

Temporal variation of diatom benthic propagules in a monsoon influenced tropical estuary

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Abstract

Temporal variations in the diatom benthic propagule (DBP) community and its role in the phytoplankton community in a monsoon-affected tropical estuary, Zuari estuary, Goa (India) is presented. The DBP from the sediments was enumerated using an extinction dilution method (Most Probable Number method), which allows estimation of resting stages through examination of germinated vegetative cells in culture. The DBP community was dominated by planktonic species belonging to the genera *Skeletonema*, *Fragilariopsis*, *Thalassiosira* and *Chaetoceros*. Benthic propagules (BP) of *S. costatum* and *Fragilariopsis* sp. were dominant throughout the year. Between these two species, only *S. costatum* showed a linear relationship between the BP and planktonic cells indicating that this species is particularly important in coupling of pelagic and benthic ecosystems. During the onset and restart of monsoon after an intermittent break, water column was stratified, with a low salinity layer arising from riverine discharge and precipitation at the surface and relatively cold, saline, low oxygen waters at the bottom. Stratification favored blooming of *S. costatum* and *Fragilariopsis* sp. in nutrient rich surface and bottom waters respectively. The decline in these blooms ensuing nitrate depletion and salinity change resulted in an increased abundance of BP. *Chaetoceros* bloom was observed during the monsoon break as well as during non-monsoon period and on both the occasions the decline in bloom was coupled with freshwater discharge. During the non-monsoon season, *Thalassiosira* blooms were encountered subsequent to high nitrate inputs. These findings suggest that in such shallow tropical regions, physical processes during monsoon (freshwater discharge) and non-monsoon seasons (currents, waves and tides) cause resuspension of diatom BP. Since light is not a limiting factor for germination in such regions, the blooming of resuspended BP depends upon nutrient availability.

Key words: estuary; planktonic diatoms; benthic propagules; monsoon; non-monsoon

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1. Introduction

Planktonic diatoms, which are major components of the phytoplankton community in coastal regions, are known to form specialized resting spores or resting cells (hereafter referred as resting stages for both types) as a survival strategy to overcome unfavorable conditions. The formation of resting stages as survival alternatives, in many diatoms, during their life histories is now a well-accepted phenomenon (Garrison, 1984; Hargraves and French, 1983). Diatom resting stages are dormant stages, produced in response to certain physico-chemical conditions, such as change in temperature, salinity, pH and especially nutrient depletion (McQuoid and Hobson, 1996). Once resting stages are formed, they sink to the sea floor and become a part of the benthos. Benthic resting stages repopulate waters if resuspended and exposed to suitable light, temperature and nutrients (McQuoid et al., 2002). This is because germination of resting stages is regulated by several environmental factors such as light, temperature, salinity and nutrients (Eilertsen et al. 1995, McQuoid and Hobson 1995, McQuoid 2005). It has been shown that such seeding from resting stages may affect the phytoplankton community structure, depending on the seeding strategy of single species. In order to have a better understanding of the influence of diatom resting stages on the phytoplankton community structure, it is important to investigate transitions between planktonic and resting stages of species, and factors influencing these transitions. *In situ* evaluation of these factors will further enhance, understanding of their role in diatom life cycles, survival strategies, prediction of blooms and species succession.

At present there are few long-term *in situ* observations of diatom resting stage production and deposition in the marine environment. These observations are from bays, coastal waters, fjords and upwelling regions (Garrison, 1981; Itakura et al., 1997; McQuoid, 2002; McQuoid and Hobson, 1996; McQuoid et al., 2002; Pitcher, 1990). The number of resting stages deposited in sediments has been compared to the number of planktonic diatoms found in overlying waters and has contributed valuable information on seasonal patterns of sporulation and germination of several diatom species. However, information to support such studies in tropical environment, where the monsoon has tremendous influence on the physico-chemical and biological characteristics of aquatic environments is limited. A recent paper which examines the role of resting stages in a tropical environment from mesocosm experiments indicated that the species composition can be altered if a population is seeded by resting stages (Härnström et al. 2007). In this study, through time series observations, the

environmental influence on temporal variations in the diatom benthic propagule (DBP) community and their influence on the planktonic community in a monsoon-affected tropical estuary are addressed.

2. Materials and Methods

2.1. Description of Study Area

The study site, Zuari estuary, sustains a diverse phytoplankton assemblage that is strongly influenced by the southwest monsoon, which brings drastic changes in hydrodynamic characteristics and is instrumental in the complete transformation of the phytoplankton community structure and production (Devassy and Goes 1988, Bhattathiri et al. 1976). During these period surplus amounts of river discharge from the Zuari River, as well as precipitation is added to the estuary resulting in marked changes in the physico-chemical nature of the water (Qasim and SenGupta, 1981). Based on this, each year has been classified into three seasons. The monsoon season (June-September) is followed by a recovery period during post-monsoon (October-January) and thereafter by a stable period of the pre-monsoon (February-May).

Monthly sampling of sediment and water was carried out from September 1999 to January 2001 in the Zuari estuary (Goa, central west coast of India) at a fixed location (Fig. 1). The depth at the study location is ~6 m. This estuary, which is a dynamic aquatic ecosystem exhibits a strong seasonal gradient, both in environmental variables and plankton assemblages because of tight physico-chemical and biological coupling.

2.2. Water sampling

Water samples were collected from surface (bucket) and 1m above the sea bed (Niskin sampler). Water temperature and secchi disc depth were recorded at the sampling site. Salinity, dissolved oxygen and nutrients (NO_3^- - N, NO_2^- - N, PO_4^- - P, and SiO_3) were analyzed by following standard procedures. For phytoplankton enumeration, a known volume (1 L) of water sample was fixed with Lugol's iodine for microscopic analysis. In addition to diatoms other phytoplankton were also enumerated in order to evaluate the contribution of diatoms to the total phytoplanktonic community. The diatom and other phytoplankton species were enumerated in triplicate and their identifications were carried out based on the identification

keys (Hasle and Syvertsen, 1997; Round et al., 1990; Desikachary, 1987; Subrahmanyam, 1946; 1959). Diatoms were most dominant and only the data relevant for this study has been presented here. For further statistical analysis, the data of diatom species >4% in abundance throughout the study period was used.

2.3. Sediment Sampling

Sediment samples were collected using a gravity corer with an inner diameter of 4.8 cm. The top sediment (0-2 cm) from 2-3 cores collected during each sampling were pooled and then sealed in air tight bags. These samples were stored in dark at 4 °C until further analysis i.e. within couple of weeks.

2.4. Meteorological parameters

Data regarding meteorological parameters like solar radiation (MW cm^{-2}), wind speed (m sec^{-1}), wind direction (degrees), air temperature ($^{\circ}\text{C}$), relative humidity (%) and atmospheric pressure (mbar) were obtained from the Marine Instrumentation and Computer Division, NIO, Goa. The rainfall (mm), day length (h: from sunrise to sunset) and sunshine hours [the time of brightness (solar radiation > 1 mw cm^{-2}) available in a day length] data were obtained from the Indian Meteorological Department, Panaji, Goa. For interpretation, the average of 7 consecutive days prior to sampling, inclusive of sampling day has been used.

2.5. Enumeration of Diatom Benthic Propagules (DBP) from the Sediments

Enumeration of viable (i.e. able to germinate) diatom cells from the sediments was carried out by an extinction dilution method (Most Probable Number method, MPN; Throndsen, 1978). A known weight (1 g) of wet sediment in triplicate was suspended in 10 ml of the f/2 culture media (Guillard and Ryther, 1962) at a concentration of $0.1 \text{ g wet wt ml}^{-1}$. Serial tenfold dilutions (10^{-2} - 10^{-5}) were made with the culture medium and then 1 ml aliquots of diluted samples were inoculated into five replicate petridishes (35 mm) and were incubated at a temperature of $20 \pm 1 \text{ }^{\circ}\text{C}$ with a 12 h light:dark cycle. The light intensity during the incubation was $50 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$. The appearance of vegetative cells of diatoms was examined microscopically (Light Microscope; Olympus BH2) after an incubation period of 6-8 d. The petridish in which vegetative cells were identified was scored as positive for each species. The MPN for a series of five tenfold dilutions of resting stage

cells in the sediment sample (MPN g⁻¹ wet sediment) was then calculated according to the statistical table (Thronsen, 1978). This table covers a range of five dilution steps, and a set of three dilutions have to be chosen out of the five cultured petridish to get the MPN. The relative diatom cell density cm⁻³ wet sediment was obtained by multiplying the MPN value with the apparent specific gravity of wet sediment (Imai and Itakura 1999). For further statistical analysis, the data of diatom species >1% in abundance throughout the study period was used.

