyssal plains (Schröder-Adams, 1988; Kaminski and Kuhnt, 1995). The presence of a nepheloid layer in the bay (Kolla et al., 1976), can be one of the causes of increased abundance of tubular forms in the deeper waters, as Kaminski et al. (1989) and Murray and Alve (2011) reported the abundant presence of these morphogroups in geostrophic currents. The bottom water currents re-suspend the particulate organic carbon from the sea floor and proliferate the abundance of tubular forms.

Although depth is the most prominent ecological factor, it alone cannot govern the abundance of morphogroups (Sztrakos, 1983; Jones and Charnock, 1985; Murray et al., 2011). Other ecological parameters (e.g., temperature, salinity, pH, food supply) also simultaneously influence the relative

abundance of various morphogroups in such a way that the effect of depth remains ambiguous (Fig. 10). The relative abundance of morphogroups A, B1, B3 and C1 is negatively correlated with ambient temperature, suggesting their preference for cold water. Incidentally, all of these morphogroups are also negatively correlated with coarse fraction as well. The negative correlation with both the temperature and CF% suggests that morphogroups A, B1, B3 and C1 are indicative of relatively cold deeper regions dominated by fine-grained sediments. The relative abundance of morphotypes B1, B3 and C1 is also negatively correlated with C_{org}/N . The negative correlation further confirms the deeper depth preference of morphotypes B1, B3 and C1 in the western Bay of Bengal, as C_{org}/N decreases with increasing water depth (Fig. 3C).

Morphogroup B2, C2 and D

Both the dead and living assemblages of morphotype B2 (coiled/flattened forms) are negatively correlated with DO and positively correlated with $\%C_{org}$. Morphotype B2 is mostly abundant in the upper slope regions where the DO concentration is within the dysoxic limit (1.0 - 0.2 ml/l). These depths have moderately high $\%C_{org}$ that is used during microbial processes utilizing the available DO and increasing the biological oxygen demand, making the region oxygen-depleted (Bristow et al., 2016). Earlier, *Ammodiscus*, one of the prominent genus of this group was reported from hypersaline and oxygen-depleted fjords (Alve, 1990). The taxa belonging to morphotype B2 have also been reported from the Arabian Sea oxygen minimum zone (555 m water depth) (Jannink et al., 1998). We report this group from shallow marine to upper continental slope oxygen-depleted environment characterized by high $\%C_{org}$ (Fig. 7C, 7D). As compared to B2, both the dead and living assemblages of morphotype C2 (quinceloculine/milioline forms) are positively correlated with DO, and negatively correlated with $\%C_{org}$. Additionally, morphotype C2 is negatively correlated with water depth, thus indicating that species belonging to this morphogroup prefer shallow environment. The relative abundance of morphotype C2 is positively correlated with temperature, CF% and C_{org}/N , thus confirming its preference for shallow warm water regions with coarse-grained sediments. The dissolved oxygen concentration and food availability are the two dominant factors that govern benthic foraminiferal abundance and diversity, especially in the deeper waters (Corliss, 1985; van der Zwaan et al., 1999). The limitation of any of the two factors, becomes detrimental for foraminiferal sustenance and its proliferation (Jorissen, 1999). Earlier, although Rao and Rao (1974) reported living *Miliammina* from the Suddagedda estuary, eastern coast of India, its ecological preferences were not discussed. Murray, (1991) reported *Miliammina* from 0 to 2000 m in the Southern Ocean. Based on the distribution of benthic foraminifera in surface sediments of the Ross Sea, Antarctica, a majority of the members of morphotype C2 were reported as infaunal and abundant in unstable and winnowed

sediments in shelf to the slope (Violanti, 2000). Although Murray et al. (2011) stated that morphotype C2 did not correspond to any specific depth habitat, our study suggests its clear preference for marginal marine regions and a close affinity for high DO and low %C_{org}. Both quinqueloculine forms and trochamminids are abundant in the shallow marginal marine environment as the food availability is quite high with temperature in these regions being favorable for reproduction (Murray, 2006; Jones, 2011). The decrease in temperature with depth is the main factor for depth zonation of species (Boltovskoy and Wright, 1976). Additionally, the relative abundance of morphotype C2 (living) and D (dead) is negatively correlated with ambient salinity, thus confirming its preference for hyposaline conditions. The hyposaline preference of these morphogroups is also evident in the PCA plot (Fig. 10). The trochospiral forms are also abundant in the riverine influx regions of the eastern Arabian Sea (Nigam et al., 1992) and northern Bay of Bengal (Manasa et al., 2016).

Taphonomic processes

The distribution and abundance of the living and dead assemblages of almost all the morphogroups of agglutinated benthic foraminifera match well in the 0-1 cm section, with only a few exceptions. The minor differences in the living and dead assemblage of a few morphogroups are attributed to the taphonomic processes or environmental changes (Murray and Pudsey, 2004). The difference in living and dead assemblages of morphotype C1 are ascribed to the very delicate soft shells as it is prone to post-depositional breakage. The difference in the dead and living assemblage of morphotype C1, as well as B3, can also arise due to post-depositional sediment transport. We do not, however, have any data to substantiate the effect of sediment transport.

Conclusions

We report exceptionally high agglutinated benthic foraminiferal abundance on the slope of the western Bay of Bengal. Both depth and temperature significantly affect the total agglutinated benthic foraminifera abundance. Morphogroups A (tubular), and morphotypes B1 (globular), and B3 (planispiral/trochospiral, only dead) are positively correlated with water depth and negatively correlated with the ambient temperature, suggesting its preference for deeper waters. Both the dead and living assemblages of morphotype B2 are negatively correlated with DO, and positively correlated with %C_{org} suggesting their preference for oxygen-depleted environments. The morphotype B4 prefers relatively deeper depths. The morphotype C1 is abundant in low oxygen regions with high productivity. Morphotype C2 (quinqueloculine/milioline forms) is positively correlated with DO, temperature, %CF and C_{org}/N, and negatively correlated with %C_{org} and water depth, thus indicating that species belonging to this morphotype prefer shallow water oxic coarse-grained environments. The

relative abundance of morphogroup D (dead) is negatively correlated with ambient salinity, thus suggesting its preference for hyposaline conditions. The above stated ecological preferences of agglutinated benthic foraminiferal morphogroups can help in reconstructing past dissolved oxygen concentrations and related changes in the western Bay of Bengal and other continental shelf-slope regions with oxygen minimum zones. The results have broader application to understand the distribution of agglutinated morphogroups and their value in interpreting the fossil record.

