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Diatom community dynamics in a tropical, monsoon-influenced environment: west coast of India

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ABSTRACT

Diatom communities are influenced by environmental perturbations, such as the monsoon system that impact the niche opportunities of species. To discern the influence of the monsoon system on diatom community structure, we sampled during two consecutive post-monsoons (2001 and 2002) and the intervening pre-monsoon at Mumbai and Jawaharlal Nehru ports along the central west coast of India. Characteristic temporal shifts in diatom community structure were observed across the sampling periods; these were mainly driven by temperature, salinity and dissolved oxygen saturation. The nutrient-poor pre-monsoon period supported low abundance yet high species richness and diversity of diatoms. *Coscinodiscus*, *Cyclotella*, *Triceratium*, *Pleurosigma* and *Surirella* were the most dominant genera. Both the post-monsoon periods, following dissimilar monsoon events, were dominated by *Skeletonema costatum*, but differed in some of the residual species. *Thalassiosira* and *Thalassionema* spp. dominated mostly during post-monsoon I whereas *Triceratium* and *Pleurosigma* spp. dominated during post-monsoon II. To understand the underlying ecological mechanisms involved in such dynamics, we focus on the dominant diatom species in post-monsoon periods, *S. costatum*, that contributes up to 60% to total diatom cell numbers. This research is relevant in light of the fluctuating monsoon regimes over the Asian continent, the confounding effects of anthropogenic eutrophication and the resulting cascading effects on trophic web dynamics.

Keywords: diatoms; monsoon; species diversity; *Skeletonema costatum*; ecological mechanisms

Introduction

Diatoms, the major phytoplankton group in coastal environments, are governed by a complex suite of regulating factors. They can be broadly classified into growth (bottom-up) and mortality (top-down) factors. Growth factors deal with the availability of favourable physical conditions and resources (e.g., currents, light, nutrients, salinity, temperature) and have been the focus of numerous studies (Aebischer et al., 1990; Frederiksen et al., 2006; Irigoien et al., 2004; Roemmich and McGowan, 1995). Mortality factors include pathogens, parasitoids and grazers (Smetacek et al., 2004) and also programmed cell death (Franklin et al., 2006). These categories of regulating factors play important but different roles in structuring phytoplankton communities.

The relative significance of the growth and mortality factors varies spatially and temporally. This is especially true in tropical environments influenced by monsoon. Monsoon events can be thought of as a disturbance, which impacts the niche opportunities available to a species in a system. This occurs either by altering the levels of available nutrients or by influencing mortality (Shea et al., 2004), through effects on physiological processes such as cell division, and also by disorienting organisms (White, 1976). The extent of nutrient inputs, dilution of the population, and the degree of turbulence in relation to the generation times of the diatoms involved are important factors to be considered. The intensity and frequency of the disturbance selects for particular 'resistant' species that will, through species succession and competitive exclusion, finally culminate in a characteristic community. The duration of the disturbance with respect to the generation times also shapes the species succession that occurs. All these factors determine the species that will survive and eventually dominate the community during and subsequent to a monsoon event.

The South West (SW) monsoon [Long term mean – 853 mm of rainfall (<http://www.tropmet.res.in>)], occurs from June to September whereas the other monsoon system affecting the Indian subcontinent, the North East (NE) monsoon, extends from October to December. The monsoons lead to a considerable input of nutrients in coastal water bodies through precipitation and run-off originating from terrigenous sources. Precipitation is accompanied by stormy weather, high wind speed and increased suspended load in the overlying waters. Cloudbursts (extreme rainfall events spanning a few minutes or hours) are sporadically reported. For example, on 26th July 2005, approximately 950 mm of rainfall was recorded over a span of eight to ten hours in Mumbai (the present study area).

Over the years, the Asian sub-continent has experienced fluctuations in the monsoon pattern. The frequency and magnitude of extreme rain events over central India from 1951 to 2000 has increased (Goswami et al., 2006). An increase in the Asian South West monsoon during the last four centuries in response to climate change has also been reported (Anderson et al., 2002). Such ‘irregular’ events, in terms of climate change, are known to affect the equilibrium between bottom-up and top-down control factors. Meserve et al. (2003) have reported that high rainfall events in semi-arid systems, caused by periodic El Niño Southern Oscillation (ENSO) events, have led to the region experiencing a trend of shifting bottom-up and top-down control. In this context, it is imperative to understand the effect of fluctuating monsoon regimes on the composition of diatom communities, through similar changes in bottom-up and top-down control factors.

Taking this into consideration, the changes in diatom community composition in a tropical, coastal environment, along the central west coast of India, are analyzed with regard to SW monsoon-driven changes in growth and mortality factors. We have focused mainly on *Skeletonema costatum*, a chain-forming species, 4-12 µm in diameter, with a cosmopolitan distribution, blooms of which have been linked with monsoons and increased run-off (Lee and Kim, 2008; Liu et al., 2005; Patil and Anil, 2008). This species has been extensively reported in Indian waters (Madhu et al., 2006; Patil and Anil, 2008). Its blooms have been observed at the onset and restart of monsoon after an intermittent break in the Zuari estuary along the west coast of India (Patil and Anil, 2008); and also in the vicinity of the study area in October (post-monsoon) during consecutive years (1984 – 1985) (Tiwari and Nair, 1998).

In this study, we addressed the following questions. (1) What are the seasonal changes observed in the diatom community in a tropical, monsoon-influenced environment? (2) What are the underlying ecological mechanisms involved? (3) How does *Skeletonema costatum* respond to variations in monsoon regimes and anthropogenic enrichment?

1. Materials and methods

1.1. Study area and sampling

Samples for phytoplankton analysis were collected at Mumbai and Jawaharlal Nehru ports, along the west coast of India (18°54'N, 72°40'E) (Fig. 1) as part of the Global Ballast Water Management Program initiative in India. Sampling was conducted during two consecutive post-monsoon periods (November

2001 and October 2002) and the intervening pre-monsoon (April-May 2002) (Table 1). Sampling during the monsoon period was not possible due to inclement weather conditions. Thirty stations including anchorages, berths, dry docks, piers, spoil grounds and ship breaking areas were selected (Table 1). Three stations (28-30) were located offshore ($18^{\circ}47'N$, $72^{\circ}49'E$; $18^{\circ}52'N$, $72^{\circ}43'E$; $18^{\circ}57'N$, $72^{\circ}49'E$) and are not shown in Fig. 1.

The currents in this area are semi diurnal; an average of one-third of the bay water is renewed per tidal cycle with the ingress of flood water (Patel et al., 1985). The details of tidal levels up to the period of the study are mentioned in Table 2. The direction of the current is northeast during the flood tide and southwest during the ebb tide. Wind direction is mainly from North to West quarter; Northeasterly winds blow for a short duration during October-November, with a significant height $< 1m$, and with a period ranging from 3 to 5 seconds. The predominant waves are the swell waves generated by deep sea storms, and arise just before and during the SW monsoon, which is the main source of climatic variation. The SW monsoon pattern from 2000-2005 at the Mumbai and Jawaharlal Nehru ports, is illustrated in Fig. 2.

These ports form a semi-enclosed basin, opening into the Arabian Sea, at the southwesterly side. They receive industrial waste from the heavily industrialized Thane-Belapur belt via the Thana Creek upstream, and also from the Dharamtar, Nhava-Sheva and Panvel Creeks on their eastern shores. The port areas are also influenced by industrial and domestic wastewater discharged in the Arabian Sea through several point sources (e.g., Mahim Creek, Back Bay in Colaba) along the west coast of Mumbai. These port areas are characterized as mesotrophic with regard to nitrate concentration. Based on Assessment of Estuarine Trophic Status (ASSETS) model, the present status is poor and the environment is degrading (Sawant et al., 2007).

1.2. Sampling and microscopy

Surface and near bottom water samples (1 L) were collected using a bucket and Niskin sampler respectively. The samples were immediately fixed with Lugol's iodine, allowed to stand undisturbed for 48 hours and concentrated to 250 mL. Aliquots of 2.5 mL, in triplicate, were analyzed using an inverted microscope, at 100 and 200 times magnification. Phytoplankton were identified based on the available literature (Desikachary and Prema, 1987; Desikachary et al., 1987; Horner, 2002; Subrahmanyam, 1946;

Tomas, 1997) and expressed as cells L⁻¹. Dinoflagellates, <25 µm, which could not be identified to generic level, were grouped together as Unidentified Tiny Dinoflagellates (UTDs).

1.3. Environmental variables

Water temperature, pH, suspended particulate matter (SPM), salinity, nutrient concentrations, dissolved oxygen (DO) and bacteria were analyzed following standard procedures and are published elsewhere (Sawant et al., 2007). The concurrent changes in zooplankton population in the study area are reported in Gaonkar et al. (*in press*). Details of the dinoflagellate community are reported in D'Costa et al. (2008).

1.4. Data analyses

The phytoplankton data were analyzed for Shannon-Wiener diversity index (H'), Margalef's species richness (d) and Pielou's evenness (J') using PRIMER - version 5 (developed by PRIMER-E Limited, UK) and the variations in these determined by one-way ANOVA. The spatial variation in the diatom community and the distribution of *Skeletonema costatum* were depicted using SURFER 6 (developed by Golden Software Inc. USA). Canonical Correspondence Analysis (CCA) was performed to evaluate the relationships between environmental variables and diatoms using the Multi-Variate Statistical Package program version 3.1 (Kovach, 1998) developed by Kovach Computing Services, Wales. Only those stations were considered for which physico-chemical variable data were available. The changes in the diatom community are discussed with regard to physico-chemical variables, zooplankton and bacterial abundance, data generated as part of the Global Ballast Water Management Program.

2. Results

2.1. Phytoplankton community

Overall, 117 species belonging to 48 genera were recorded in the water column. Phytoplankton abundance ranged from 2.7 x 10² to 1.2 x 10⁶ cells L⁻¹ in surface waters and from 2.3 x 10² to 1.3 x 10⁵ cells L⁻¹ in near bottom waters (average and standard deviation values in Fig. 3A). Species richness (d),

Pielou's evenness (J') and Shannon-Wiener diversity (H') of the phytoplankton community in surface and near bottom waters were highest in pre-monsoon (Fig. 3B-D) whereas abundance was lowest (Fig. 3A). One-way ANOVA indicated significant temporal variation in Margalef's species richness (d , $p \leq 0.001$ in surface and near bottom waters), Pielou's evenness (J' , $p \leq 0.01$ in surface and $p \leq 0.025$ in near bottom waters) and Shannon-Wiener diversity (H' , $p \leq 0.001$ in surface and near bottom waters) of the phytoplankton community.