2.6. Data analysis

2.6.1. Cluster analysis of sampling periods

The fourth root ($\sqrt[4]{}$) transformed abundance data of diatoms, both planktonic diatoms and that of DBP was then used to construct a lower triangular similarity matrix using Bray-Curtis coefficients. This similarity matrix was then subjected to clustering by group average method and ordination by non-metric multidimensional scaling (NMDS). There are advantages in applying more than one method, since each is based on different assumptions and may give different insights (Gray et al., 1988). In case of cluster analysis, a) the individual, once placed in a group loses its identity, b) the sequence of individuals is arbitrary and c) only the inter group relationships are shown. In view of these disadvantages, it is advisable to employ an additional method of presentation to show individual relationships such as NMDS (ordination). Cluster and ordination (NMDS) analysis were made using the software PRIMER ver. 5.

2.6.2. Cluster analysis of species abundance

The fourth root ($\sqrt[4]{}$) transformed abundance data of diatoms (both planktonic cells and DBP) was then used to construct a lower triangular dissimilarity matrix using Euclidean distance. This matrix was then subjected to clustering and ordination techniques similarly as described earlier.

2.6.3. Spearman's rank correlation test

Spearman's rank correlation test was performed to evaluate the relationships between the BP and PC (dominant forms) with various observed environmental parameters that may be

responsible for regulating their population. This test was performed using the software Statistica release 5.0 by Statsoft, after transformation of only biological data i.e. fourth root ($\sqrt[4]{\cdot}$).

3. Results

3.1. Meteorological conditions

Temporal variation in wind speed is shown in Fig. 2A. Maximum wind speed was observed during the onset of monsoon in April and June 2000 and in the late monsoon period (September 2000). Wind speed showed a small increase during November in both the years. Monthly profiles of wind direction are shown in the Fig. 3B and reveals that during monsoon the winds are in the southwest direction. Temporal variations in the duration of sunshine hours and solar radiation showed a definite seasonal trend (Figs. 2C-D). Low sunshine hours and solar radiation were observed during June 2000 and thereafter increased to a maximum of 10.5 h in April 2000 (Figs. 2C-D). Maximum rainfall was observed during June (38 mm) and decreased thereafter. During non-monsoon periods, except October 2000, the study region received traces/no rainfall (Fig. 2E). The temporal variations in air temperature, relative humidity and atmospheric pressure are shown in Figs. 2F-H. During monsoon, air temperature and atmospheric pressure was low whereas the relative humidity was high.

3.2. Hydrographic conditions

Surface and bottom seawater temperature ranged from a maximum of 33 °C and 31 °C (March 2000) to a minimum of 28 °C (December 1999 and August 2000) and 22 °C (August 2000) respectively (Fig. 3A). Thermal stratification, as judged by the difference in surface and bottom temperatures, developed from June to September 2000 and the water was vertically mixed during rest of the months. Salinity ranged between a high of ~36.5 in April 2000 and a low of 17 and 18 in August and June 2000 respectively. Low salinity in the surface layer was due to freshwater influx from the Zuari River during the monsoon period. During this period, salinity stratification was also observed and existed till early post-monsoon season (except July 2000; Fig. 3B). The DO concentrations ranged from 5.6 ml L⁻¹ (July 2000) – 3.3 ml L⁻¹ (September 1999) in surface and 4.35 ml L⁻¹ (March 2000) - 2.2 ml L⁻¹ (August 2000) in bottom waters respectively (Fig. 3C). DO concentrations in bottom

waters were lower than in surface waters. The maximum difference was observed during the monsoon season. The measurement of water transparency using secchi disc, revealed that the water was less transparent during the monsoon season except during July 2000 and during the end of the post-monsoon (Fig. 3D). Secchi disc depth showed an increasing trend up to February 2000 (196 cm) except in December 1999 (45 cm), which was then followed by a decline till June 2000 (87 cm).

Nutrient concentrations showed a definite seasonal trend over the sampling period (Figs 3E-H). Maximum nutrient concentrations were found during the early phase of the monsoon. A second peak of nitrate and nitrite was observed in the years 2000 and 2001 during November-December and thus was not a mere coincidence. In addition, a surface and bottom high of $\sim 7\mu\text{M}$ nitrate was observed during April 2000. The temporal variation in nutrient concentrations at both depths followed almost a similar pattern (Figs. 3E-H).

3.3. Diatoms from the water column and sediments

In the present study, 89 species of diatoms have been recorded. Altogether 74 (37-centrales and 37-pennales) and 73 (38-centrales and 35-pennales) diatom species were recorded from surface and bottom waters respectively (Table 1). Amongst them, maximum cell densities of 6 species (*Skeletonema costatum*, *Chaetoceros curvisetus*, *Thalassiosira* spp, *Leptocylindrus danicus*, *Cerataulina bicornis*, *Fragilariopsis* sp. and *Thalassionema nitzschioides*) in surface and 8 species (*S. costatum*, *C. curvisetus*, *Thalassiosira* spp, *L. danicus*, *C. bicornis*, *Fragilariopsis* sp., *Nitzschia angularis*, *Pseudonitzschia* sp. and *T. nitzschioides*) in bottom waters was greater than $10000\text{ cells L}^{-1}$. From the sediment, benthic propagules of 41 species (21-centrales and 20-pennales) belonging to 23 genera were recorded (Table 1). Of the 41 species, resting stage formation for 16 species belonging to 12 genera are known, while formation of resting stages for other species are unknown (Table 1). In this study, the BP of only 7 species (*S. costatum*, *C. curvisetus*, *Thalassiosira* spp, *Fragilariopsis* sp., *Navicula transitans* and *Nitzschia panduriformis*) occurred in > 100 propagules cm^{-3} wet wt. of sediment. Amongst them *N. transitans* and *N. panduriformis* are the benthic diatoms. Comparison of planktonic cells and BP showed that the diatom species (except *L. danicus*, *C. bicornis*, *N. angularis*, *Pseudonitzschia* spp. and *T. nitzschioides*) which were found above $10,000\text{ cells L}^{-1}$ in the water column were the ones dominating the benthic propagule community.

In the water column, diatoms dominated the phytoplankton community in the surface waters (30 to 99%) as well as in the bottom waters (77 to 99%). The percentage of diatom abundance was maximum during monsoon, followed by post- and pre-monsoon for surface waters and, for bottom waters during post-monsoon, monsoon and pre-monsoon. The total diatom densities ranged from $8.8 \times 10^2 - 9.9 \times 10^5$ cells L^{-1} in surface and $2.2 \times 10^3 - 1.8 \times 10^5$ cells L^{-1} in bottom waters (Fig. 4A). The relative abundance of DBP ranged up to 10^4 cells cm^{-3} wet wt. of sediment (Fig. 4B) with maximum abundance during monsoon and early post-monsoon periods. The relative abundance of BP was maximum during the post-monsoon period of 2000 as compared to that of 1999 indicating an inter-annual variation.

The distribution of dominant diatom species exhibited significant temporal variations in the both sediment and water column. During onset (June 2000) and restart of monsoon after an intermittent break (August 2000), a single species bloom of *S. costatum* was observed in the surface waters whereas *Fragilariopsis* bloom was observed only during the onset of monsoon in bottom waters (Fig. 5A and B). Blooms of both these species were responsible for the observed high cell densities. The BP of *S. costatum* and *Fragilariopsis* were present throughout the study period and the occurrence of highest densities coincided with their blooms in the water column (Fig. 5A and B). *Chaetoceros* and *Thalassiosira* were the other dominant diatoms which formed blooms on certain occasions (Fig. 5C and D). Mixed blooms were encountered on two occasions i.e. during the monsoon break and the pre-monsoon wherein *Chaetoceros* was the most dominant diatom. On both the occasions, the decline in bloom coincided with an increase in the BP of *Chaetoceros curvisetus* (Fig. 5D). The highest abundance of *Chaetoceros* BP were observed after the monsoon season and thereafter their population declined as the season progressed (Fig. 5D). The highest abundance of *Thalassiosira* was observed during the end of post-monsoon (January 2001; Fig. 5D). The distribution of *Thalassiosira* in the water column showed oscillations during the non-monsoon period. However such oscillations in the distribution of *Thalassiosira* BP were not observed as they persisted for most part of the year.