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Legend to Figures and Tables

- Figure 1: Location of surface sediment samples (black-filled inverted triangles) in the western Bay of Bengal. The inset map shows the location of the sampling area in the western Bay of Bengal. The major rivers are marked in blue in the inset map. The bathymetric contours are marked in meters.
- Figure 2: The dissolved oxygen (ml/l) (A), pH (B), salinity (psu) (C), and temperature (°C) (D) at the sediment water interface in the western Bay of Bengal. The plots are based on the measurements made on bottom water retrieved in multicore tops. The dissolved oxygen data is annual average, downloaded from the World Ocean Atlas. The sample locations are marked in black-filled inverted triangles and black numbered contours are bathymetry.
- Figure 3: The surface distribution of coarse fraction (CF%) (A), organic carbon (%C_{org}) (B), organic carbon/nitrogen (C_{org}/N) (C), and inorganic carbon (TIC%) (D) in the western Bay of Bengal.
- Figure 4: The relative abundance of dead (A) and living (B) agglutinated and calcareous benthic foraminifera in the western Bay of Bengal. The relative abundance of agglutinated is reciprocal to that of the calcareous benthic foraminifera.
- Figure 5: The surface distribution of the absolute abundance of dead agglutinated (A) and calcareous (B) as well as living agglutinated (C) and calcareous (D) benthic foraminifera in the western Bay of Bengal.
- Figure 6: The surface distribution of the relative abundance of dead (A) and living (B) morphogroup A in the western Bay of Bengal.
- Figure 7: The surface distribution of the relative abundance of dead (A, C, E, and G) and living (B, D, F and H) morphogroup B (B1-B4) in the western Bay of Bengal.
- Figure 8: The surface distribution of the relative abundance of dead (A and C) and living (B and D) morphogroup C (C1-C2) in the western Bay of Bengal.
- Figure 9: The surface distribution of dead (A) and living (B) morphogroup D in the western Bay of Bengal.
- Figure 10: The principal component analysis biplot of agglutinated morphogroups and the environmental variables from the western Bay of Bengal. The red squares denote the morphogroups and the blue circles with blue dashed lines denote the environmental variables. DO=Dissolved oxygen, Sal=Salinity, Temp=Temperature, CF=Coarse fraction, %C_{org}=Organic carbon, C_{org}/N=Organic carbon/total nitrogen. D=Dead, L=Living. Morphogroup abbreviations: A (Tub) (D, L)=Morphogroup A (tubular), B1 (Glo) (D, L)=Morphotype B1 (Globular), B2 (Coil/Flat) (D, L)=Morphotype B2 (Coiled/Flattened), B3 (Plan/Troc) (D, L)=Morphotype B3 (Planispiral/Trochospiral), B4 (Irr) (D, L)=Morphotype B4 (Irregular), C1 (Elon) (D, L)=Morphotype C1 (Elongated), C2 (Elon) (Q) (D, L)=Morphotype (Elongated) (*Quinqueloculina*), D (Troc) (D, L)=Morphogroup D (Trochospiral). Agg (D, L)=Agglutinated benthic foraminifera, Calc (D, L)=Calcareous benthic foraminifera.
- Table 1: The details of surface samples and the absolute as well as relative abundance of both dead and living calcareous and agglutinated benthic foraminifera. The relative abundance of all the agglutinated benthic foraminiferal morphogroups is also given.
- Table 2: Details of correlation analysis. The marked correlations are significant at p<0.05. The significant values are marked in red.