2.2. Diatom community

The changes in abundance and univariate measures of the phytoplankton community (Fig. 3A-D) were reflected in diatoms (Fig. 3E-H), which constituted 76-99% of the phytoplankton community in the water column (Fig. 4). The maximum diatom abundance sampled was 1.2×10^6 cells L^{-1} in surface waters (Fig. 5A-C) and 1.3×10^5 cells L^{-1} in near bottom waters (Fig. 5D-F). One-way ANOVA indicated significant temporal variation in diatom abundance in surface waters ($p \leq 0.05$). A total of 86 diatom species belonging to 35 genera (18 centric, 17 pennate) were recorded (Table 3). Margalef's species richness, Pielou's evenness and Shannon-Wiener diversity of the diatom community varied significantly (one-way ANOVA; d , $p \leq 0.001$ in surface and near bottom waters; J' , $p \leq 0.001$ in surface and $p \leq 0.025$ in near bottom waters; H' , $p \leq 0.001$ in surface and $p \leq 0.005$ in near bottom waters).

Among the genera contributing $>2\%$ to the diatom community, *Coscinodiscus*, *Cyclotella*, *Triceratium*, *Pleurosigma* and *Surirella* spp. dominated in pre-monsoon (Table 4). *Skeletonema costatum* constituted 11-13% of the diatom community in pre-monsoon but dominated the diatom community in post-monsoon (approx. 42-60%) (Table 4), with very high abundance recorded at stations 11 in post-monsoon I and at stations 13 and 14 in post-monsoon II (Fig. 6). Differences in species composition of the diatom community during the 2 post-monsoon periods were also observed. *Thalassiosira* and *Thalassionema* spp. were most dominant during post-monsoon I whereas *Triceratium* and *Pleurosigma* spp. showed highest dominance during post-monsoon II (Table 4).

2.3. Effect of environmental variables on diatoms

During pre-monsoon, the water column was warmer by $2^\circ C$ ($30^\circ C$) (Fig. 7A). Surface and near bottom waters were production-dominated, with average dissolved oxygen saturation values in the range

of 104-106% (Fig. 7D). Salinity, SPM and bacterial abundance were high compared to post-monsoon periods (Fig. 7B,C,E) Nutrient levels (except nitrate) were lower than in the post-monsoon periods (Fig. 7F-I).

In the CCA biplots for surface waters (Fig. 8A,B), 3 axes explaining 70% of the relationship between diatoms and environmental variables were extracted. Temperature, salinity, SPM and dissolved oxygen saturation were the most important environmental variables influencing diatom community structure in surface waters. Three groups were recognized within the diatom community (Table 3, Fig. 8A). Group A diatoms showed preference for elevated salinity, SPM and dissolved oxygen saturation levels and lower concentrations of nutrients. These species were either restricted to or most abundant in the pre-monsoon period, characterized by the above environmental conditions. The majority of diatoms constituted Group B and preferred moderate to elevated levels of temperature. These species were most abundant in both post-monsoon periods. Group C diatoms were either restricted to or were most abundant in post-monsoon I, indicating differences in diatom community structure during both post-monsoon periods. The difference between the two post-monsoon periods is also evident in the accompanying station biplot (Fig. 8B).

In the CCA biplots for near bottom waters (Fig. 9A,B), 3 axes explaining 73% of the relationship between diatoms and environmental variables were extracted. Temperature, salinity, dissolved oxygen saturation and nitrite concentration were the most important environmental variables influencing diatom community structure in near bottom waters. Three diatoms groups could be discerned (Fig. 9A). Group A diatoms were associated with elevated conditions of temperature, salinity, SPM and lower concentration of nutrients, and were restricted to or most abundant in pre-monsoon period. Group B diatoms were abundant during post-monsoon II. Group C diatoms were associated with elevated nitrite concentration and lower dissolved oxygen saturation levels and preferentially occurred in post-monsoon I period. As in surface waters, the accompanying station biplot for near bottom waters (Fig. 9B) revealed the differences between the two post-monsoon periods.

3. Discussion

The pre-monsoon period

The pre-monsoon period supported the lowest phytoplankton abundance in surface and near bottom waters but highest values of Margalef's species richness (d), Pielou's evenness (J') and Shannon-Wiener diversity (H') (Fig. 3A-D). These trends were mirrored in diatoms, and even in species richness and diversity of dinoflagellates in surface and near bottom waters (D'Costa et al., 2008). These similarities in diatoms and dinoflagellates, even though both groups of organisms differ in their mode of nutrition and physiological characteristics, indicate the consistent nature of these trends over different physiological groups.

The diverse and species-rich pre-monsoon period was characterized by dominance of multiple species (*Coscinodiscus*, *Cyclotella*, *Triceratium*, *Pleurosigma* and *Surirella*) (Table 4). Nitrite (NO_3), phosphate (PO_4) and silicate (SiO_4) concentrations decreased (Fig. 7G-I). However, silica concentrations ranged from 2.3 – 23.9 $\mu\text{mol L}^{-1}$ and were above the limiting level required for diatom growth, i.e., 2 $\mu\text{mol L}^{-1}$ (Egge and Aksnes, 1992). However, according to Redfield ratios, diatom growth in marine waters is limited by Si:N ratios less than 1 (Piehler et al., 2004). Si:N ratios of 1:1 and below were reported at the majority of the stations in pre-monsoon whereas they peaked to much higher levels during post-monsoon (approximately 2:1 and 4:1 in post-monsoons I and II respectively).

Another important factor to be considered is the increased SPM in surface and near-bottom waters during pre-monsoon (Fig. 7C). Light availability plays an important role in regulating phytoplankton communities, especially when turbidity is high (Cloern, 1987). In the present study area, it is particularly important in surface waters. It is one of the important environmental variables regulating diatom community structure in surface waters along with temperature, salinity and dissolved oxygen saturation (Fig. 8).

These changes in environmental conditions were reflected in altered species composition of the diatom community in pre-monsoon and are clearly evident in CCA species biplots (Group A species in surface and near bottom waters; Figs. 8A, 9A).

The multiple genera that dominated in pre-monsoon could possibly have favourable resource acquisition strategies (e.g., low half-saturation constants for uptake that optimize nutrient acquisition under low nutrient conditions). Using resource competition models, Huisman and Weissing (1999) have

shown that oscillations and chaotic population fluctuations are generated when species compete for three or more resources. This allows many species to co-exist on just a handful of resources. In addition, these genera may also have the ability to produce allelopathic substances that allow them to survive the biotic interactions, predominant in the nutrient-poor pre-monsoon (Fistarol et al., 2005), including interactions with the same and other trophic levels.

The high species richness, diversity and evenness of the diatom community in pre-monsoon (Fig. 3F-H) has important consequences for the resistance of the community to predation. Firstly, phytoplankton tend to be more resistant to grazing under nutrient-stressed conditions (especially P-stressed conditions, as in pre-monsoon) compared to nutrient-replete conditions (van Donk and Hessen, 1993). Secondly, diverse prey assemblages have a higher chance of containing less edible species (Duffy, 2004). Thirdly, high prey diversity maximizes the utilization of limiting resources in a way that facilitates recovery from the impacts of grazing. Fourthly, positive species interactions such as facilitation are often stronger and more likely to be expressed in diverse assemblages (Cardinale et al., 2002), especially when many species contribute significantly to the total community, i.e., high evenness (Hillebrand and Cardinale, 2004). This holds true for the pre-monsoon period, with high evenness (0.76) compared to both post-monsoon periods (0.57). Such internal, community-led (autogenic) processes (competitive interactions) tilt the system towards biotic interaction-driven succession (Reynolds, 1980) and strengthen the organization of the system (Reynolds, 1993).

In view of this, the observed increase in heterotrophic dinoflagellates (mainly peridinioids), (D'Costa et al., 2008) and carnivorous (*Tortanus barbatus*) and omnivorous (*Centropages furcatus*, *Oithona* sp., *Corycaeus* sp.) copepods (Gaonkar et al., *in press*) maybe be attributed to the microbial loop. This is supported by the observations of increased bacterial abundance (Fig. 7E) and SPM (Fig. 7C) in the water column, conditions typical of the warmer summer months. The microbial loop has been reported earlier in the northeastern Arabian Sea (west coast of India) where it supports the high-biomass mesozooplankton community in the oligotrophic, warm, summer months (Madhupratap et al., 1996) (corresponding to pre-monsoon in this study).

***Skeletonema costatum* and the post-monsoon period**

Skeletonema costatum, an inferior competitor in the pre-monsoon period, contributed substantially to the diatom community (max. 60%) in both post-monsoon periods (Table 4) and could be considered a keystone species. *S. costatum* shows large fluctuations in cell density in response to nutrient pulses (Yamamoto and Hatta, 2004). It has a higher growth rate and nitrate uptake rate, and can adapt to warmer temperatures and lower salinity compared to many diatom species (Liu et al., 2005 and references therein; Mitbavkar and Anil, 2000). Its ‘affinity’ for nutrients is corroborated by its occurrence in high numbers (approx. 10^5 - 10^6 cells L^{-1}) at station no. 11 (3 m depth) in post-monsoon I (Fig. 6A,D) and stations 13 (3 m depth) and 14 (10 m depth) in post-monsoon II (Fig. 6. C,F), that had comparatively higher concentrations of nitrate (upto 47.2 μM), phosphate (upto 9.5 μM) and silicate (upto 31.1 μM). It is interesting to note that *S. costatum* was conspicuously absent in pre-monsoon at all these stations, when nutrient concentrations were lower. *Surirella ovata*, *Thalassiosira* spp., *Triceratium caudatum* and *Coscinodiscus* spp. dominated these stations in the pre-monsoon period.

Such characteristics allow *S. costatum* to proliferate in response to nutrient pulses and lowered salinity in the ensuing post-monsoon periods before its grazers have a chance to grow to levels high enough to be able to control it. In fact, as mentioned in the introduction, *S. costatum* blooms have been reported earlier in the vicinity of the study area in the post-monsoon period (Tiwari and Nair, 1998).