3.4. Cluster analysis

Cluster analysis of the sampling months based on abundance of planktonic diatoms at 50% similarity level revealed four and two groups for surface and bottom waters respectively. In the sediments, cluster analysis based on relative abundance of DBP at 50% similarity level

revealed two groups (Fig. 6A-C). Clusters I and IV for surface waters, cluster I for bottom waters and cluster II for sediments were represented by sampling periods characterized by high cell densities. The planktonic diatoms and DBP distribution portrayed a similar pattern as that of the cluster analysis when subjected to 2D NMDS ordinations (Fig. 6A'-C').

Cluster analysis divided the 29 diatom species from surface waters into 1 group and 5 ungrouped individuals (Fig. 7A). The 5 ungrouped individuals were represented by *S. costatum*, *Fragilariopsis* sp., *Thalassiosira* spp., *C. curvisetus* and *T. nitzschioides*. Blooms of these species were encountered in the surface waters. For bottom waters, cluster analysis divided the 29 species into 4 groups and two ungrouped individuals (Fig. 7B). *Fragilariopsis* sp. and *N. angularis* represented the ungrouped individuals as they formed blooms in the bottom waters. The species representing groups I to II formed the next major components of the bottom community in terms of abundance. Cluster analysis divided the BP of 40 diatom species into 2 clusters (Fig. 7C). Cluster I consisted of 3 species, *S. costatum*, *Fragilariopsis* sp. and *Thalassiosira* spp., the most dominant groups which occurred during most of the study period. Cluster II was dominated by *C. curvisetus* and its distribution was sporadic. Rest of the species formed a minor group as they occurred once or twice during the study period. Diatom distribution for both planktonic and DBP portrayed a similar pattern as that of the cluster analysis when subjected to 2D NMDS ordinations (Fig. 7 A'-C').

3.5. Relationship between diatoms (both planktonic cells and BP) with observed environmental variables

The results of Spearman's rank correlation test are presented in Table 2. The abundance of *S. costatum*, both planktonic cells as well as BP showed a significant negative correlation with surface salinity (SS) and nitrate (SNO_3) and a positive relationship with rainfall (RF). The BP of *Fragilariopsis* sp. showed a significant negative correlation with surface salinity (SS) and nitrate (SNO_3). The planktonic cells of this species showed a negative relationship between sunshine hours (SH) and atmospheric pressure (PR) and positive relationship with bottom phosphate (BPO_4) and silicate (BSi), wind direction (WD) and relative humidity (RH). In case of *Thalassiosira* spp, the BP of *Thalassiosira* sp.1 showed a significant negative correlation with surface nutrients (nitrate (SNO_3), nitrite (SNO_2) and phosphate (SPO_4)) and bottom nitrate (BNO_3) whereas its planktonic cells did not show any relation with the observed environmental parameters. The BP of *T. subtilis* showed negative

correlation with solar radiation (SR) while its planktonic cells in surface waters showed a positive relationship with surface dissolved oxygen (SDO) and a positive relationship with BPO_4 and RF were observed in bottom waters. However, the BP of *Thalassiosira* sp. 2 showed a negative correlation with surface phosphate (SPO_4) and BNO_3 . The BP of *C. curvisetus* showed a significant positive correlation with ST, BT, RF and a negative correlation with SNO_2 and BPO_4 .

4. Discussion

In the water column, blooms of 9 species (*S. costatum*, *C. curvisetus*, *Thalassiosira* spp, *L. danicus*, *C. bicornis*, *Fragilariopsis* sp., *Nitzschia angularis*, *Pseudonitzschia* sp. and *T. nitzschioides*) were observed during the study period (Table 1; Figure 7A and B). However out of these, benthic propagules of only 4 species were found in the sediments. These benthic propagules (DBP) persisted round the year and their dominance followed the order of *Skeletonema*>*Fragilariopsis*>*Thalassiosira*>*Chaetoceros* (Fig. 7C). The dominance of these species, except *Fragilariopsis*, in sediments was also reported in temperate regions (Itakura et al. 1997) suggesting that only planktonic forms contribute significantly to the pool of DBP in the coastal sediments. During monsoon, the period of decline in blooms of *Skeletonema* and *Fragilariopsis* coincided with the maximum abundance of their propagules in the sediment.

The abundance of benthic propagules of *S. costatum* was negatively correlated with nitrate and salinity (Table 2A) revealing that depletion in nitrate concentrations and change in salinity may be the likely cue, which induced *S. costatum* to form BP. Whereas for *Fragilariopsis* sp., although a strong relation between environmental parameters could not be established statistically, it is possible that the combined effects like temperature decrease and nutrient depletion (especially nitrate and nitrite) in bottom waters could be the inducing factors. The decline of *C. curvisetus* bloom with the onset of monsoon and restart of the monsoon after an intermittent break was coupled with an increase in the abundance of its BP. This event coincided with the decrease in salinity due to freshwater discharge from the Zuari River (Figs. 3B and 5D). Earlier it was hypothesized that the resting stage formation is initiated by poor growth conditions in the water column (Gran, 1912). Once formed, they sink to the sediments, where they remain as benthic stages. This hypothesis is by far the most widely used interpretation for the role of resting stages in the marine environment (French and Hargraves, 1980; Garrison, 1981; Hollibaugh et al., 1981). Most authors have reported

nitrogen depletion to be the most important environmental variable causing the dormancy in marine diatoms (Davis et al., 1980; Durbin, 1978; Hollibaugh et al., 1981; Kuwata and Takahashi, 1990; review by McQuoid and Hobson, 1996). Maximum number of resting stages may be formed during or just after a period of maximum vegetative cell division (McQuoid and Hobson, 1996; Zohary et al., 1998). The formation of resting stages can take hours, days or weeks but it is not certain how long it takes after an environmental trigger to begin sporulation (see review by McQuoid and Hobson, 1996). Once formed, most of them sink faster out of the euphotic zone into the sediments. The maximum sedimentation rate recorded for diatoms in the near by region i.e. a few kilometers away from the study site (Dona Paula Bay) was 121.5×10^4 cells $m^{-2} d^{-1}$ (Garg and Bhaskar 2000). It has also been reported that (von Bodungen et al., 1981) such sedimentation process will be a crucial part in diatom survival strategies, as it represents the transition from a surface growing stage to a benthic or deep-water resting stage in their life cycles (Smetacek, 1985).

The diatom resting stages, which are deposited at the bottom are known to survive for a long time in the sediments (Lewis et al., 1999; McQuoid et al., 2002) and their prolonged survival (even more than a century in some freshwater species) is common but not universal (Sick-Goad et al., 1989). The resting stages of the dominant species *Skeletonema*, *Thalassiosira* and *Chaetoceros* recorded in the study are known not only to survive for a long term under dark conditions (Itakura et al. 1997) but also to seed the surface waters for further primary production (Carrick et al 1993). Additionally, in sediments the diatom pool persists for several months in spite of the abundance of benthic macrofauna (Hansen and Josefson, 2001). Among the dominant species, only *S. costatum* showed a linear relationship between the BP and planktonic cells i.e. both fugitive and vegetative cells (data not shown), indicating that this species is particularly important in coupling pelagic and benthic ecosystems. As the coupling between the benthic and pelagic stages were not studied directly (eg. via sedimentation trap), and as the sampling of the sediment included the top 2 cm, the germinated stages might have also originated from the BP formed during previous blooms.

