

Phytoplankton community structure is governed by salinity gradient and nutrient composition in the tropical estuarine system

M. D. Bharathi^{a,b}, V. Venkataramana^{a,c}, V.V.S.S. Sarma^{a,*}

^aNational Institute of Oceanography, Council of Scientific and Industrial Research, Regional Centre, 176 Lawsons Bay Colony, Visakhapatnam, India

^bPresently at: National Centre for Coastal Research (NCCR), MoES, 2nd Floor, NIOT Campus, Pallikaranai, Chennai - 600100, India.

^cPresently at: National Centre for Polar and Ocean Research (NCPOR), MoES, Government of India

* Corresponding author (sarmav@nio.org)

Abstract

Primary production in the estuarine ecosystems is principally represented by phytoplankton. The presence or function of phytoplankton in estuarine production is mainly regulated by factors such as salinity, light, turbidity, temperature, nutrients, grazers and the dynamics of the water basin. In order to understand the impact of salinity and hydrological characteristics on phytoplankton community structure in tropical estuaries, surface water samples for phytoplankton and biogeochemical parameters were collected from 26 estuaries along the Indian coast during non monsoon/ no discharge period. Large spatial gradient in salinity was observed within the estuary (upper, middle and lower regions of estuary) from 2 to > 15 due to sea water intrusion through tidal currents. A higher concentration of suspended particulate matter (SPM) is observed in the lower estuarine regions, such as Tapti, and Narmada due to higher tidal amplitude. Higher phytoplankton biomass/abundances in upper estuarine region is associated with higher concentration of nutrients, and lower salinity whereas higher SPM, grazers and salinity is noticed associating with lower phytoplankton abundance in lower estuarine region. Phytoplankton community structure is found to vary significantly with reference to salinity as green algae and diatoms were dominated in the low saline upper estuary, diatoms and blue-green algae were abundant in the moderate saline region of middle estuary and diatoms alone were prominent in the high saline lower estuarine region. Moreover, diatoms in the upper estuarine region is exhibiting high heterogeneity with *Melosira* spp., *Thalassiosira* spp., *Navicula* spp. and *Nitzschia* spp. while the middle estuary and lower estuary were homogenous, mainly dominated by *Thalassiosira* spp. Higher species diversity (lower species dominance) was observed in upper estuary due to the diverse taxa of green algae and blue-green algae along with diatoms, whereas lower diversity was noticed in the lower estuarine region. Present study reveals that availability of light and grazing pressure is predominately governing phytoplankton abundance, while variations in nutrient concentrations and salinity is more influencing phytoplankton community structure.

Keywords: Phytoplankton, Tropical estuaries, diversity, salinity, Nutrients

1. Introduction

Estuaries are considered to be unique and are the transition zone between river and sea. They receive land driven nutrients through rivers and modify them before delivering to the adjacent ocean (Ketchum, 1967). The shallow water column in estuary facilitates rapid exchange of material (including nutrients) between sediments and water. These prominent features make estuaries the most productive zone among the marine ecosystems (Gameiro et al., 2004). Phytoplankton lies at the bottom of the food chain and support secondary and tertiary production in the estuary. Phytoplankton growth is governed by the combined interactions of physical, chemical and biological components of an estuary (Dayala et al., 2014). Land driven nutrients and light availability support rich phytoplankton production in estuaries (Crouzet et al., 1999; Neill, 2005). The light penetration into the estuarine waters is subjected to the magnitude of suspended solids. There are many abiotic factors that influence the growth of phytoplankton community of an estuarine ecosystem, the monsoonal runoff and tidal activity being the major contributors (Cloern, 1996; Sin et al., 1999).

Indian subcontinent houses several estuaries (Godavari, Krishna, Narmada etc.) which are influenced by monsoonal rainfall; hence they are called monsoonal estuaries (Sarma et al., 2014). Indian subcontinent has wide differences in the monsoonal system and precipitation pattern (Soman and Kumar, 1990). However, the discharge of each river, in terms of quantity and timing is tuned to the precipitation. During monsoon period seasonal runoff far exceeds the total volume of the estuary resulting non-steady state behavior and displays riverine conditions with no vertical salinity gradients (Sarma et al. 2009; 2010; 2011; Acharyya et al., 2012). Rivers bring huge amount of nutrients from several sources especially agricultural lands and the concentrations of these nutrients exhibit spatial variation because of the differences in the state wise fertilizer usage (Krishna et al. 2016). River discharge also carries SPM and the magnitude of SPM is depending on the texture of the sediment in the river bed and flow rate of discharge (Krishna et al. 2019). Besides seasonality in precipitation, dam constructions on the river also modify the discharge pattern. Several dams have been constructed on almost all major monsoonal rivers in India and water is stored over 6 month's period to use for irrigation and domestic purposes. The dams release water with concentrated flow during a short span of time when water levels in the dam reservoir exceeds its capacity (Sarma et al., 2012b). On the other hand, during no discharge period, dominant seawater intrusion can be observed in estuaries due to drying of upstream river because of reduced monsoonal precipitation. It is important to note that when there is complete cessation of discharge due to closing of the dam gates, the flushing time in estuary is solely governed by tides. Hence, tidal mixing can be responsible for significant changes in salinity,