According to Irigoien et al. (2005), some phytoplankton species grow explosively to form dense blooms when perturbations (nutrients and light) open a ‘loophole’ in the microbial loop. These potential ‘blooming’ species must escape predatory pressure at the critical point of entry into the loophole i.e., they have the potential to escape microzooplankton grazing. *Skeletonema costatum* produces aldehydes that affect copepod egg viability and sea urchin egg division (d’Ippolito et al., 2002). This strategy could be part of the triggering mechanism for *S. costatum* blooms in post-monsoon, i.e., nutrient pulses in the preceding monsoon period (bottom-up control) as well as escape from microzooplankton grazing (top-down control) and could be playing a far more important role in the system than previously thought.

There are several mechanisms by which *Skeletonema costatum* survives unfavourable conditions, in this case, the nutrient-poor, warm surface waters in pre-monsoon. Seeding by fugitive cells (Kilham and Kilham, 1980) and deep-living refuge populations (Smetacek, 1985) that have been transported by currents (Saravanane et al., 2000) are some of the mechanisms involved. Another survival strategy is

the formation of resting stages, induced by nitrate depletion and changes in salinity (Patil and Anil, 2008). Such a mechanism incorporating meroplanktic behavior is an efficient life strategy in shallow waters (Carrick et al., 1993). Post-bloom sedimentation provides nutrient-depleted diatoms with the opportunity to take up minerals from the sediment surface and restart photosynthesis immediately after resuspension (Sicko-Goad et al., 1986). The study area with depths ranging from 3 m to 18 m, possibly supports a similar scenario, wherein monsoon-driven turbulence causes repopulation of the water column with *S. costatum* in post-monsoon.

Surviving unfavourable conditions through benthic propagule formation is a common strategy in several phytoplankton groups and has been reported for dinoflagellates in the study area (D'Costa et al., 2008). It is reminiscent of the storage effect in Intermediate Disturbance Hypothesis (IDH) terminology (Connell, 1978) according to which species with low tolerance of competition, can endure unfavourable periods in a dormant life stage. This mechanism is also referred to as 'temporal niche sharing' wherein species coexist in the same space and use the same resources but avoid direct competition in some periods through unsynchronized life-history schedules (Shea et al., 2004).

Incidentally, the mechanisms discussed above may also be used by other species that usually dominate in pre-monsoon (*Coscinodiscus*, *Cyclotella*, *Triceratium*, *Pleurosigma* and *Surirella*) to survive the unfavourable post-monsoon periods. *Coscinodiscus* and *Pleurosigma* are known to be tychopelagic, i.e., they inhabit both the sediments as well as the water column during their life-cycle and have been reported from both environments (Mitbavkar and Anil, 2002; Patil and Anil, 2008). All these genera have also been observed in sediments collected from the current study area (personal observation).

Effect of fluctuations in the SW monsoon

Fluctuations in the SW monsoon impact the phytoplankton community. High abundance of *Skeletonema costatum* was observed at different stations during both post-monsoon periods (Fig. 6). Additionally, *Thalassiosira* and *Thalassionema* spp. dominated in post-monsoon I whereas *Triceratium* and *Pleurosigma* spp. dominated in post-monsoon II (Table 4). Occurrence of characteristic diatom species in both post-monsoon periods is also evident in the CCA species biplots (Figs. 8A, 9A). Among dinoflagellates, gonyaulacoids and prorocentroids dominated in post-monsoon I whereas dinophysoids and Unidentified Tiny Dinoflagellates (UTDs) dominated in post-monsoon II (D'Costa et al., 2008).

The differences in dominant phytoplankton in the 2 post-monsoons reflect variations in the duration and intensity of the SW monsoon during the sampling period. In 2001, the monsoon was prolonged. It started in May, peaked during June-July and ended in October. The 2002 monsoon was erratic; it started in June, dipped sharply in July (monsoon break), and ended in September (Fig. 2). These changes were reflected in physico-chemical variables, bacterial abundance and grazing pressure. Contrary to the trend in post-monsoon I, DO saturation levels in near bottom waters were higher (production-dominated) than in surface waters (respiration-dominated) in post-monsoon II (Fig. 7D). Bacterial abundance was low in post-monsoon II compared to post-monsoon I (Fig. 7E). Differences in the copepod population were also observed. *Microsetella* sp. and *Oncea* sp. were absent in post-monsoon I; *Acartia centrura* and *Nanocalanus* sp. were absent in post-monsoon II (Gaonkar et al., *in press*).

This study spanning two monsoon events, revealed differences in the phytoplankton community subsequent to two differing monsoon events. However, fluctuations in the SW monsoon, both long-term and short-term, have been observed (Anderson et al., 2002; Goswami et al., 2006). In the study area, maximum rainfall (up to 1200 mm) was recorded in the year 2000 (Fig. 2). In the subsequent years, maximum rainfall was much lower (in the range of 500-800 mm). The SW monsoon pattern also varied over the years (Fig. 2). As mentioned in the introduction, a cloudburst occurred on 26th July 2005 wherein approximately 950 mm of rainfall was recorded over a span of eight to ten hours. This is not reflected in Fig. 2 that takes into account the average rainfall for each month.

The nature of monsoon fluctuations, whether press (sustained) or pulsed (relatively instantaneous), is very important, as both have different effects on communities. Communities usually adapt to a gradual change in conditions, i.e., pressed perturbations, with corresponding gradual changes in structure and function. However, it is possible that at some critical point, they may collapse and form a completely new system (Shea et al., 2004). Thus, in fluctuating environments, the rate of environmental change (fluctuations) is more important than its magnitude, known as the critical-rate hypothesis (Scheffer et al., 2008).

Several studies (documented in Heil et al., 1998) have reported diatom blooms after anomalous rainfall and run-off events. However, such effects depend on the resilience of the system. Two factors affecting the resilience of the system need to be considered here: (1) intra-annual variability in resilience of the system; and (2) the mesotrophic nutrient status of the study area. Concerning the former, post-monsoon periods are less diverse compared to pre-monsoon, and dominated by *Skeletonema costatum*, that shows “boom-and-bust” population cycles in response to resource availability. Such

synchronization of population cycles heightens the susceptibility of the system to disturbance (Stachowicz et al., 1999). Concerning the mesotrophic nutrient status of the study area (Sawant et al., 2007), the increase in nitrate concentration and corresponding decrease in DO observed over the years, further compromises the resilience of the system.

Presently, the study area is characterized by bloom-like conditions of *Skeletonema costatum* at some stations along the coast in post-monsoon and a diverse phytoplankton assemblage in pre-monsoon. The abundance of *S. costatum* decreases in the nutrient-poor pre-monsoon as it is sensitive to a dip in nutrient concentrations. It is tempting to speculate whether continuing nutrient enrichment in the study area will alter the dynamics of *S. costatum*, especially since it is a better competitor than many diatoms under eutrophication conditions (Liu et al., 2005). Additionally, if nutrient concentrations increase above a certain threshold value, will *S. costatum* dominate throughout the year? This aspect can be addressed only through long-term studies in the study area. However, it is evident that anthropogenic enrichment has the potential to confound the effects of variations in the SW monsoon on the population dynamics of *S. costatum*, particularly the exact point of entry into the loophole, as suggested by Irigoien et al. (2005), and must be considered in future studies. This is especially important in view of the consequences for trophic dynamics, as many intermittently-breeding invertebrates like bivalves, interpret *Skeletonema* blooms as signals for release of their larvae. Thus, the effects of fluctuating monsoon regimes on diatom communities will ripple through higher trophic levels as well.

4. Conclusions

To our knowledge, though several studies on phytoplankton communities from this monsoon-influenced region exist, very few have attempted to unravel the underlying ecological mechanisms in addition to species distribution patterns. This is the first detailed study that emphasizes the relevance of incorporating ecological mechanisms into studies on diatom dynamics. This approach provides valuable insights into the pathways regulating diatom community structure in response to monsoon-influenced changes. This is especially necessary for dominant species such as *Skeletonema costatum*, due to its response to anthropogenic enrichment prevalent in the study area and its relevance to trophic web dynamics. The results of this study draw attention to the need for long-term studies, with improved, overlapping sampling regimes and robust methodologies (e.g., analyses of pigments through High Performance Liquid Chromatography and picoplankton through flow cytometry), to decipher the

response of diatoms, and phytoplankton in general, to monsoon variations. Similar studies in different geographical regimes characterized by unique monsoon cycles, would be a useful tool in understanding the effects of fluctuating monsoons on diatom and phytoplankton communities on a global scale.

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LEGENDS TO FIGURES

Fig. 1. Location of sampling stations at Mumbai and Jawaharlal Nehru ports, India.

Fig. 2. Variation in SW monsoon from 2000-2005 at Mumbai and Jawaharlal Nehru ports, India. (PM-I) Post-monsoon I, (PreM) Pre-monsoon, (PM-II) Post-monsoon II.

Fig. 3. Temporal variation in abundance (N) (A,B), Margalef's species richness (d) (C,D), Pielou's evenness (J') (E,F) and Shannon-Wiener diversity (H') (G, H) of the phytoplankton and diatom communities in surface and near bottom waters in Mumbai and Jawaharlal Nehru ports, India. (PM-I) Post-monsoon I, (PreM) Pre-monsoon, (PM-II) Post-monsoon II. Values in graph represent average values across 20-25 stations in surface waters and 18-25 stations in near bottom waters. Error bars: standard deviation values.

Fig. 4. Phytoplankton community composition in (A-C) surface and (D-F) near bottom waters in Mumbai and Jawaharlal Nehru ports, India. (PM-I) Post-monsoon I, (PreM) Pre-monsoon, (PM-II) Post-monsoon II.

Fig. 5. Spatial variation in abundance of diatoms (cells L^{-1}) in (A-C) surface and (D-F) near bottom waters in Mumbai and Jawaharlal Nehru ports, India. Nos. 1-27 indicate the stations where sampling was carried out. (PM-I) Post-monsoon I, (PreM) Pre-monsoon, (PM-II) Post-monsoon II. The asterisk at station 13 in PM-II represents 1.20×10^6 cells L^{-1} .

Fig. 6. Spatial variation in abundance of *Skeletonema costatum* (cells L^{-1}) in (A-C) surface and (D-F) near bottom waters in Mumbai and Jawaharlal Nehru ports, India. Nos. 1-27 indicate the stations where sampling was carried out. (PM-I) Post-monsoon I, (PreM) Pre-monsoon, (PM-II) Post-monsoon II. The asterisk at station 13 in PM-II represents 1.18×10^6 cells L^{-1} .