In this study, during monsoon, the blooms of *S. costatum* in surface and *Fragilariopsis* sp. in bottom waters were observed when the water column was stratified, with a nutrient rich low salinity layer arising from riverine discharge and precipitation at the surface and the nutrient rich cold, saline and oxygen depleted water at the bottom (Figs. 3B,E-H and 5A and B). Based on density data, it was observed that *S. costatum* bloomed twice (June and August

2000; Fig. 5A) under similar conditions, whereas *Fragilariopsis* sp. bloomed once (June 2000; Fig. 5B). From these observations we hypothesize that the events during monsoon such as increased freshwater discharge supplies the nutrients and resting stages from the sediments to the surface. The resuspended cells are kept in suspension due to the presence of stratification thus giving an ample opportunity for the resting stages to grow. This may be the probable reason for the occurrence of *S. costatum* and *Fragilariopsis* sp. blooms during monsoon along the west coast of India (Gopinathan 1974, Mitbavkar and Anil 2002, Personal observation). Since, diatom resting stages are known to germinate only under light conditions (French and Hargraves, 1985; Hollibaugh et al., 1981), resuspension of bottom sediments into the water column is a prerequisite for the cells to germinate and grow. The resuspension might be accomplished by specific hydrodynamic conditions, which have sufficient energy to transport benthic sediments, like upwelling, strong waves, currents etc. The upwelling events have been correlated with the formation of red tides (Figueiras and Pazos, 1991) and *Chaetoceros* blooms (Pitcher et al., 1991). McQuoid et al. (McQuoid et al., 2002) reported that in their study area wind forcing, baroclinic waves and northward flow of water is a vector for the resuspension of benthic propagules and assumes that the blooms could develop if conditions were favorable for their growth.

During post and pre-monsoon periods, blooms of *Thalassiosira* sp. and *C. curvisetus* were observed (Fig. 5 C and D). The current speed in the study area is greater during spring tide (Jayakumar S., personal communication) than the critical current speed ($>20 \text{ cm s}^{-1}$), which is required to resuspend the bottom sediments (Bloesch, 1994). These physical forcings could be one of the factors affecting the distribution of BP in the sediments through frequent resuspension. It was reported that the currents (velocity as low as 10 cm s^{-1}), under natural conditions in shallow waters and waves (Beaulieu, 2003) are sufficient enough to resuspend benthic diatoms, settled phytodetritus and other sticky organic flocs to the water column. The frequent resuspension of DBP and fugitive cells (if present) due to water movements could be the reason why there were no long periods where a species is absent from the surface waters (Fig. 5C and D). Moreover, such frequent resuspension and sinking could provide cells with 'recharging' periods of brief photosynthesis without inducing germination (French and Hargraves, 1980) and it provides opportunities for diatoms with a resting stage to exploit favorable conditions for their germination and subsequent vegetative growth (Ishikawa and Furuya, 2004). The nitrate input, through regeneration (Nair, 1980) or localized origin (Qasim and SenGupta, 1981), during post and premonsoon (Figs. 3E-H) might have fueled

the observed blooms. Interestingly, *C. curvisetus* bloom was observed (Fig. 5D) even though the system was nitrate limited i.e. $\text{NO}_3:\text{PO}_4$ ratio <1 (data not shown) which could be because of its adaptation to high light and low nitrate conditions (Anderson and Roels, 1981). The observations from this study indicate that in such shallow tropical regions, physical processes during monsoon (freshwater discharge) and non-monsoon season (currents, waves and tides) cause resuspension of BP. Since light is not a limiting factor for germination and growth in this area, the subsequent growth of germinated BP depends upon the nutrient availability.

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Table 1. List of diatoms (both planktonic diatoms and diatom benthic propagules) recorded from the sediments and the abbreviations. * indicates the resting stages reported for the respective species or genera (Garrison 1981, Sicko-Goad et al. 1989, McQuoid and Hobson 1996, McQuoid et al. 2002, Ishikawa and Furuya 2004)

S. No.	Taxon	Abbrev.	Water column (Cells L ⁻¹)		Sediment (Cells g ⁻¹ wet wt.)
			Surface	Bottom	
CENTRICS					
1	<i>Asteromphalus</i> sp.	Ast.sp	27	27	
2	<i>Bacteriastrum delicatulum</i> Cleve	Bac.del	53		
3	<i>Bacteriastrum fusus</i>	Bac.fus		27	
4	<i>Bacteriastrum hyalinum</i> Lauder	Bac.hya	533	347	
5	<i>Bacteriastrum varians</i>	Bac.var		27	
6	<i>Biddulphia granulata</i>	Bid.gra			3
7	<i>Biddulphia rhombus</i> (Ehrenberg) W. SM.	Odt.rho	33	107	20
8	<i>Cerataulina bicornis</i>	Cer.bic	12100	22167	
9	<i>Chaetoceros calcitrans</i>	Cha.cal			2 *
10	<i>Chaetoceros curvisetus</i> Cleve	Cha.cur	18413	13627	599 *
11	<i>Chaetoceros diversus</i> Cleve	Cha.div	7787	1493	
12	<i>Chaetoceros lacinosus</i> Schütt	Cha.lac		227	
13	<i>Chaetoceros lorenzianus</i> Grunow	Cha.lor	867	2160	35 *
14	<i>Chaetoceros socialis</i> Lauder	Cha.soc	2440	333	
15	<i>Chaetoceros tenuissimus</i> Meunier	Cha.tes	27		
16	<i>Climacodium frauenfeldianum</i> Grunow	Cli.fra	13	13	
17	<i>Corethron criophilum</i> Castracane	Cor.cri	267	347	
18	<i>Coscinodiscus marginatus</i> Ehrenberg	Cos.mar	427	4720	2
19	<i>Coscinodiscus radiatus</i>	Cos.rad	30	13	
20	<i>Coscinodiscus</i> sp.	Cos.sp	340	133	2
21	<i>Ditylum brightwellii</i> (West) Grunow	Dit.bri	880	880	5 *
22	<i>Eucampia zodiacus</i> Ehrenberg	Euc.zoo	267	2333	
23	<i>Guinardia flaccida</i> (Castracane) H. Peragallo	Gui.fla	7120	240	
24	<i>Helicotheca tamesis</i> (Shrubssole) Ricard	Hel.tha	1240	4827	9
25	<i>Hemiaulus sinensis</i> Greville	Hem.sin	1013	300	
26	<i>Hemidiscus</i> sp.	Hem.sp	80	133	
27	<i>Lauderia annulata</i> Cleve	Lau.bor	613	267	
28	<i>Leptocylindrus danicus</i> Cleve	Lep.dan	12133	21033	3 *
29	<i>Melosira granulata</i>	Mel.gra			4 *
30	<i>Melosira nummuloides</i> C.A. Agardh	Mel.num	600	260	3
31	<i>Odontella aurita</i> (Lyngbye) Agardh	Odt.aur			5 *
32	<i>Odontella regia</i>	Odt.reg	33	300	1
33	<i>Odontella sinensis</i> (Greville) Grunow	Odt.sin	1000	495	12
34	<i>Paralia sulcata</i> (Ehrenberg) Cleve	Par.sul	107	107	2 *
35	<i>Planktoniella sol</i> (Wallich) Schutt	Pln.sol	67	400	
36	<i>Proboscia alata</i> (Brightwell) Sundstrom	Rhi.ala	1373	1307	
37	<i>Rhizosolenia imbricata</i> Brightwell	Rhi.imb	53		
38	<i>Rhizosolenia styliformis</i> Brightwell	Rhi.sty		187	
39	<i>Rhizosolenia stouterfothii</i> H Peragallo	Rhi.sto	1067	300	2 *
40	<i>Schroederella schroederi</i> (Bergon) Pavillard	Sch.sch	267	1040	
41	<i>Skeletonema costatum</i> Greville (Cleve)	Ske.cos	992667	22720	6144 *
42	<i>Thalassiosira subtilis</i> (Ostenfeld) Gran	Tha.sub	2113	827	2581 *
43	<i>Thalassiosira eccentrica</i> (Ehrenberg) Cleve	Tha.exc	320	320	
44	<i>Thalassiosira</i> sp1.	Tha.sp1	30360	10707	891 *
45	<i>Thalassiosira</i> sp2.	Tha.sp2	453	453	996 *

Continued.....