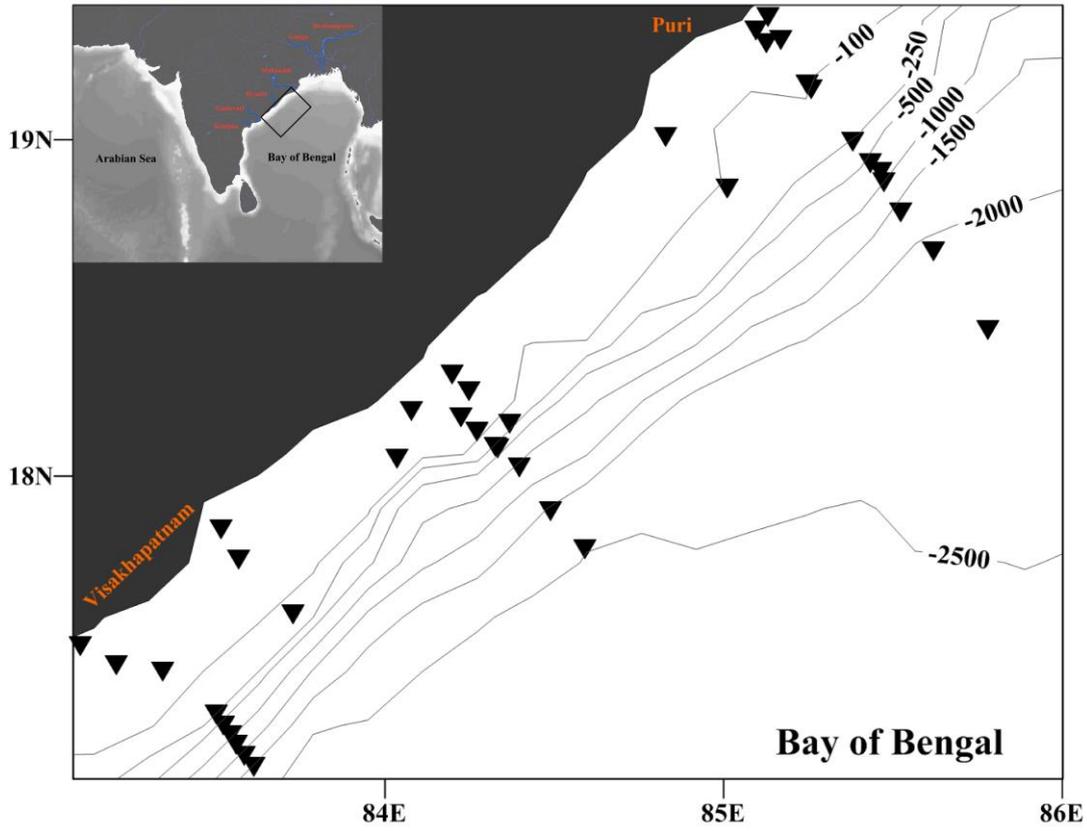


Figure 1

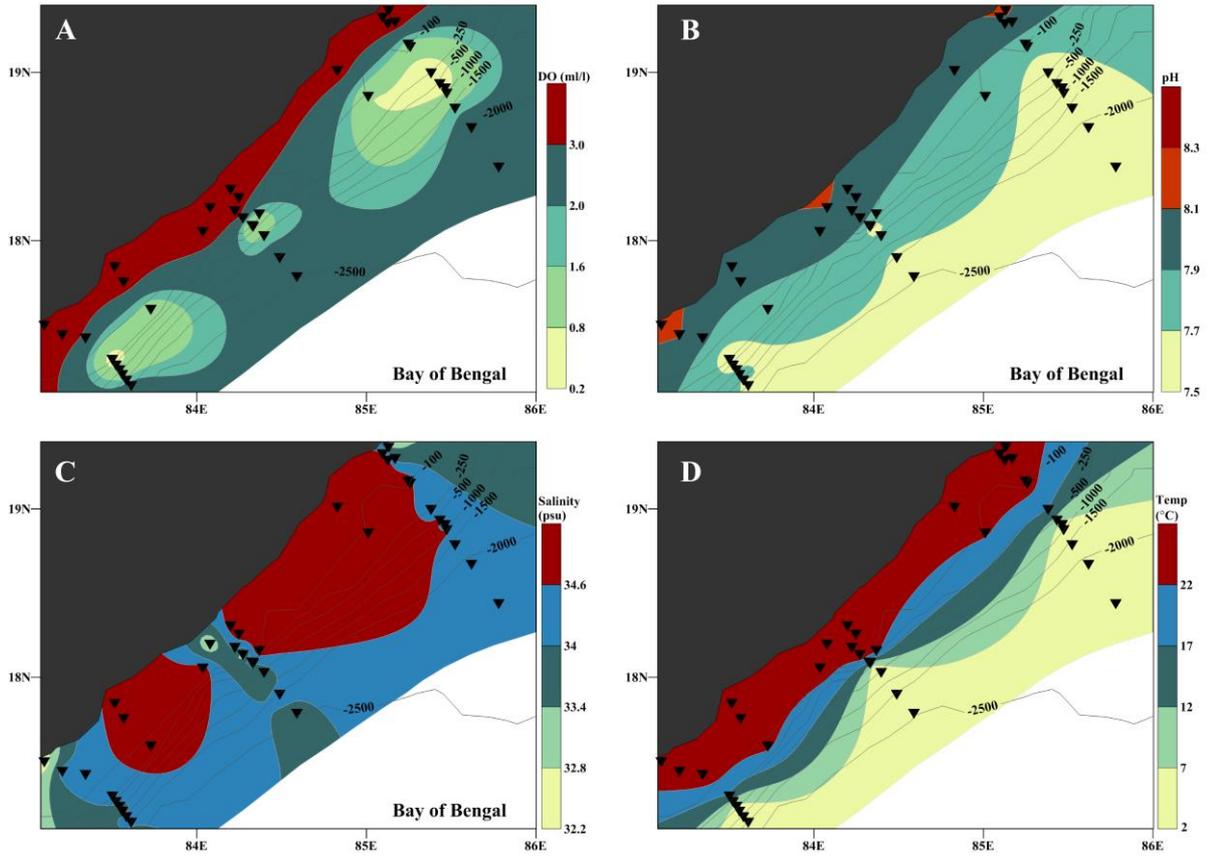


Figure 2

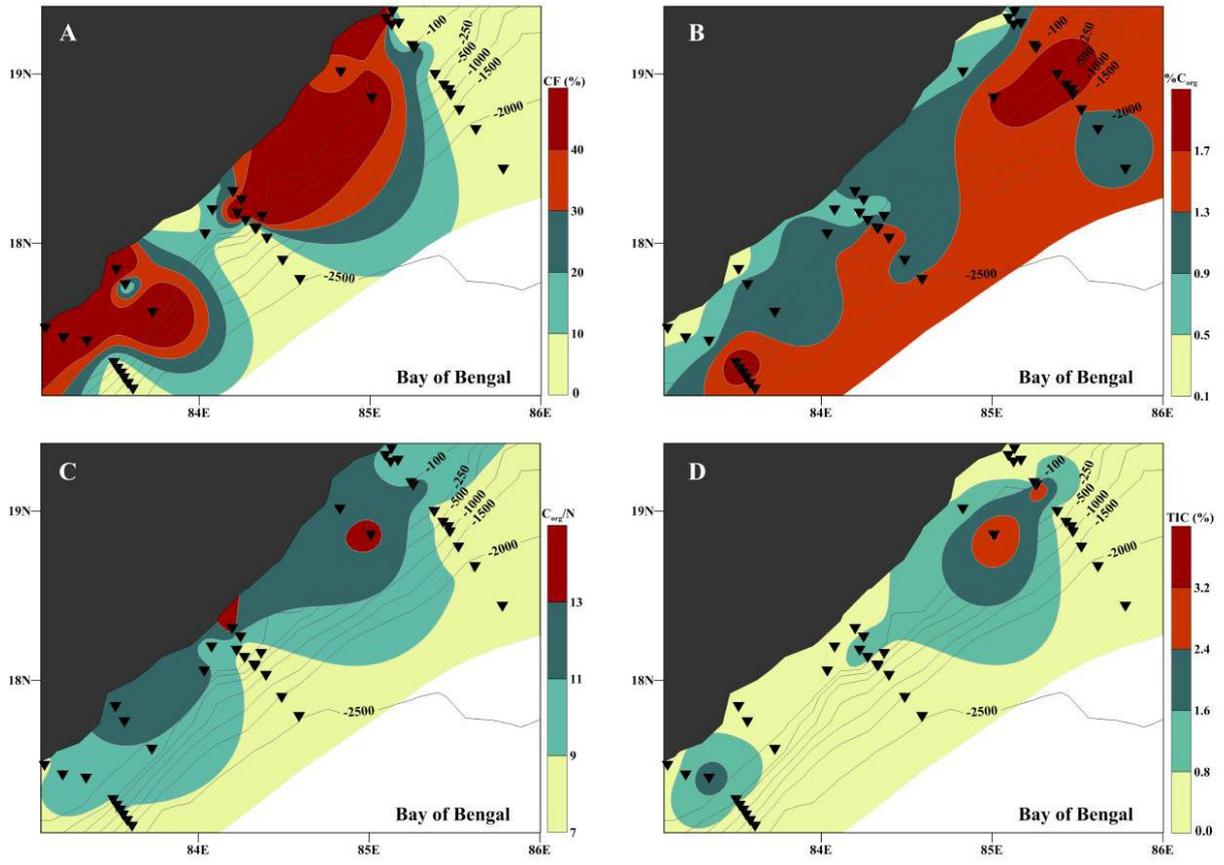


Figure 3

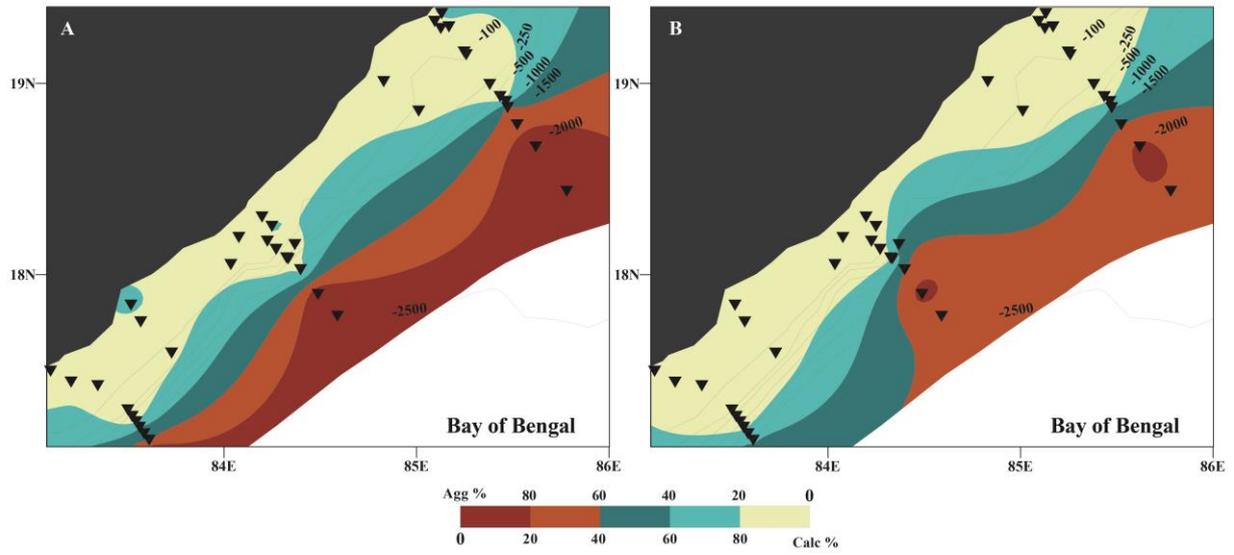


Figure 4

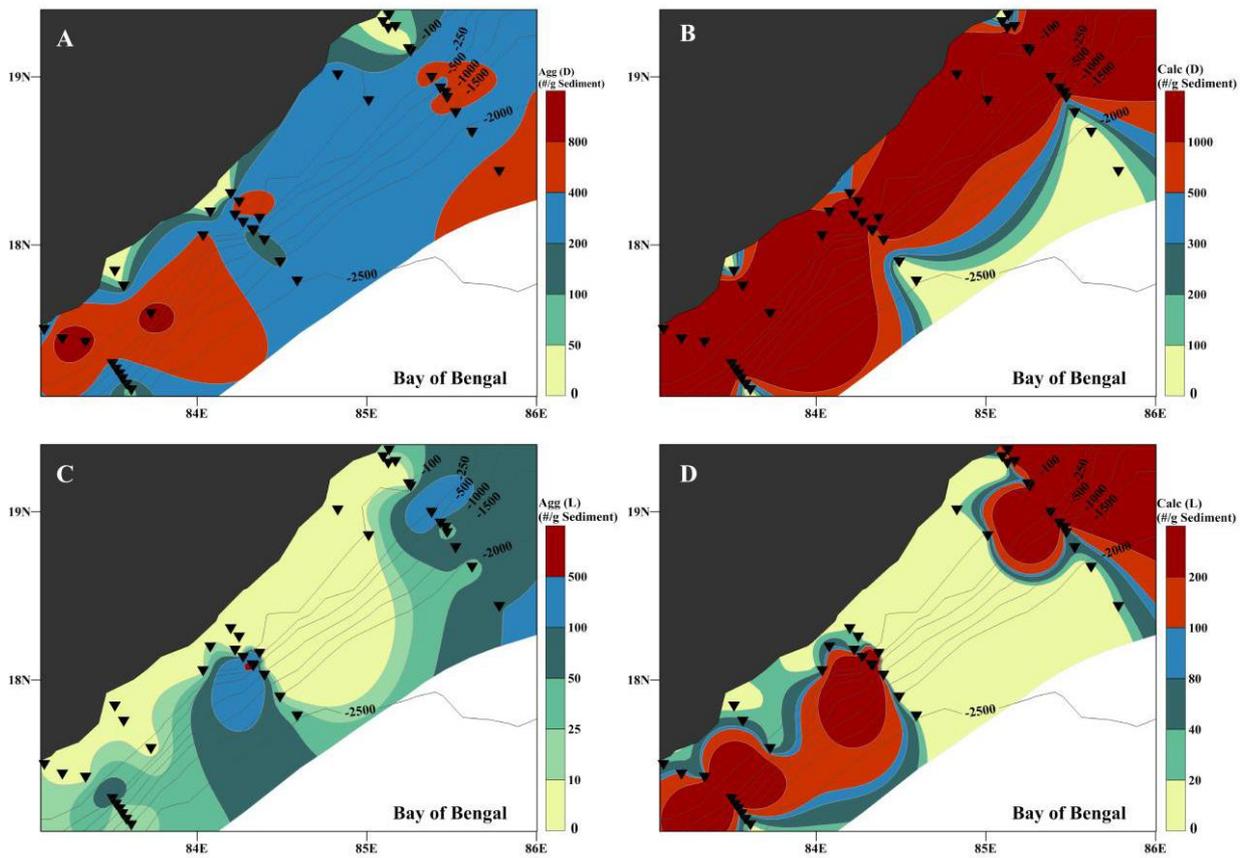


Figure 5

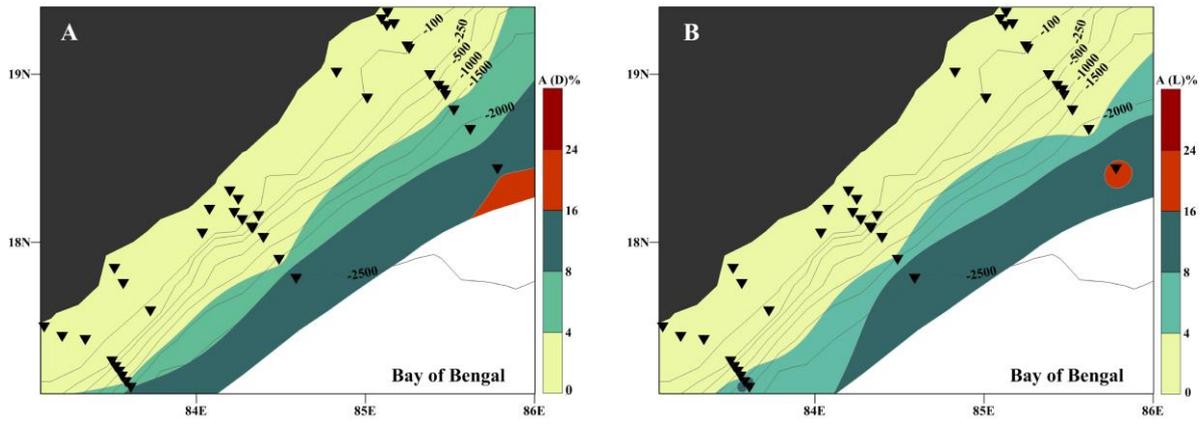


Figure 6

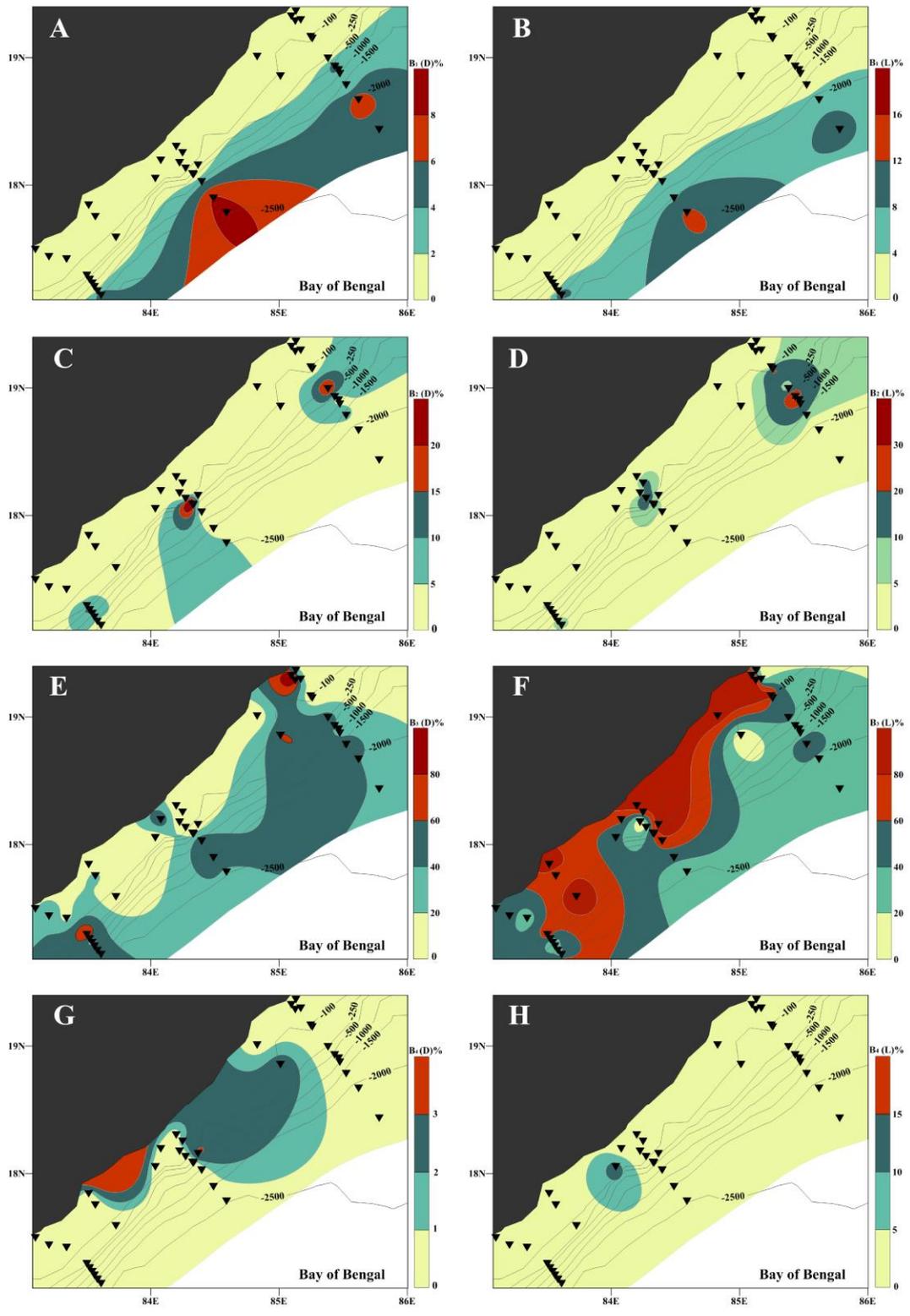


Figure 7

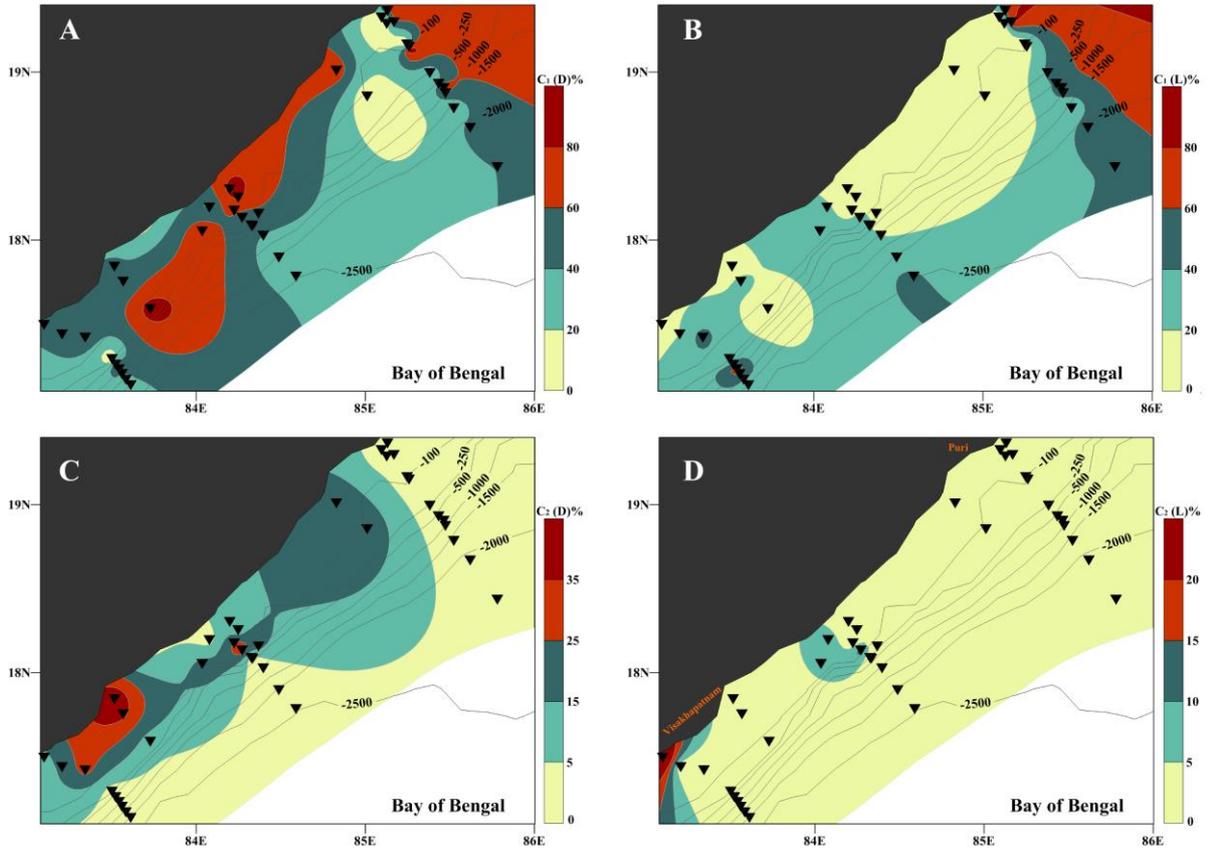


Figure 8

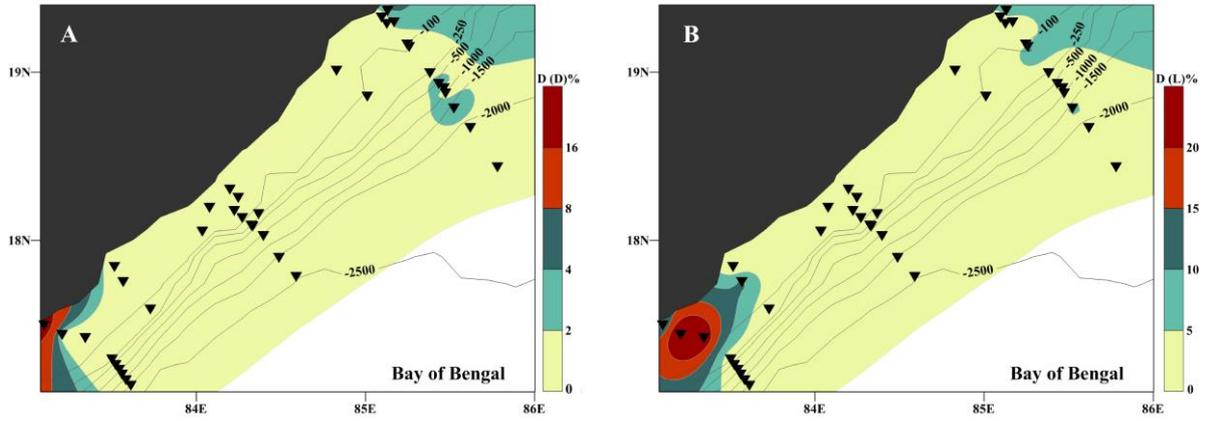


Figure 9

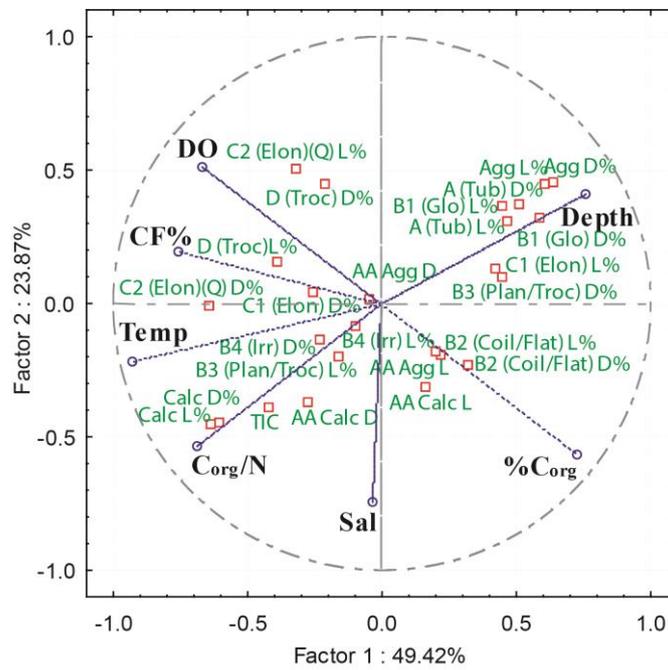


Figure 10

Sample	Longitude (E)	Latitude (N)	Depth (m)	Dead Benthic (#)	Living Benthic (#)	Dead Agglut./g Sed.	Living Agglut./g Sed.	