Fig. 7. Variation in (A) temperature ($^{\circ}C$), (B) salinity (S), (C) suspended particulate matter ($mg L^{-1}$), (D) DO saturation levels (%), (E) total bacterial count (CFU mL^{-1}), (F) nitrate concentration ($\mu mol L^{-1}$), (G) nitrite concentration ($\mu mol L^{-1}$), (H) phosphate concentration ($\mu mol L^{-1}$), and (I) silicate concentration in

the water column in Mumbai and Jawaharlal Nehru ports, India. (PM-I) Post-monsoon I, (PreM) Pre-monsoon, (PM-II) Post-monsoon II. Values in graph represent average values. Error bars: standard deviation values.

Fig. 8. Ordination diagrams for (A) species and (B) stations based on Canonical Correspondence Analysis (CCA) of the diatom community in surface waters. The physico-chemical variables (temperature, salinity, SPM, dissolved oxygen saturation percentage, nitrate, nitrite, phosphate and silicate) are indicated by arrows, labeled Temp, Sal, SPM, OSat%, NO₃, NO₂, PO₄ and Si respectively. General grouping of species are indicated. Station codes are given in Table 1, species codes (nos) and grouping details are presented in Table 3. See text for interpretation of ordination diagrams.

Fig. 9. Ordination diagrams for (A) species and (B) stations based on Canonical Correspondence Analysis (CCA) of the diatom community in near bottom waters. The physico-chemical variables (temperature, salinity, SPM, dissolved oxygen saturation percentage, nitrate, nitrite, phosphate and silicate) are indicated by arrows, labeled Temp, Sal, SPM, OSat%, NO₃, NO₂, PO₄ and Si respectively. General grouping of species are indicated. Station codes are given in Table 1, species codes (nos) and grouping details are presented in Table 3. See text for interpretation of ordination diagrams.