S. No.	Taxon	Abbrev.	Water column (Cells L ⁻¹)		Sediment (Cells g ⁻¹ wet wt.)
			Surface	Bottom	
PENNATES					
46	<i>Achnanthes longipes</i> Agardh	Ach.lon	1453	107	
47	<i>Achnanthes subsessilis</i> Kützing	Ach.sub		13	
48	<i>Amphiprora gigantea</i>	Amp.gig	80	27	
49	<i>Amphora coffeaeformis</i> (Ag.) Kützing	Amp.cof		27	47 *
50	<i>Amphora rostrata</i>	Amp.ros		80	6
51	<i>Amphora</i> sp.	Amp.Sp	213	507	9
52	<i>Asterionellopsis glacialis</i> (Castracane) Round	Ast.jap	1920	1200	50 *
53	<i>Cocconeis scutellum</i> Ehrenberg	Coc.scu	33	133	2
54	<i>Cylindrotheca closterium</i> (Ehrenberg) Smith	Cy.clos	2787	1493	14
55	<i>Cymbella gastroides</i> Kütz	Cym.gas	13	80	
56	<i>Diploneis</i> sp.	Dip.sp	27	80	
57	<i>Fragilariopsis</i> sp.	Frag.sp	13733	116587	5712 *
58	<i>Grammatophora marina</i> (Lyngbye) Kützing	Gra.mar	93		
59	<i>Haslea</i> sp.	Has. sp	213	267	
60	<i>Licmophora juergensii</i> Agardh	Lic.jeu	7813	27	
61	<i>Licmophora paradoxa</i>	Lic.par	400		
62	<i>Meuniera membranacea</i> (Cleve) P. C. Silva comb. nov	Meu.mem			26
63	<i>Navicula crucicula</i> (Wm. Smith) Donkin	Nav.cru			17
64	<i>Navicula transitans</i> var. <i>derasa</i> f. <i>delicatula</i> Heimdal	Nav.del	8333	2053	172
65	<i>Navicula subinflata</i> Grun	Nav.sub	50	67	11
66	<i>N. inflexa</i>	Nav.inf			41
67	<i>Navicula</i> sp. 1	Nav.sp1	573	693	33
68	<i>Navicula</i> sp. 2	Nav.sp2	53	13	23
69	<i>Navicula</i> sp. 3	Nav.sp3	27		
70	<i>Navicula</i> sp. 4	Nav.sp4	367		
71	<i>Nitzschia angularis</i>	Nit.ang	507	53627	31
72	<i>Nitzschia bilobata</i>	Nit.bil	213	427	81
73	<i>Nitzschia longissima</i> Ralfs in Pritchard.	Nit.lon	347	213	
74	<i>Nitzschia panduriformis</i> Gregory	Nit.pan	160	213	130
75	<i>Nitzschia sigma</i> (Kützing) Wm.smith	Nit.sig	507	667	
76	<i>Pleurosigma angulatum</i> Sensus W. Smith	Ple.ang	6373	7680	
77	<i>Pleurosigma elongatum</i> WM Smith	Ple.elo	133	33	
78	<i>Pseudo-nitzschia</i> (Seriata group)	Pnit.ser	3767	30987	5
79	<i>Pseudo-nitzschia</i> sp. 1	Pnit.sp1	393	160	
80	<i>Pseudo-nitzschia</i> sp. 2	Pnit.sp2	67		
81	<i>Surirella ovata</i>	Sur.ova	133	213	
82	<i>Surirella</i> sp.	Sur.sp	27	80	
83	<i>Synedra gallioni</i> (Bory) Ehrenberg	Syn.gal	53	53	
84	<i>Synedra affinis</i> Kützing	Syn.aff	53	107	
85	<i>Synedra</i> sp.	Syn.sp	93	53	
86	<i>Thalassionema frauenfeldii</i> (Grunow) Hallegraeff	Thx.fre	3120	960	
87	<i>Thalassionema nitzschioides</i> (Grunow)	Thn.nit	27067	12587	45
88	<i>Thalassiothrix longissima</i> Cleve and Grunow	Thx.lon	1920	1493	
89	Unidentified sp.	UI			10

Table 2. Results of Spearman's rank correlation test between 24 environmental variables and total diatom benthic propagules (DBP) as well as the benthic propagules and planktonic cells of *Skeletonema costatum*, *Fragilariopsis* sp., *Thalassiosira subtilis*, *T. sp.1*, *T. sp.2* and *Chaetoceros curvisetus*. Only the combinations with significance level >95% are shown.

Note: ST-surface temperature; SS-surface salinity; SNO₃-surface nitrate; SNO₂-surface nitrite; SPO₄-surface phosphate; SSi-surface silicate; BT-bottom temperature; BDO-bottom dissolved oxygen; BNO₃-bottom nitrate; BPO₄-bottom phosphate; BSi-bottom silicate; WV-wind velocity; WD-wind direction; SH-sunshine hours; SR-solar radiation; RF-rainfall; RH-relative humidity; PR-atmospheric pressure

a. Sediment

Parameters	DBP		<i>S. costatum</i>		<i>Fragilariopsis</i> sp.		<i>T. subtilis</i>		<i>T. sp.1</i>		<i>T. sp.2</i>		<i>C. curvisetus</i>	
	R	p	R	p	R	p	R	p	R	p	R	p	R	p
ST													0.65	0.006
SS	-0.58	0.018	-0.57	0.023	-0.52	0.041								
SNO ₃			-0.57	0.022	-0.62	0.011			-0.66	0.005				
SNO ₂									-0.54	0.033			-0.51	0.042
SPO ₄									-0.50	0.048	-0.50	0.048		
BT													0.50	0.049
BNO ₃			-0.54	0.029					-0.70	0.003	-0.49	0.052		
BPO ₄													-0.51	0.046
SR							-0.57	0.02						
RF			0.51	0.045									0.52	0.041

B. Surface water

Parameters	<i>S. costatum</i>		<i>Fragilariopsis</i> sp.		<i>T. subtilis</i>		<i>T. sp.2</i>		<i>C. curvisetus</i>	
	R	p	R	p	R	p	R	p	R	p
SS	-0.69	0.003								
SDO					0.80	0.000			0.53	0.035
SNO ₃	-0.52	0.039								
SSi			0.53	0.034						
WV							0.58	0.02		
WD			0.50	0.046						
SH			-0.67	0.004						
RF	0.51	0.046								
RH			0.52	0.040						
PR			-0.61	0.013						

C. Bottom water

Parameters	<i>S. costatum</i>		<i>Fragilariopsis</i> sp.		<i>T. subtilis</i>	
	R	p	R	p	R	p
BDO			-0.54	0.030		
BPO ₄			0.61	0.012	0.50	0.050
BSi			0.68	0.004		
WD			0.56	0.025		
SH			-0.67	0.004		
RF	0.69	0.003			0.56	0.024
RH			0.58	0.018		
PR			-0.54	0.029		

Legends to figures

Fig. 1. Geographic location of the study site Zuari estuary (Goa), located on the west coast of India.

Fig. 2. Temporal variations in meteorological parameters. A) Wind speed, B) Wind direction, C) Day length, D) Solar radiation, E) Rainfall, F) Air temperature, G) Relative humidity and H) Atmospheric pressure. Shaded region represents monsoon season.

Fig. 3. Temporal variations in water parameters. A) Temperature, B) Salinity, C) Dissolved oxygen, D) Secchi disc depth, E) Nitrate (NO₃-N), F) Nitrite (NO₂-N), G) Phosphate (PO₄-P) and H) Silicate (Si). Shaded region represents monsoon season.

Fig. 4. Temporal variations in diatom abundance A) water column and B) sediment. Shaded region represents monsoon season. The error bars shown are standard deviations.

Fig. 5. Comparison between planktonic and benthic propagules of diatoms. A) *Skeletonema costatum*, B) *Fragilariopsis sp.*, C) *Thalassiosira* spp. and D) *Chaetoceros curvisetus*

Fig. 6. Cluster dendrograms based on diatom abundance in Surface water (A and A'), Bottom waters (B and B') and sediments (C and C'). Dendrograms (A, B and C) of sampling periods using the Bray-Curtis similarity coefficient and group average method and Non-metric Multidimensional scaling (NMDS) ordination based on the Bray-Curtis similarity coefficient (A', B' and C').

Fig. 7. Cluster dendrograms based on diatom abundance in Surface water (A and A'), Bottom waters (B and B') and sediments (C and C'). Species relationships (A, B and C) using Euclidean distance and group average method And Non-metric Multidimensional scaling (NMDS) ordination based on Euclidean distance of the DBP community (A', B' and C').

Note: Please see Table 1 for the details of the species abbreviations.