Agglut. D (%)	Calc D (%)	Agglut. L (%)	Calc L (%)	Morphogroup A (D) (%)	Morphotype B1 (D) (%)	Morphotype B2 (D) (%)	Morphotype B3 (D) (%)	Morphotype B4 (D) (%)	Morphotype C1 (D) (%)	Morphotype C2 (D) (%)	Morphogroup D (D) (%)	Morphogroup A (L) (%)
MC 39	83.21	17.44	54.7	407	239	1197	5	17.4	82.6	4.2	95.8	0.0	0.0	0.0	39.4	0.0	43.7	16.9	0.0	0.0
MC 40	83.10	17.50	28.7	303	59	39	10	5.3	94.7	18.6	81.4	0.0	0.0	0.0	18.8	0.0	43.8	12.5	25.0	0.0
MC 41	83.34	17.42	72.9	353	86	922	2	13.6	86.4	4.7	95.3	0.0	0.0	0.0	10.4	0.0	60.4	29.2	0.0	0.0
MC 42	83.50	17.29	280.1	454	363	368	114	3.3	96.7	4.7	95.3	0.0	0.0	6.7	93.3	0.0	0.0	0.0	0.0	0.0
MC 43	83.52	17.26	520.4	343	646	38	11	7.3	92.7	11.5	88.5	0.0	0.0	16.0	36.0	0.0	48.0	0.0	0.0	0.0
MC 44	83.54	17.23	763.4	327	686	462	12	19.6	80.4	9.3	90.7	0.0	0.0	4.6	27.7	0.0	67.7	0.0	0.0	0.0