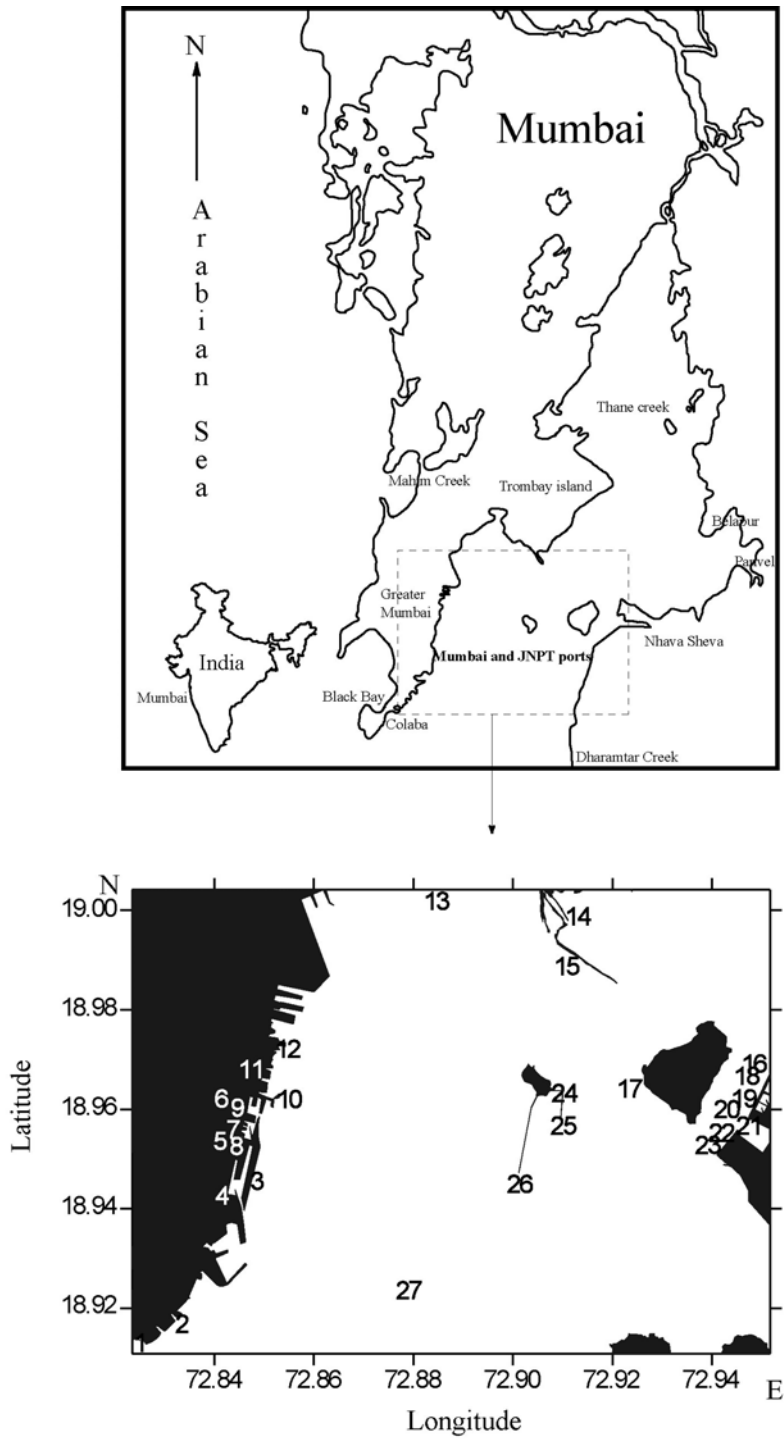


Fig. 1

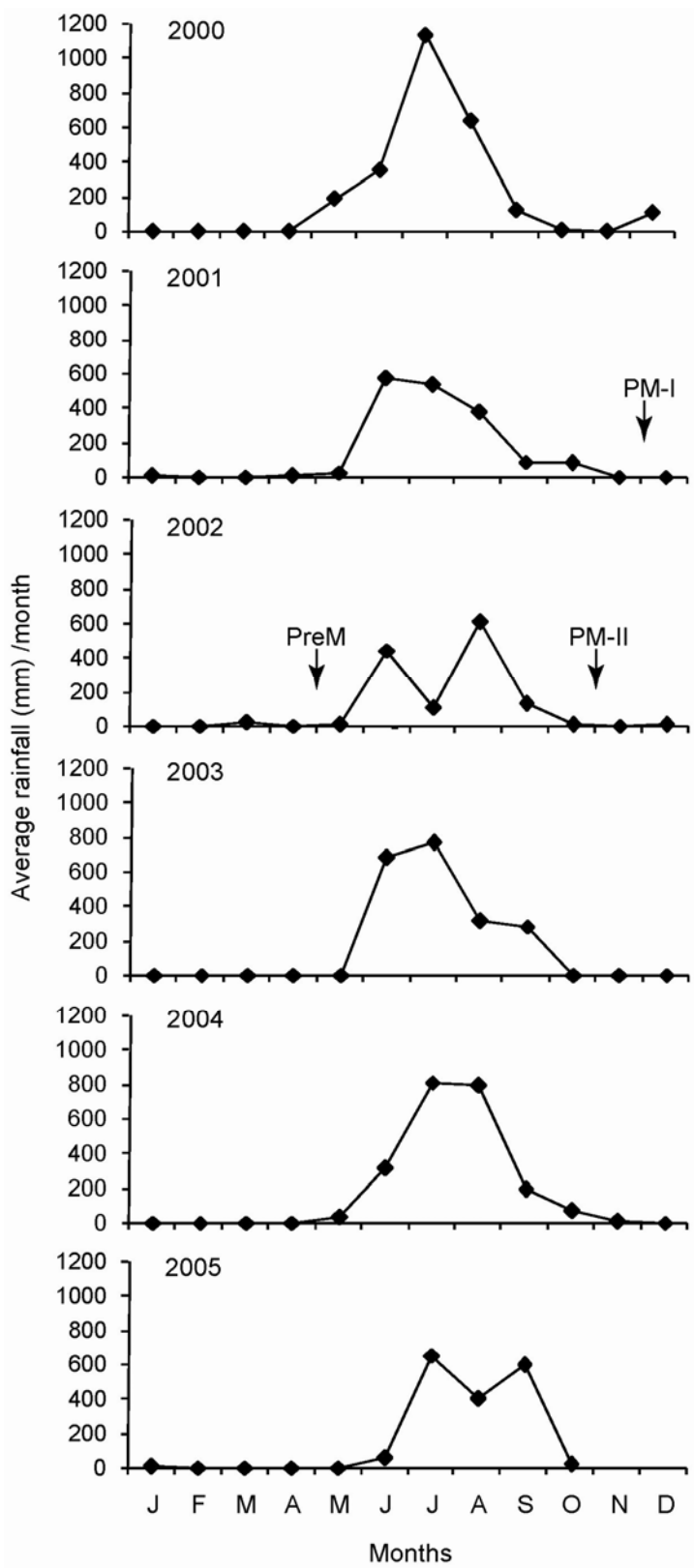


Fig. 2

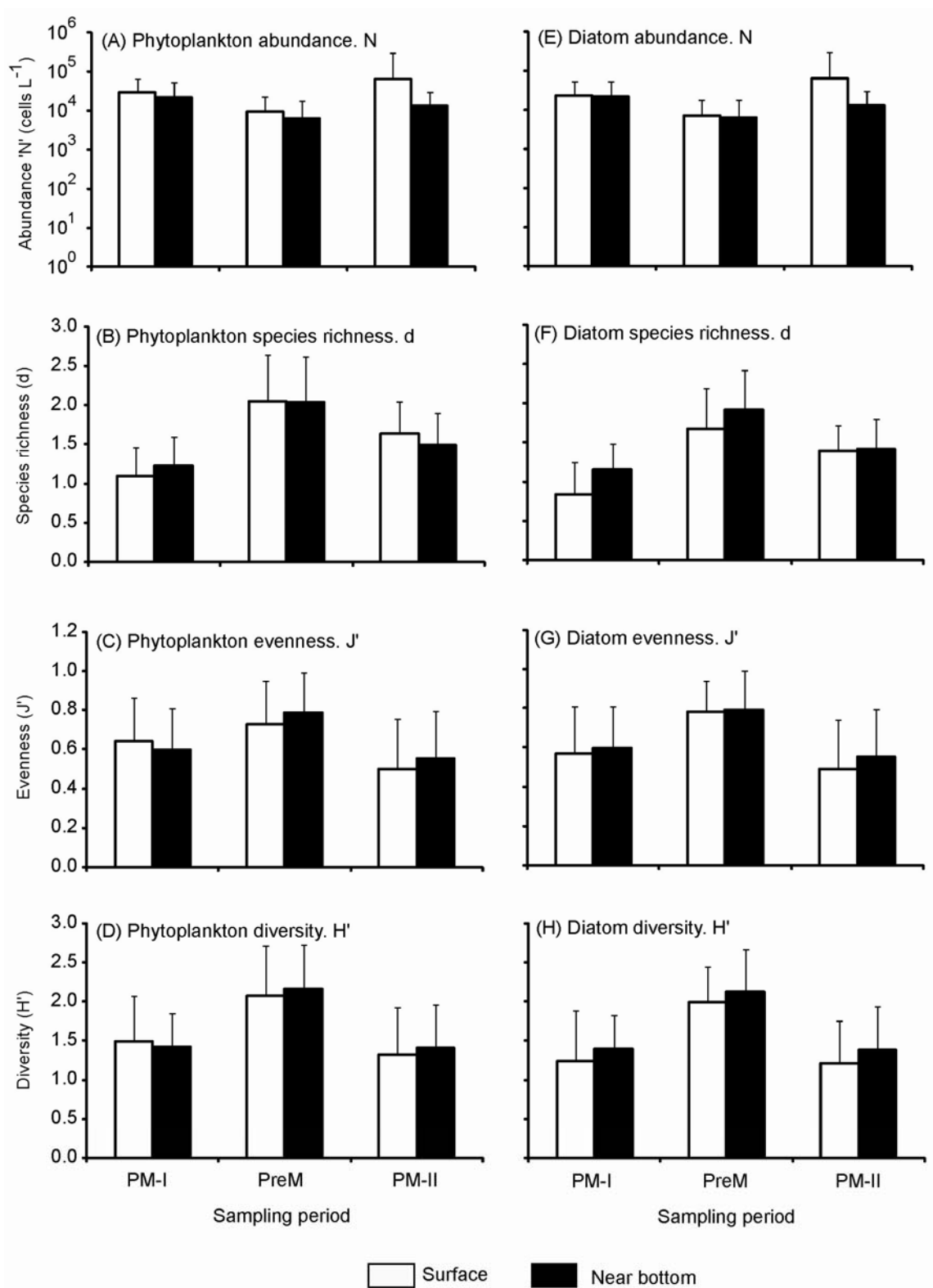


Fig. 3

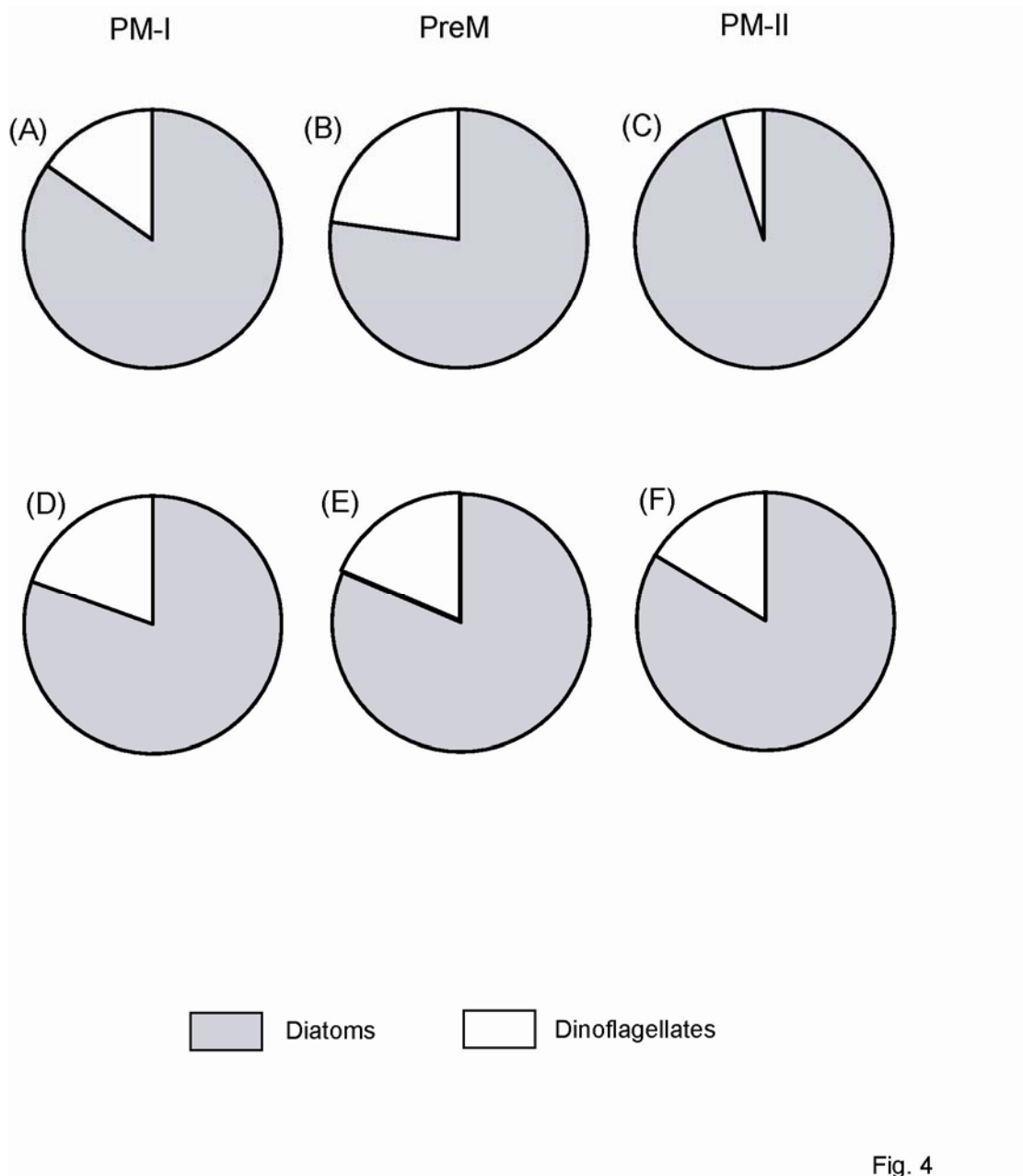


Fig. 4

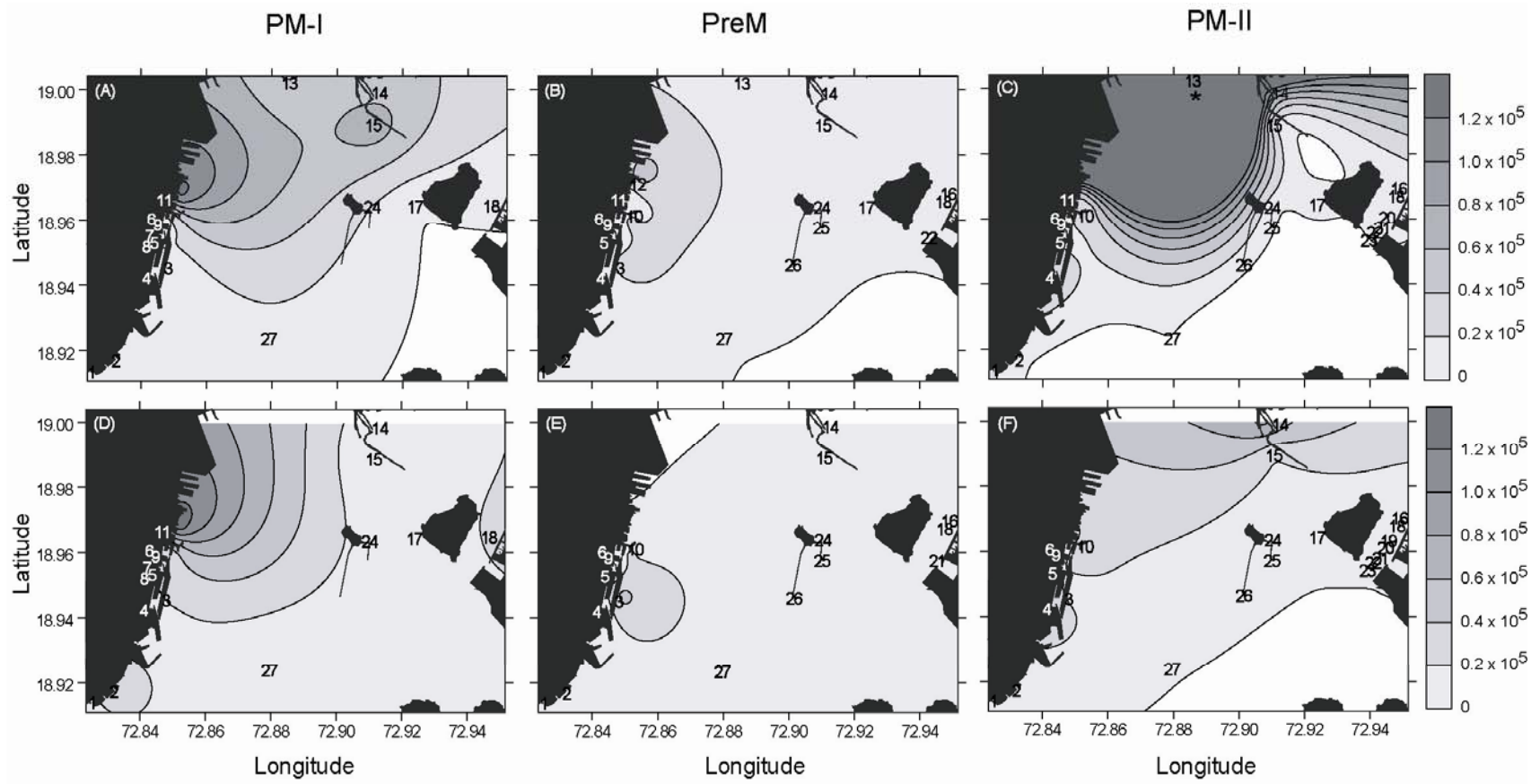


Fig. 5

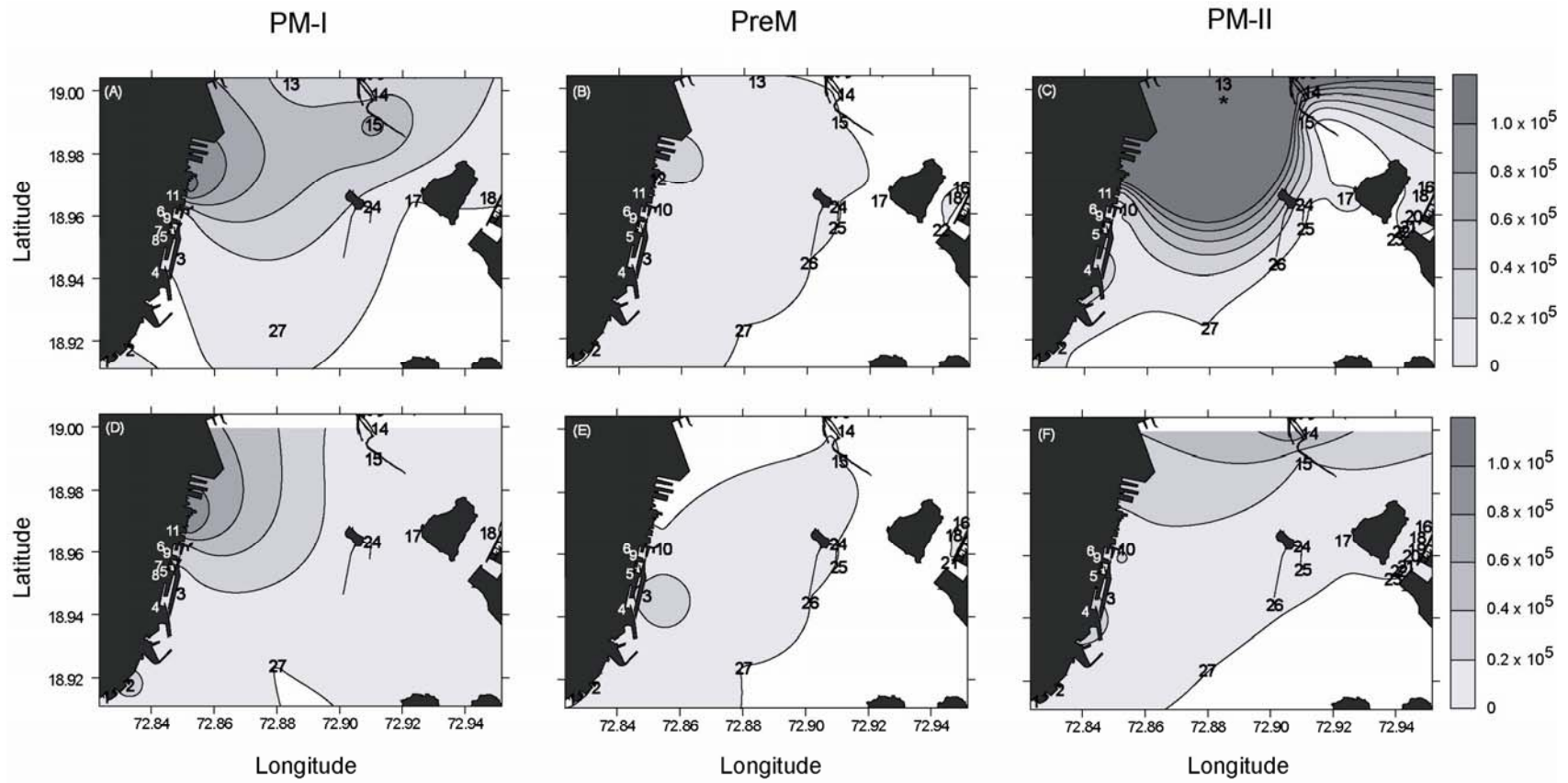


Fig. 6

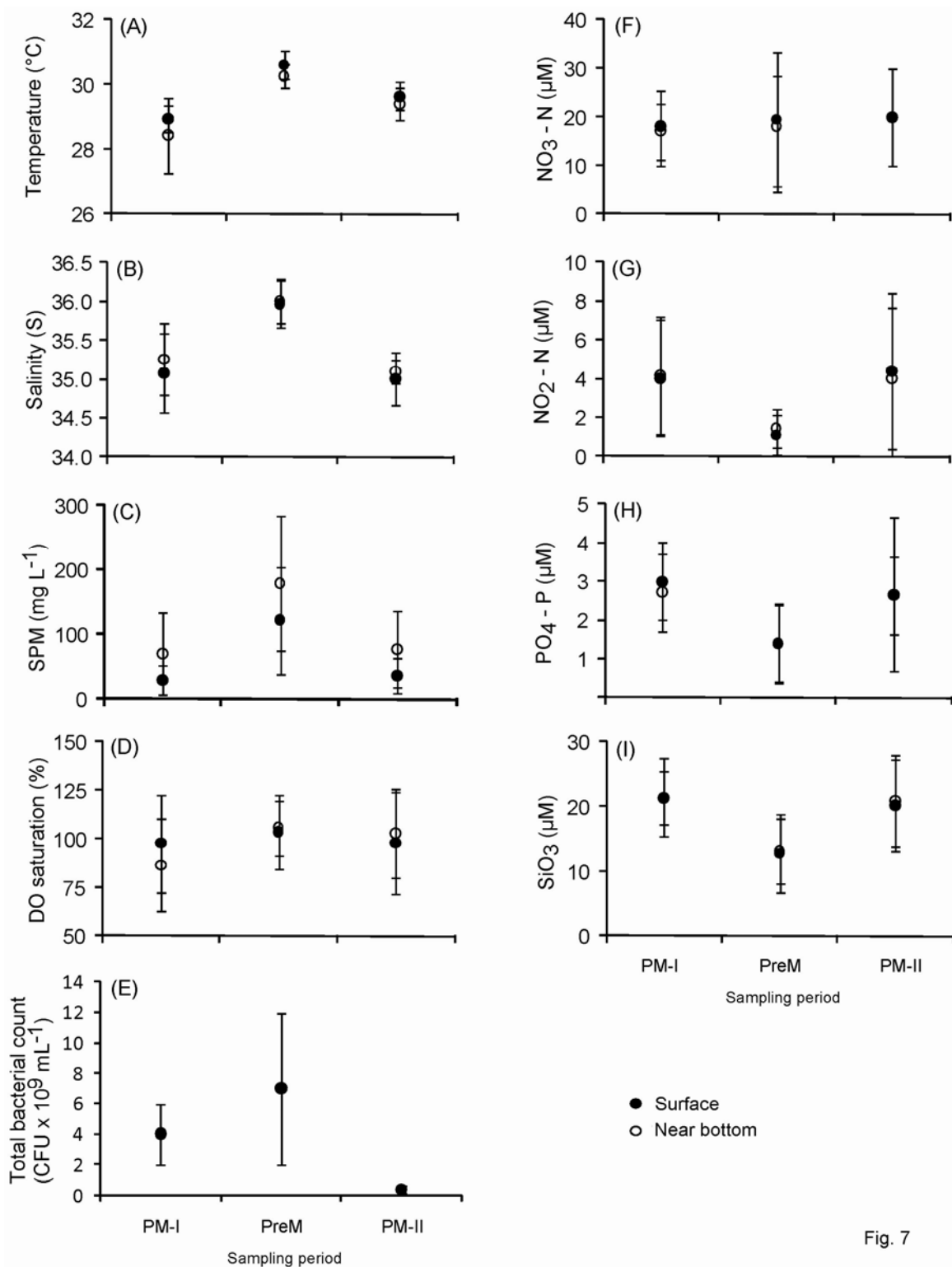


Fig. 7

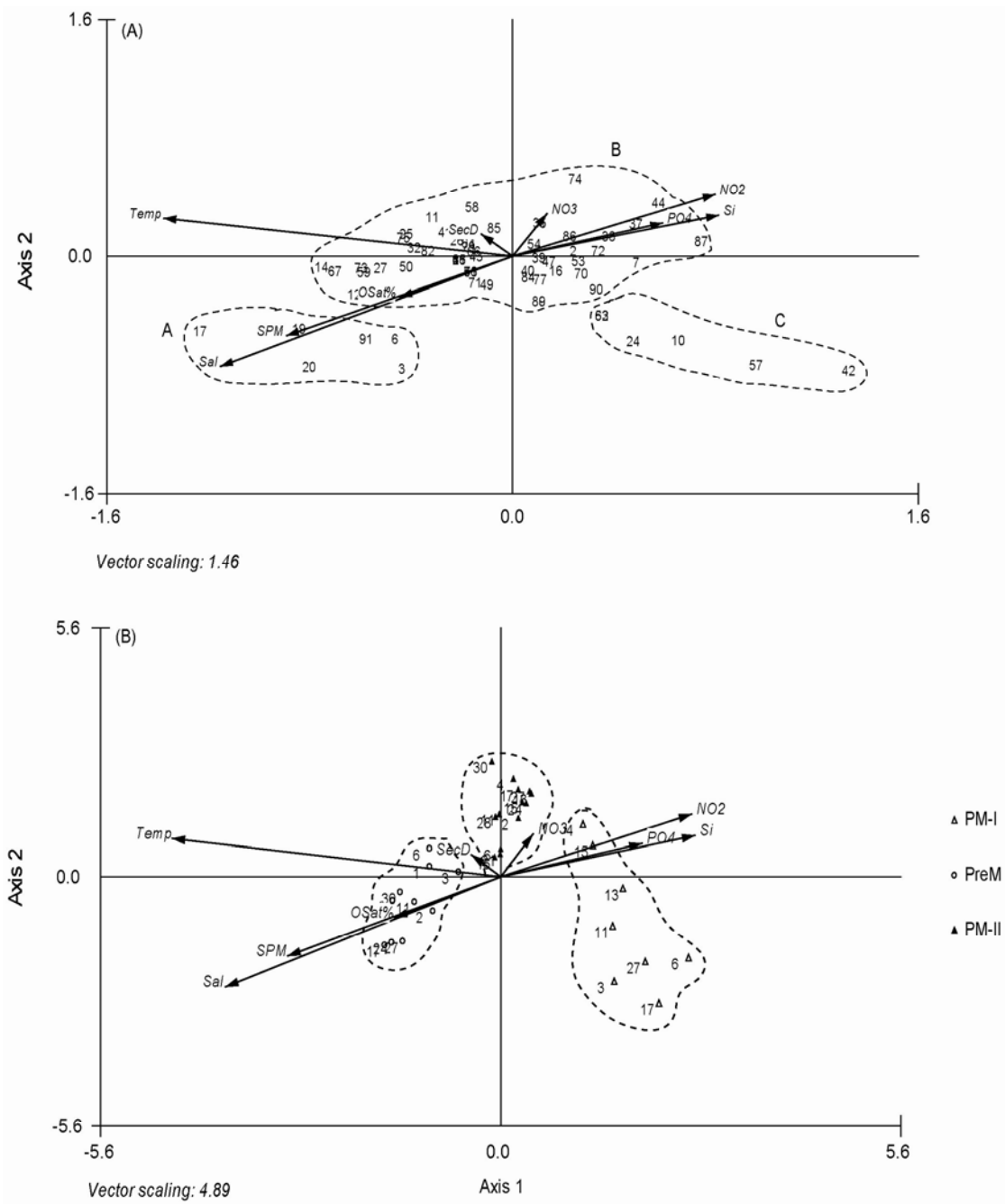


Fig. 8

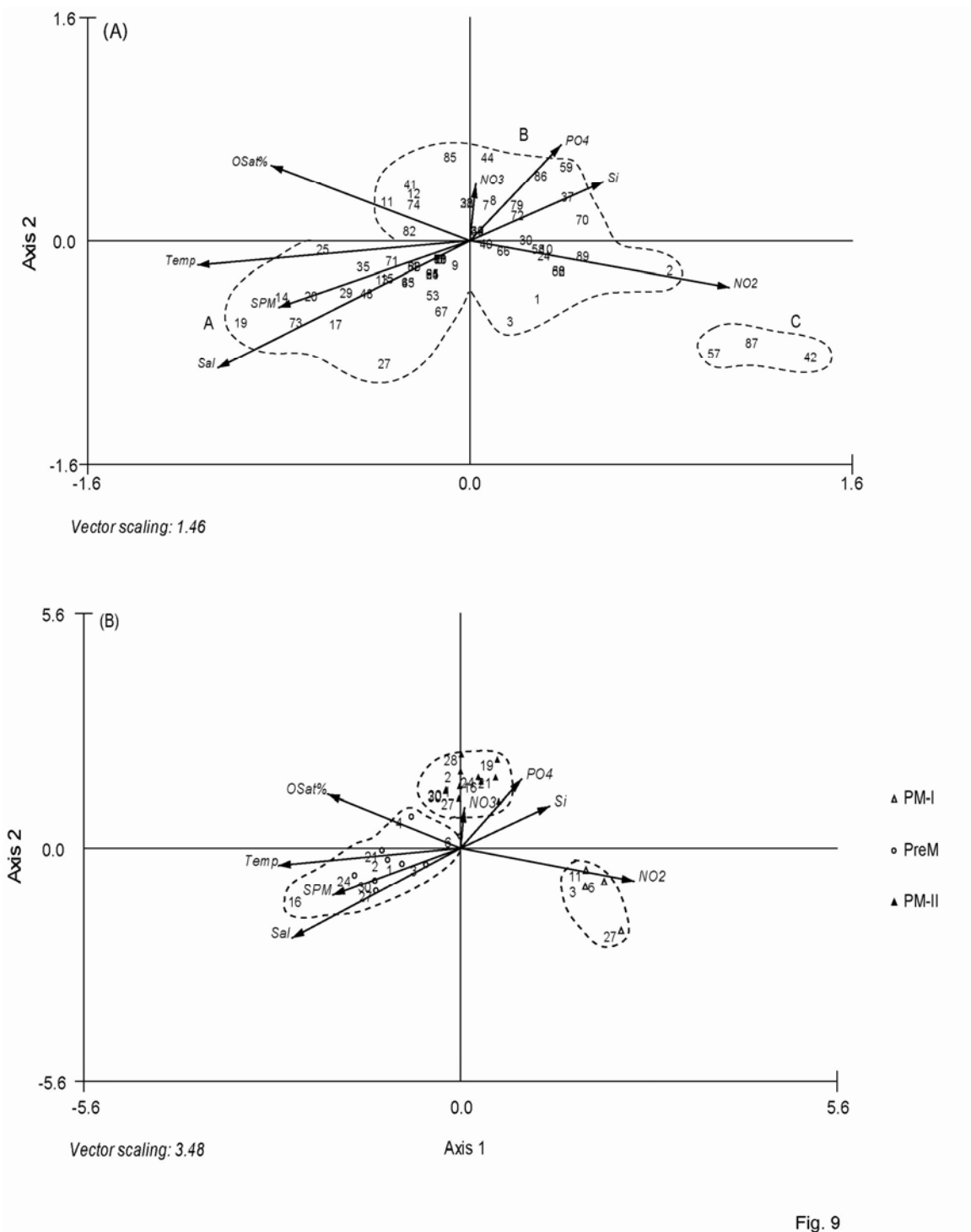


Table 1

Details of stations and sampling dates in Mumbai and Jawaharlal Nehru ports, India.

Station code	Station name	Date of sampling		
		PM-I	PreM	PM-II
1	Sasoon Dock	04/11/2001	27/04/2002	25/10/2002
2	Apollo Bandar	04/11/2001	27/04/2002	25/10/2002
3	Harbour Wall Berth 20	03/11/2001	27/04/2002	26/10/2002
4	Indira Dock 1	06/11/2001	28/04/2002	30/10/2002
5	Victoria Dock 1	06/11/2001	29/04/2002	29/10/2002
6	Princess Dock 1	04/11/2001	29/04/2002	29/10/2002
7	Princess Dock 2	04/11/2001	29/04/2002	29/10/2002
8	Princess Dock 3	04/11/2001	29/04/2002	-
9	Ferry Wharf 1	05/11/2001	27/04/2002	26/10/2002
10	Ferry Wharf 2	05/11/2001	27/04/2002	25/10/2002
11	Kasara Basin	02/11/2001	28/04/2002	26/10/2002
12	Break Yard	09/11/2001	27/04/2002	26/10/2002
13	Mahul Creek	09/11/2001	29/04/2002	29/10/2002
14	Old Pirpau 1	03/11/2001	29/04/2002	28/10/2002
15	New Pirpau 1	08/11/2001	29/04/2002	28/10/2002
16	JNPT Marker Buoy	-	30/04/2002	27/10/2002
17	Elephanta 1	05/11/2001	29/04/2002	28/10/2002