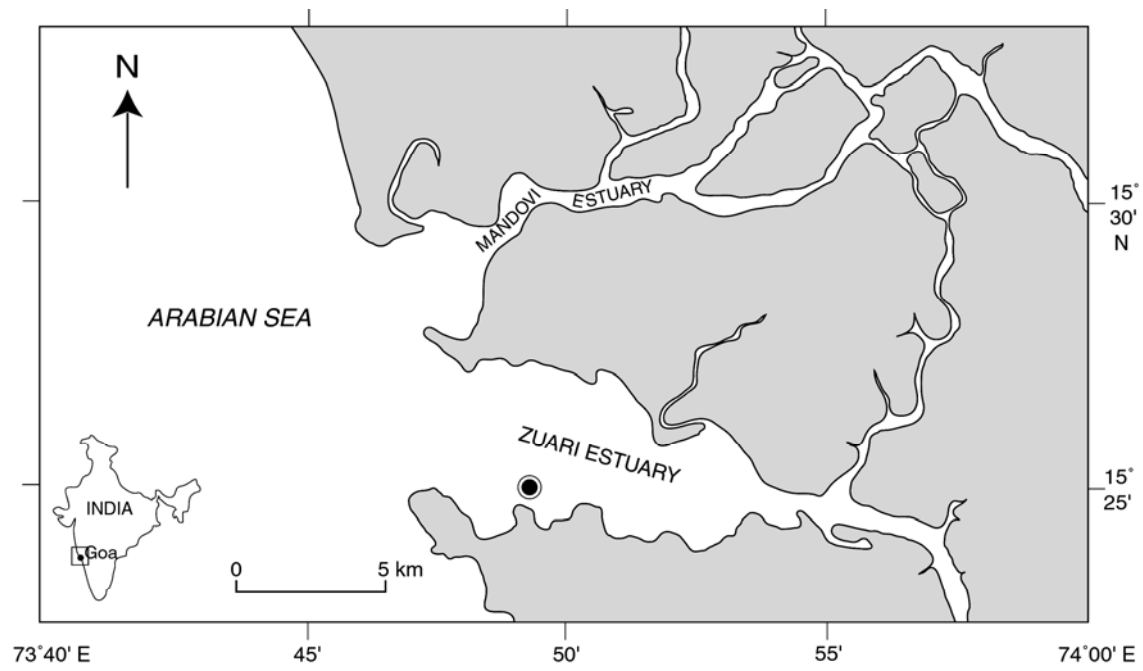


Fig. 1.

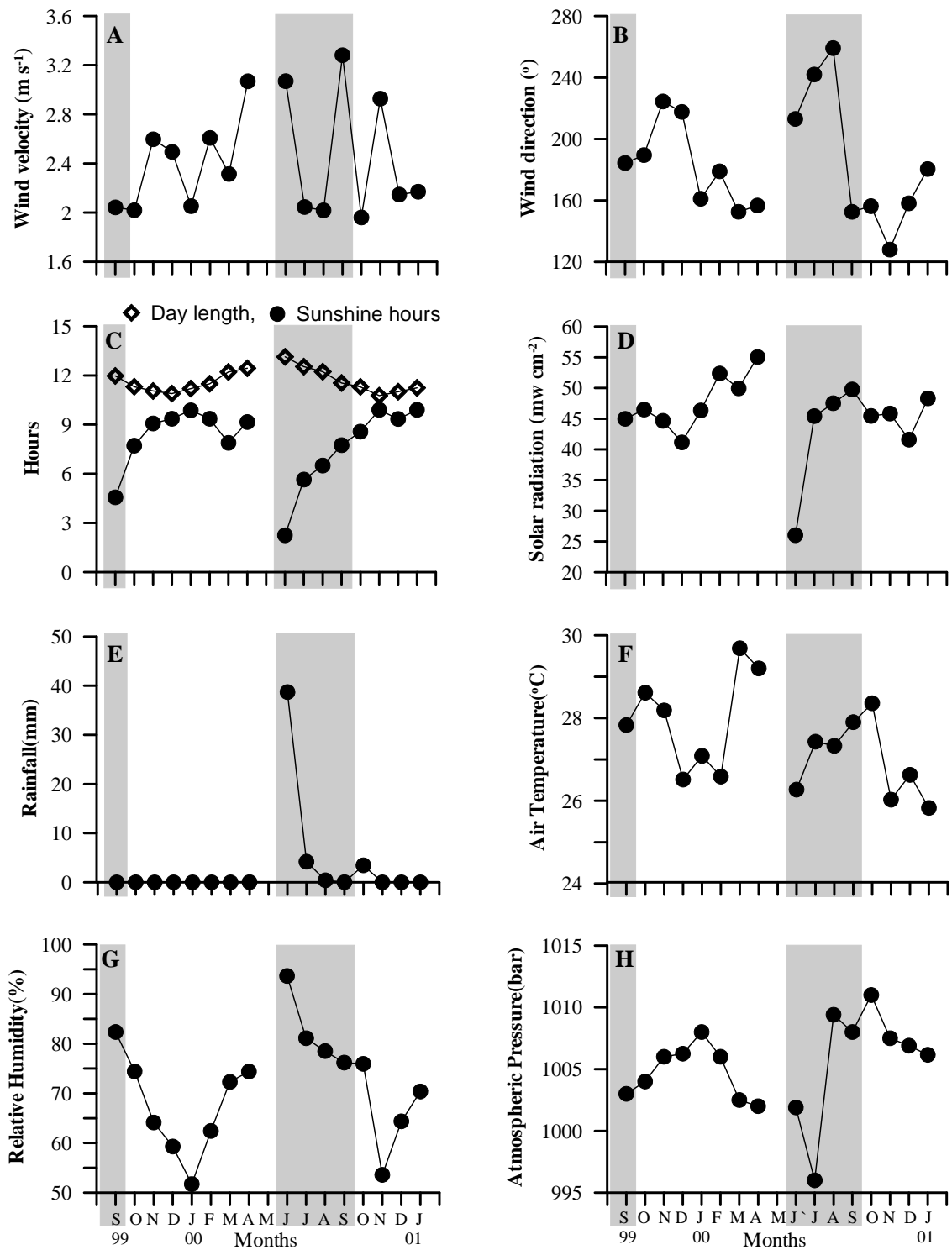


Fig. 2.

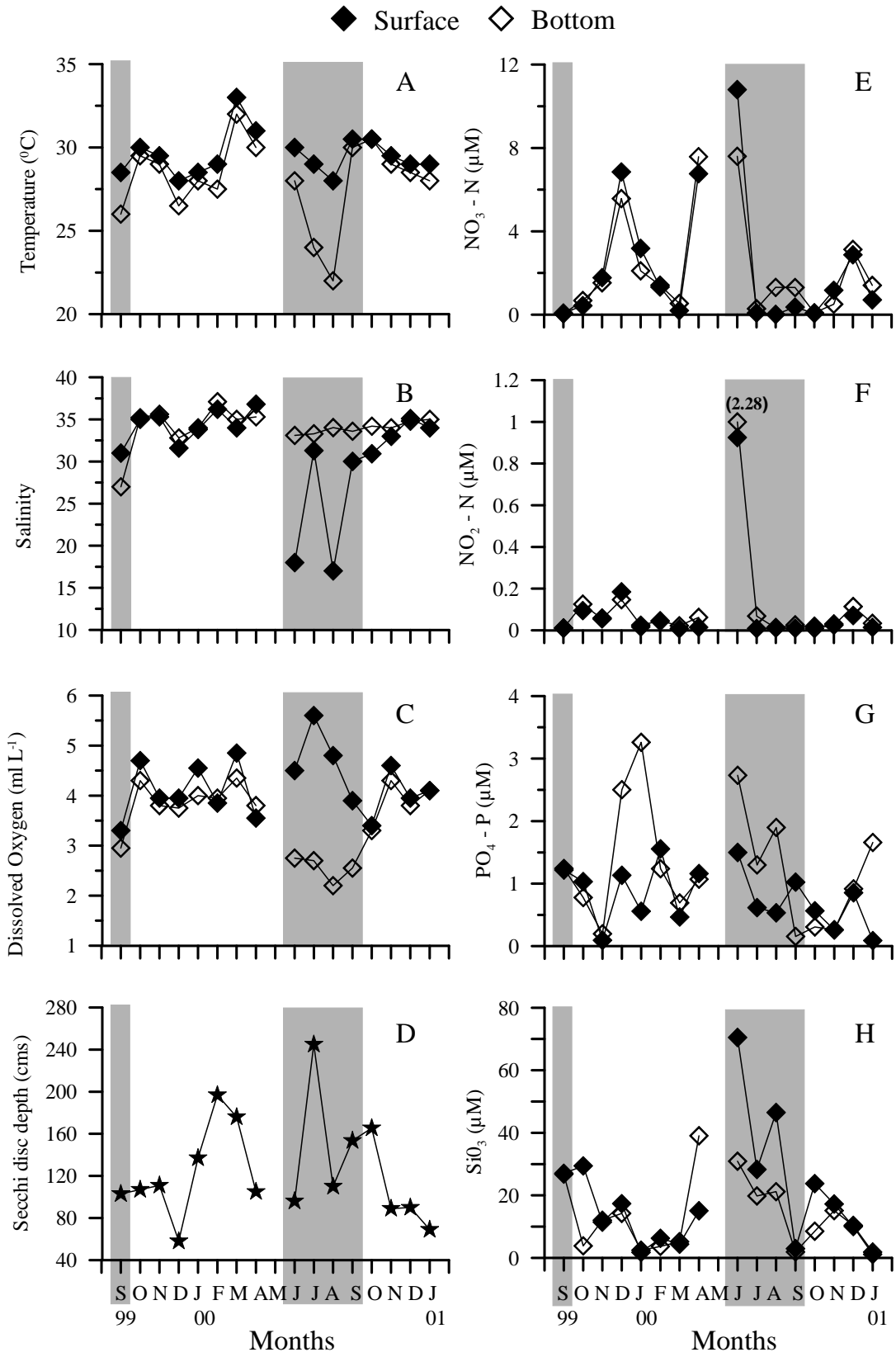


Fig. 3.