MC 45	83.56	17.20	1034.9	301	757	238	10	35.5	64.5	13.7	86.3	2.8	0.0	7.5	54.2	0.0	35.5	0.0	0.0	1.0
MC 46	83.58	17.17	1510.6	355	338	100	30	62.5	37.5	37.6	62.4	3.2	1.4	4.1	56.8	0.0	34.7	0.0	0.0	16.5
MC 47	83.61	17.13	2029.8	342	337	72	6	48.8	51.2	31.8	68.2	7.8	7.2	3.6	43.7	0.0	37.1	0.0	0.6	6.5
MC 48	83.63	17.10	2540.2	303	277	93	19	92.4	7.6	60.6	39.4	12.1	3.9	3.2	49.6	0.0	30.4	0.0	0.7	5.4
MC 49	84.08	18.19	29.5	301	72	38	17	3.7	96.3	16.7	83.3	0.0	0.0	0.0	63.6	0.0	36.4	0.0	0.0	0.0
MC 50	84.23	18.17	57.8	325	4	398	0	8.0	92.0	0.0	100.0	0.0	0.0	0.0	3.8	0.0	69.2	26.9	0.0	0.0
MC 51	84.27	18.13	73.3	382	162	187	20	6.3	93.7	8.6	91.4	0.0	0.0	0.0	20.8	0.0	45.8	33.3	0.0	0.0