18	JNPT Container Berth 1	07/11/2001	30/04/2002	27/10/2002
19	JNPT Container Berth 2	07/11/2001	30/04/2002	27/10/2002
20	JNPT Container Berth 3	07/11/2001	30/04/2002	27/10/2002
21	JNPT Bulk Berth 1	07/11/2001	30/04/2002	27/10/2002
22	JNPT Bulk Berth 2	07/11/2001	30/04/2002	27/10/2002
23	JNPT Bulk Berth 3	07/11/2001	30/04/2002	27/10/2002
24	Jawahar Dweep Berth 1	08/11/2001	29/04/2002	28/10/2002
25	Jawahar Dweep Berth 3	09/11/2001	29/04/2002	28/10/2002
26	Jawahar Dweep Berth 4	08/11/2001	29/04/2002	28/10/2002
27	Mumbai Channel Marker Buoy	05/11/2001	27/04/2002	26/10/2002
28	Spoil Ground Ebb	-	-	31/10/2002
29	Spoil Ground Flood	08/11/2001	01/05/2002	31/10/2002
30	Offshore Station	-	01/05/2002	31/10/2002

Table 2

Tidal details at the study area.

Tide	Above (+) or Below (-) Chart Datum (m)
Highest High water recorded	+ 5.39
Mean High water spring tides	+ 4.42
Mean High water neap tides	+ 3.30
Mean sea level	+ 2.51
Mean Low water neap tides	+ 1.86
Mean Low water spring tides	+ 0.76
Lowest low water recorded	- 0.46
Highest low water	+ 2.74

Table 3

Diatoms recorded in surface and near bottom waters in Mumbai and Jawaharlal Nehru ports, India. PM-I, PreM and PM-II represent post-monsoon I, pre-monsoon and post-monsoon II sampling periods respectively. CCA codes for species are also indicated.

Centric diatoms	CCA codes	CCA group (su/nb)							
			PM-I _{su}	PM-I _{nb}	PreM _{su}	PreM _{nb}	PM-II _{su}	PM-II _{nb}	
<i>Asteromphalus</i> sp.	1	-/B		+					