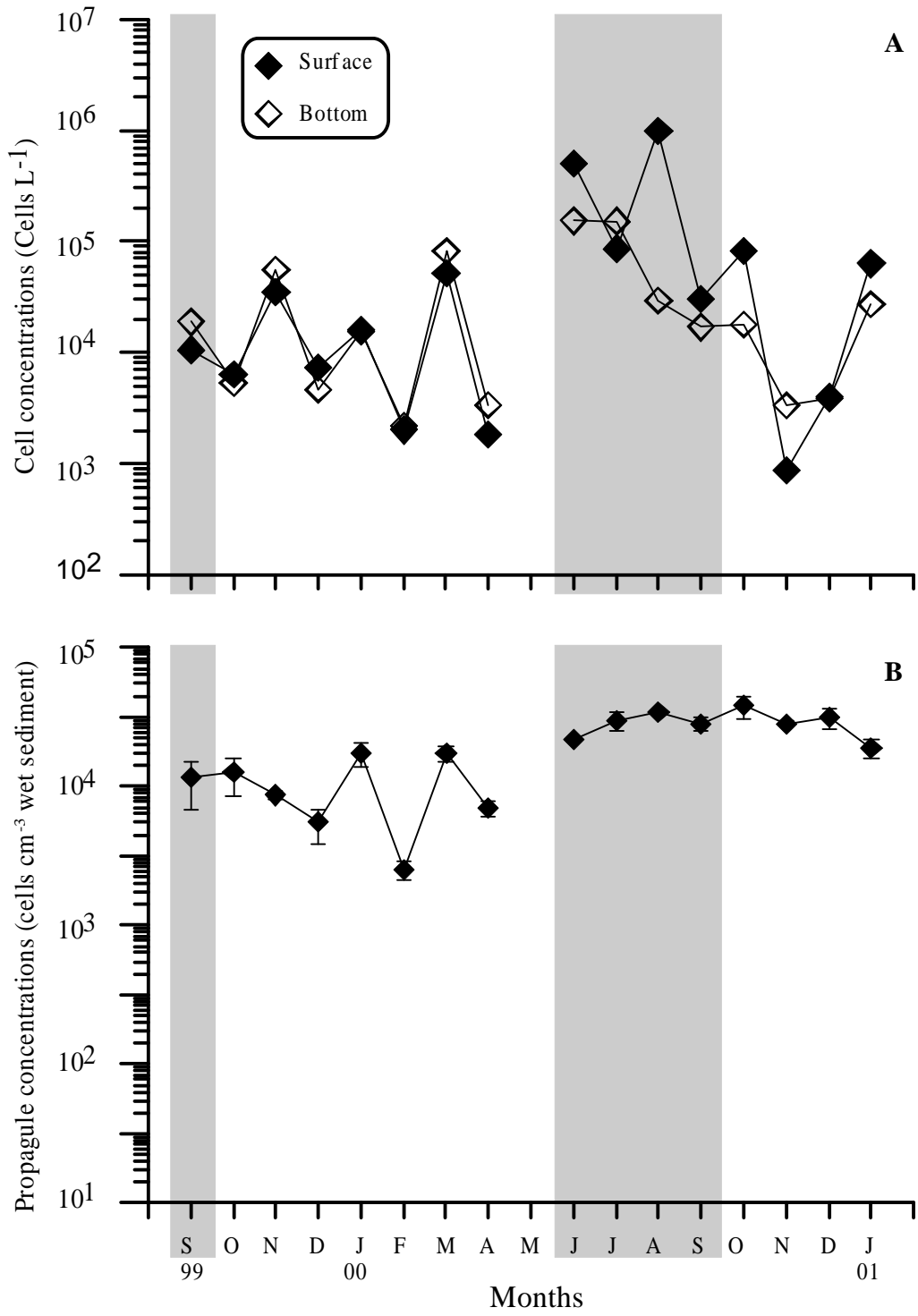


Fig. 4.

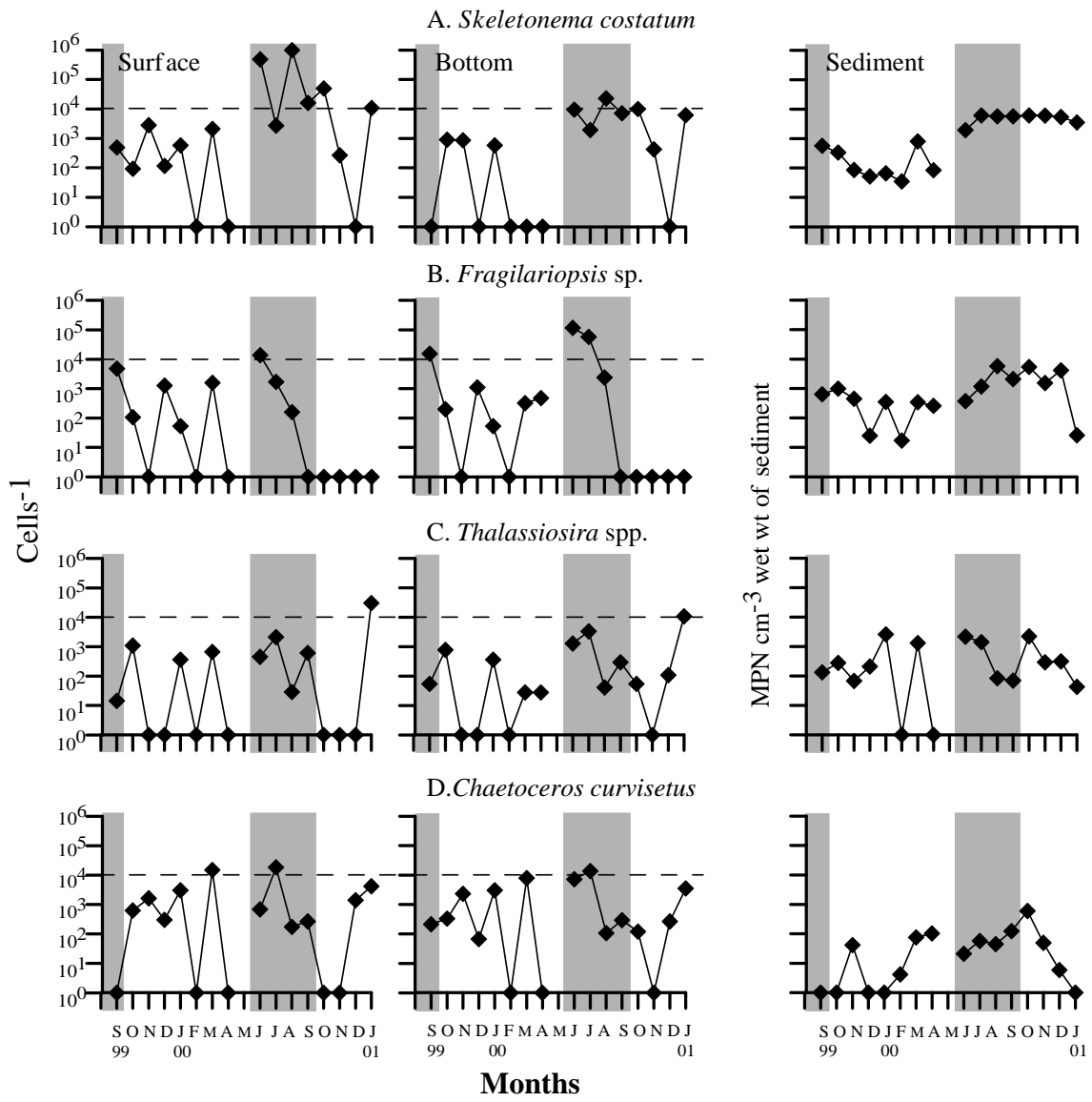


Fig. 5.