MC 52	84.33	18.09	225.4	392	354	217	1068	10.2	89.8	22.9	77.1	0.0	0.0	57.5	5.0	0.0	37.5	0.0	0.0	0.0
MC 53	84.33	18.08	644.8	500	385	163	86	23.0	77.0	21.6	78.4	0.0	0.0	12.2	24.3	0.0	63.5	0.0	0.0	0.0
MC 55	84.40	18.03	1487.0	359	359	162	73	15.0	85.0	63.2	36.8	0.0	3.7	0.0	59.3	0.0	37.0	0.0	0.0	0.0
MC 56	84.49	17.90	2098.0	305	332	179	20	98.0	2.0	89.8	10.2	2.0	8.4	3.3	56.9	2.3	27.1	0.0	0.0	4.7
MC 57	84.59	17.78	2488.5	381	345	280	40	95.0	5.0	63.2	36.8	13.0	8.6	5.8	36.2	0.3	35.6	0.0	0.6	14.2
MC 58	86.03	18.07	2386.4	312	309	452	126	77.9	22.1	70.6	29.4	21.0	3.7	3.7	23.0	0.0	48.1	0.0	0.4	7.3
MC 59	85.78	18.44	2239.8	302	313	550	98	92.4	7.6	78.3	21.7	15.4	4.7	2.5	36.9	0.0	40.5	0.0	0.0	18.8
MC 60	85.62	18.67	2072.6	325	316	166	36	95.4	4.6	85.1	14.9	3.9	7.4	0.0	40.6	0.0	47.4	0.0	0.6	2.2
MC 61	85.52	18.78	1537.9	347	341	336	78	72.0	28.0	58.7	41.3	5.6	2.0	6.4	62.8	0.0	19.6	0.0	3.6	2.5
MC 62	85.47	18.87	1073.1	325	304	669	37	68.9	31.1	47.0	53.0	2.2	3.6	5.4	32.1	0.0	55.4	0.0	1.3	1.4
MC 63	85.46	18.91	763.4	419	307	631	25	23.4	76.6	21.2	78.8	2.0	3.1	1.0	19.4	0.0	73.5	0.0	1.0	0.0
MC 64	85.43	18.93	499.6	749	309	118	47	6.3	93.7	13.6	86.4	2.1	6.4	6.4	44.7	0.0	36.2	0.0	4.3	2.4
MC 65	85.38	18.99	260.2	386	329	563	266	9.1	90.9	8.2	91.8	0.0	0.0	22.9	54.3	0.0	22.9	0.0	0.0	0.0
MC 66	85.26	19.15	104.6	353	106	172	21	1.1	98.9	7.5	92.5	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0
MC 67	85.17	19.30	55.4	501	302	53	5	13.0	87.0	2.0	98.0	0.0	0.0	0.0	30.8	0.0	60.0	6.2	3.1	0.0