<i>Biddulphia rhombus</i> (Ehrenberg) Wm. Smith	2	B/B	+	+				+	+
<i>Cerataulina bicornis</i> (Ehrenberg) Hasle	3	A/B	+	+	+	+		+	+
<i>Corethron criophilum</i> Castracane	4	B/A			+	+			
<i>Corethron</i> sp.	5	-/A				+			
<i>Coscinodiscus lineatus</i> Ehrenberg	6	A/A			+	+		+	+
<i>Coscinodiscus marginatus</i> Ehrenberg	7	B/B	+	+	+	+		+	+
<i>Coscinodiscus nodulifer</i> A. Schmidt	8	-/B							+
<i>Coscinodiscus oculus-iridis</i> Ehrenberg	9	-/A				+			
<i>Coscinodiscus radiatus</i> Ehrenberg	10	C/B	+	+	+	+		+	+
<i>Coscinodiscus</i> spp.	11	B/B	+		+	+		+	+
<i>Cyclotella caspia</i> Grunow	12	B/B			+	+		+	+
<i>Cyclotella litoralis</i> Lange & Syvertsen	13	B/A			+	+			
<i>Cyclotella striata</i> (Kutzing) Grunow	14	B/A			+	+		+	+
<i>Cyclotella stylonum</i> Brightwell	15	-/A				+			
<i>Cyclotella</i> spp.	16	B/A	+	+		+			
<i>Detonula</i> sp.	NI								+
<i>Ditylum brightwellii</i> (West) Grunow in Van Heurck	17	A/A		+	+	+			+
<i>Ditylum sol</i> Grunow in Van Heurck	18	-/A				+			
<i>Helicotheca tamesis</i> (Shrubsole) Ricard	19	A/A			+	+		+	
<i>Hyalodiscus</i> sp?	20	A/A			+	+		+	
<i>Lauderia annulata</i> Cleve	21	-/A				+			
<i>Lauderia</i> sp.	22	-/B							+
<i>Melosira nummuloides</i> C.A. Agardh	23	B/-			+			+	

su, surface; nb, near bottom. + indicates presence during particular sampling periods; A, B and C represent CCA groups; NI indicates that the species were not included in the CCA analysis.

Table 3. contd.