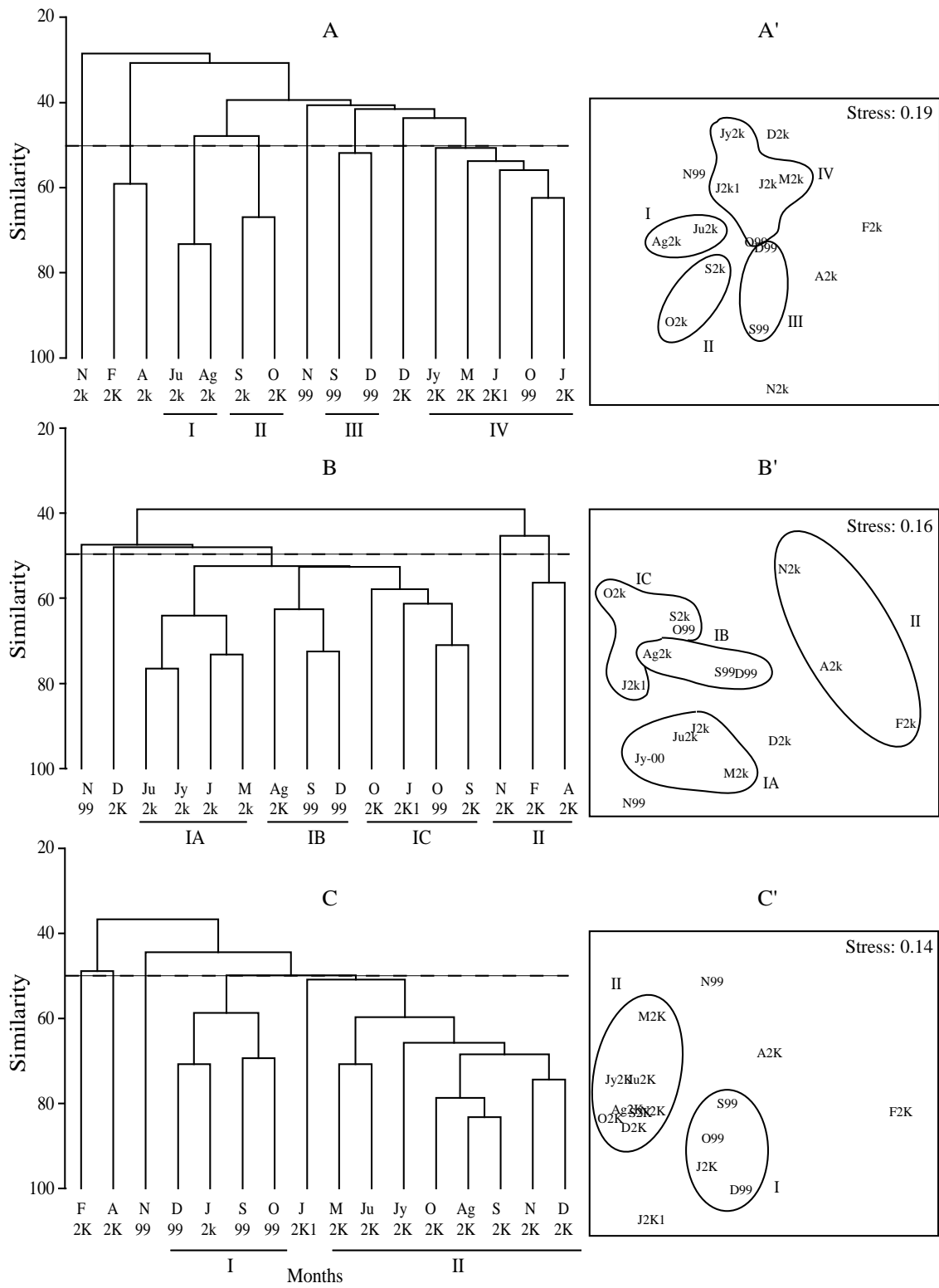


Fig. 6.

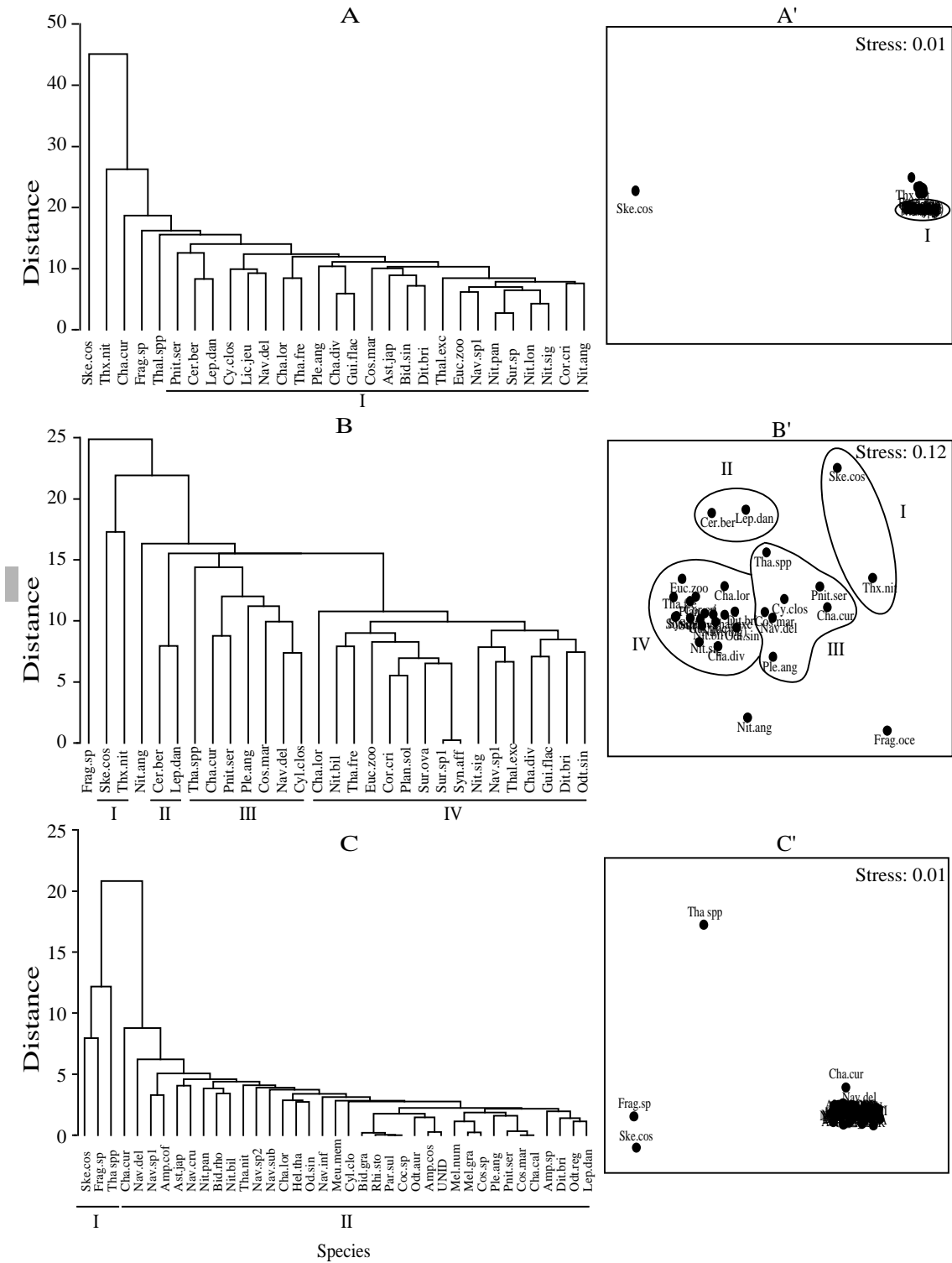


Fig. 7.