MC 68	85.13	19.36	29.2	391	321	73	32	26.1	73.9	9.0	91.0	0.0	0.0	3.9	26.5	0.0	62.7	2.9	3.9	0.0
SPC-23	85.09	19.32	33.5	153	43	5	1	3.9	96.1	2.3	97.7	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0
SPC-24	85.13	19.29	55.0	303	53	22	3	2.3	97.7	15.1	84.9	0.0	0.0	0.0	85.7	0.0	14.3	0.0	0.0	0.0
SPC-25	85.25	19.16	106.0	319	316	0	3	0.0	100.0	4.1	95.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SPC-26	85.01	18.85	122.0	317	39	264	0	12.3	87.7	0.0	100.0	0.0	0.0	0.0	61.5	15.4	0.0	23.1	0.0	0.0
SPC-27	84.83	19.01	55.0	314	73	261	0	9.6	90.4	1.4	98.6	0.0	0.0	0.0	0.0	0.0	76.7	23.3	0.0	0.0
SPC-28	84.37	18.16	99.5	341	6	410	2	10.6	89.4	50.0	50.0	0.0	0.0	0.0	2.8	22.2	55.6	19.4	0.0	0.0
SPC-29	84.25	18.25	54.0	339	108	642	3	24.8	75.2	6.5	93.5	0.0	0.0	0.0	0.0	9.5	82.1	8.3	0.0	0.0
SPC-30	84.20	18.30	36.0	403	122	19	3	3.7	96.3	9.8	90.2	0.0	0.0	0.0	0.0	0.0	86.7	13.3	0.0	0.0
SPC-31	83.65	18.13	33.3	332	156	5	5	0.6	99.4	8.3	91.7	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0
SPC-32	84.04	18.05	55.0	313	308	459	2	13.7	86.3	4.9	95.1	0.0	0.0	0.0	2.3	0.0	79.1	18.6	0.0	0.0
SPC-33	83.73	17.59	114.0	359	33	1011	2	15.0	85.0	6.1	93.9	0.0	0.0	0.0	0.0	0.0	90.7	9.3	0.0	0.0
SPC-34	83.57	17.75	54.0	301	312	56	7	2.7	97.3	11.5	88.5	0.0	0.0	0.0	25.0	0.0	37.5	37.5	0.0	0.0
SPC-35	83.52	17.84	31.0	89	15	20	1	30.3	69.7	6.7	93.3	0.0	0.0	0.0	7.4	0.0	48.1	44.4	0.0	0.0

Table 1

Table 2

	DO (ml/1)	Salinity (psu)	Temp (°C)	C_{org}/N	%C_{org}	CF%	Depth (m)
Agg D%	-0.01	-0.04	-0.77	-0.53	0.05	-0.36	0.92
Calc D%	0.01	0.04	0.77	0.53	-0.05	0.36	-0.92
Agg L%	-0.05	-0.09	-0.78	-0.56	0.07	-0.44	0.90
Calc L%	0.05	0.09	0.78	0.56	-0.07	0.44	-0.90
A (Tub) D%	0.04	-0.02	-0.61	-0.44	0.10	-0.31	0.82
B1 (Glo) D%	-0.11	-0.01	-0.71	-0.44	0.12	-0.39	0.82
B2 (Coil/Flat) D%	-0.50	0.07	-0.15	-0.26	0.34	-0.28	-0.01
B3 (Plan/Troc) D%	-0.27	-0.21	-0.40	-0.34	0.35	-0.33	0.33
B4 (Irr) D%	0.21	0.21	0.21	0.31	-0.18	-0.01	-0.15
C1 (Elon) D%	0.22	-0.01	0.15	0.19	-0.18	0.29	-0.17
C2 (Elon)(Q) D%	0.39	0.06	0.59	0.42	-0.46	0.59	-0.47
D (Troc) D%	0.22	-0.51	0.13	-0.16	-0.29	0.40	-0.11
A (Tub) L%	0.01	0.06	-0.57	-0.42	0.05	-0.30	0.72
B1 (Glo) L%	0.04	-0.06	-0.59	-0.33	0.00	-0.30	0.75
B2 (Coil/Flat) L%	-0.39	0.02	-0.12	-0.17	0.32	-0.11	-0.05
B3 (Plan/Troc) L%	0.13	0.22	0.24	0.21	-0.07	-0.16	-0.20
B4 (Irr) L%	0.16	0.16	0.10	0.15	-0.05	-0.06	-0.04
C1 (Elon) L%	-0.14	-0.22	-0.39	-0.35	0.31	-0.42	0.27
C2 (Elon)(Q) L%	0.31	-0.62	0.27	-0.14	-0.38	0.42	-0.22
D (Troc)L%	0.25	-0.07	0.27	0.20	-0.41	0.47	-0.18
TIC	-0.14	0.21	0.42	0.55	-0.02	0.58	-0.41
Agg D (#g/Sediment)	-0.09	0.15	-0.03	-0.12	-0.10	0.33	-0.01
Agg L (#g/Sediment)	-0.36	0.11	-0.05	-0.19	0.19	-0.20	-0.02
Calc D (#g/Sediment)	-0.21	0.15	0.38	0.34	0.07	0.33	-0.41
Calc L (#g/Sediment)	-0.45	0.06	0.08	-0.14	0.34	-0.17	-0.20