Centric diatoms	CCA codes	CCA group (su/nb)	PM-Isu	PM-Inb	PreMsu	PreMnb	PM-IIsu	PM-IIInb
<i>Odontella aurita</i> (Lyngbye) C.A. Agardh	24	C/B	+	+	+	+	+	+
<i>Odontella mobiliensis</i> (Bailey) Grunow	25	B/A	+	+	+	+	+	+
<i>Odontella regia</i> (Schultze) Simonsen	26	B/B			+	+		
<i>Odontella sinensis</i> (Greville) Grunow	27	B/A	+	+	+	+	+	
<i>Paralia sulcata</i> (Ehrenberg) Cleve	28	-/B				+		
<i>Planktoniella blanda</i> (A. Schmidt) Syvertsen & Hasle	29	-/A				+		
<i>Podosira stelliger</i> (Bailey) Mann	30	B/B					+	+
<i>Podosira</i> sp.	NI						+	
<i>Rhizosolenia alata</i> f. <i>indica</i> (Peragallo) Gran	31	B/-					+	
<i>Rhizosolenia hebetata</i> f. <i>semispina</i> (Hensen) Gran	32	B/B			+	+		
<i>Rhizosolenia imbricata</i> Brightwell	33	B/A			+	+		
<i>Rhizosolenia robusta</i> Norman in Pritchard	34	-/B						+
<i>Rhizosolenia setigera</i> Brightwell	35	B/A			+	+	+	+
<i>Rhizosolenia</i> sp.	36	-/A		+		+		
<i>Skeletonema costatum</i> (Greville) Cleve	37	B/B	+	+	+	+	+	+
<i>Thalassiosira eccentrica</i> (Ehrenberg) Cleve	38	B/B	+	+			+	+
<i>Thalassiosira gravida</i> Cleve	39	B/-	+					
<i>Thalassiosira punctigera</i> (Castracane) Hasle	NI						+	
<i>Thalassiosira</i> spp.	40	B/B	+	+	+	+	+	+
<i>Triceratium caudatum</i> Witt	41	B/B			+	+	+	+
<i>Triceratium</i> sp.	42	C/C	+	+				
Unidentified centric spp.	43	B/B	+	+	+		+	+

su, surface; nb, near bottom. + indicates presence during particular sampling periods; A, B and C represent CCA groups; NI indicates that the species were not included in the CCA analysis.

Table 3. contd.

Pennate diatoms	CCA codes	CCA group (su/nb)	PM-I _{su}	PM-I _{nb}	PreM _{su}	PreM _{nb}	PM-II _{su}	PM-II _{nb}
<i>Achnanthes longipes</i> Agardh	NI		+					
<i>Achnanthes subsessilis</i> Kutzing	NI			+				
<i>Amphiprora angustata</i> spec. nov.	44	B/B	+				+	+
<i>Amphiprora</i> sp.	NI				+			
<i>Amphora coffeaeformis</i> (Agardh) Kutzing	NI			+				
<i>Amphora</i> sp.	45	-/A				+		
<i>Caloneis permagna</i>	NI					+		
<i>Caloneis westii</i> (Wm. Smith) comb. nov.	46	B/B			+		+	+
<i>Caloneis</i> spp.	NI					+		
<i>Cylindrotheca closterium</i> (Ehrenberg) Lewin & Reimann	47	B/B	+	+	+		+	+
<i>Diploneis crabro</i> Ehrenberg	48	B/A			+	+		
<i>Diploneis crabro</i> var. <i>gloriosa</i> (Grun.)	49	B/B			+			+
<i>Diploneis</i> sp.	NI			+				
<i>Grammatophora marina</i> var. <i>tropica</i> (Kutz.) Grun.	NI						+	+
<i>Grammatophora marina</i> var. <i>undulata</i> (Ehrenberg) Perag. & Perag.	NI				+			
<i>Gyrosigma balticum</i> (Ehrenberg) Cleve	50	B/-			+		+	
<i>Gyrosigma wansbeckii</i> (Donkin) Cleve	51	B/B			+		+	+
<i>Gyrosigma</i> sp.	52	C/B	+	+			+	

su, surface; nb, near bottom. + indicates presence during particular sampling periods; A, B and C represent CCA groups; NI indicates that the species were not included in the CCA analysis.

Table 3. contd.

Pennate diatoms	CCA codes	CCA group (su/nb)	PM-I _{su}	PM-I _{nb}	PreM _{su}	PreM _{nb}	PM-II _{su}	PM-II _{nb}
<i>Navicula abrupta</i>	NI			+				
<i>Navicula alpitia</i>	NI				+			
<i>Navicula directa</i> (W. Smith) Ralfs in Pritchard	53	B/A	+	+	+	+	+	+
<i>Navicula distans</i> (W. Smith) Ralfs in Pritchard	54	B/-			+		+	
<i>Navicula elegans</i> Wm. Smith	55	-/A				+		
<i>Navicula granii</i> (Jorgensen) Gran	NI				+			
<i>Navicula lyra</i> Ehrenberg	56	-/A				+		
<i>Navicula subinflata</i> Grunow	NI			+				
<i>Navicula transitans</i> var. <i>derasa</i> (Grunow, in Cleve and Grunow) Cleve	57	C/C	+	+	+	+		
<i>Navicula transitans</i> var. <i>derasa</i> f. <i>delicatula</i> Heimdal	58	B/B	+	+	+	+	+	+
<i>Navicula</i> spp.	59	B/B	+	+	+	+	+	+
<i>Nitzschia angulata</i> Wm. Smith	60	-/B		+				
<i>Nitzschia bilobata</i> Wm. Smith	61	-/B		+				
<i>Nitzschia levidensis</i> (Wm. Smith) van Heurck	62	B/-			+			
<i>Nitzschia longissima</i> (Brebisson, in Kutzing) Ralfs in Pritchard	63	C/A	+	+		+		+
<i>Nitzschia panduriformis</i> Gregory	64	B/A			+	+		
<i>Nitzschia seriata</i> Cleve	65	B/A			+	+		+
<i>Nitzschia sigma</i> (Kutzing) Wm. Smith	66	B/B			+	+	+	+
<i>Nitzschia</i> spp.	67	B/A	+	+	+	+	+	+
<i>Pinnularia rectangularata</i> (Gregory) Rabenhorst	68	B/B				+	+	
<i>Pinnularia</i> sp.	69	-/B		+				

su, surface; nb, near bottom. + indicates presence during particular sampling periods; A, B and C represent CCA groups; NI indicates that the species were not included in the CCA analysis.

Table 3. contd.

Pennate diatoms	CCA codes	CCA group (su/nb)						
			PM-I _{su}	PM-I _{nb}	PreM _{su}	PreM _{nb}	PM-II _{su}	PM-II _{nb}
<i>Pleurosigma angulatum</i> sensu W. Smith emend. Sterrenburg	70	B/B	+	+	+	+	+	+
<i>Pleurosigma directum</i> Grunow in Cleve & Grunow	71	B/A			+	+	+	+
<i>Pleurosigma elongatum</i> Wm. Smith	72	B/B	+	+	+	+	+	+
<i>Pleurosigma naviculaceum</i> Breb.	73	B/A		+	+	+	+	+
<i>Pleurosigma normanii</i> Ralfs in Pritchard	74	B/B			+	+	+	+
<i>Pleurosigma</i> sp.	75	B/-			+			
<i>Pseudo-nitzschia delicatissima</i> (Cleve) Heiden in Heiden & Kolbe	76	B/-			+			
<i>Pseudo-nitzschia fraudulenta</i> (Cleve) Hasle	77	B/B					+	+
<i>Pseudo-nitzschia lineola</i> (Cleve) Hasle	78	B/A			+	+		
<i>Pseudo-nitzschia</i> spp.	79	B/B	+	+	+	+	+	+
<i>Surirella fastuosa</i> (Ehrenberg) Kutzing	80	B/B	+	+				
<i>Surirella ovalis</i> Kutzing	81	B/A			+	+		
<i>Surirella ovata</i> Kutzing	82	B/B	+	+	+	+	+	+
<i>Surirella spiralis</i>	83	-/A				+		
<i>Synedra</i> sp?	84	B/B					+	+
<i>Thalassionema bacillare</i> (Heiden in Heiden & Kolbe) Kolbe	85	B/B			+	+	+	+
<i>Thalassionema frauenfeldii</i> (Grunow) Hallegraeff	86	B/B	+	+	+	+	+	+
<i>Thalassionema nitzschioides</i> (Grunow)	87	B/C	+	+	+	+	+	+
Mereschkowsky								
<i>Thalassionema pseudonitzschioides</i> (Schuette & Schrader) Hasle comb. nov.	88	-/B		+				
<i>Thalassionema</i> sp.	89	B/B	+	+				
<i>Thalassiothrix</i> spp.	90	B/A	+	+	+	+	+	
Unidentified pennate spp.	91	A/A			+	+	+	+

su, surface; nb, near bottom. + indicates presence during particular sampling periods; A, B and C represent CCA groups; NI indicates that the species were not included in the CCA analysis.

Table 4.

Percentage contribution of dominant (>2%) genera to the diatom community in surface and near bottom waters in Mumbai and Jawaharlal Nehru ports, India. PM-I, PreM and PM-II represent post-monsoon I, pre-monsoon and post-monsoon II sampling periods respectively. Minor species represent those that contribute <2%.

Genera	PM-I _{su}	PM-I _{nb}	PreM _{su}	PreM _{nb}	PM-II _{su}	PM-II _{nb}
<i>Coscinodiscus</i>	7.31	7.00	9.58	12.21	-	4.11
<i>Cyclotella</i>	-	-	9.39	11.02	-	-
<i>Ditylum</i>	-	-	-	2.10	-	-
<i>Hyalodiscus</i>	-	-	2.89	-	-	-
<i>Odontella</i>	-	-	4.17	3.34	2.21	-
<i>Skeletonema</i>	41.53	44.68	10.63	12.57	60.52	52.58
<i>Thalassiosira</i>	13.98	13.46	11.80	8.83	3.10	3.89
<i>Triceratium</i>	4.50	5.25	17.58	10.23	9.76	10.09
<i>Navicula</i>	5.66	3.73	-	-	3.56	2.08
<i>Nitzschia</i>	-	-	2.18	2.76	-	-
<i>Pleurosigma</i>	6.24	7.66	8.19	11.31	9.70	12.40
<i>Pseudo-nitzschia</i>	-	-	2.11	2.86	-	2.64
<i>Surirella</i>	-	2.31	11.81	12.18	-	2.31
<i>Thalassionema</i>	15.85	11.02	2.21	-	4.65	5.63
Minor spp.	4.93	4.90	7.45	10.58	6.50	4.25

su, surface; nb, near bottom.