turbidity and nutrients composition during dry period, and they act as key factors to regulate phytoplankton community in the estuaries.

Flow events such as river discharge, astronomical tide and atmospheric winds, regulate estuarine residence time, nutrient advection and vertical mixing (Xia et al., 2011; Jiang et al., 2015; Jiang and Xia, 2018). These flow events cause significant heterogeneity in habitat conditions at both the spatial and temporal scales (Xia et al., 2010; Xia and Jiang, 2015; Jiang and Xia, 2017). Sarma et al. (2009) noticed that monsoon fed Godavari estuary turns into a river (nearly zero salinity) during high discharge period ($>2000 \text{ m}^3 \text{ s}^{-1}$). In monsoonal estuarine system, water was highly turbid with SPM concentration and displayed positive relationship with river discharge during peak discharge period (Acharya et al., 2012). High concentrations of nutrients are reported to be associated with river discharge compared to no discharged period in monsoonal estuaries (Mandovi Zuari estuary (Ram et al., 2003), Cochin estuary (Gupta et al., 2009), Godavari estuary (Sarma et al., 2010) and Hoogly estuary (Mukhopadhyay et al., 2006)). River discharge and associated changes bring significant changes in phytoplankton community in monsoonal estuarine system (Sarma et al., 2014).

Previous studies noticed that lower phytoplankton biomass was associated with high concentrations of nutrients and SPM during peak discharge period, while enhanced phytoplankton biomass was associated with lower turbidity and nutrient concentrations during no discharge period (Sarma et al., 2009; Pednekar et al., 2011). Many estuaries (Kaduviyar estuary (Perumal et al., 2009); Mahanadi estuary (Naik et al., 2009) and Godavari estuary (Bharathi et al., 2018)) dominated by diatoms during dry period, whereas it is replaced by green algae and blue-green algae during discharge period. Indian estuaries are reported to exhibit considerable variations in phytoplankton biomass due to significant disparity in river discharge and associated changes (Sarma et al., 2014; Bharathi and Sarma, 2019) during discharge period. In addition to variation in magnitude of river discharge, Indian estuaries experience variable tidal amplitudes that govern the magnitude of mixing of seawater with freshwater in the estuary leading to modifications in the biogeochemical properties during no discharge period. No attempts have been made so far to identify the variations in the phytoplankton community in the Indian estuaries during no discharge period. Individual estuaries in India were studied with reference to biogeochemistry, however the variability in all major and medium estuaries were never studied in India. The present work is the first of this kind to study 26 major and medium Indian estuaries in India to assess the influence of nutrient concentrations and salinity gradients on the phytoplankton community structure during no discharge period.

2. Material and methods

2.1 Study area

India has extensive coastline of about 6100 km (it will be 7517 km including of Lakshadweep Islands in Arabian Sea and Andaman and Nicobar Islands in Bay of Bengal). Indian River system has total catchment of 3.02×10^6 km² with an estuarine water-spread area of 2.7×10^4 km². The total annual discharges by all peninsular rivers comes to 1.56×10^{12} m³ (Zingde, www.nio.res.in/past_events/mandovi_zuari/zingde.pdf). The west and east coast of India is enveloped by an intricate estuarine system comprising around 14 major, 44 medium and 162 minor estuaries. Even though India located in the tropical region, Indian estuaries exhibit different hydrological conditions, caused by monsoonal precipitation. The annual precipitation over the Indian subcontinent is about 4000 km³, including snowfall. Out of this, 3000 km³ is precipitated during monsoon (June to September) period (Kumar et al., 2005). Rainfall in India mostly depends upon intensity of monsoon, shallow cyclonic depressions, disturbances and local storms. The two monsoonal seasons that primarily affect the rainfall pattern of Indian sub-continent are the Southwest monsoon (June-September) and Northeast monsoon (October –December). The maximum rainfall is received along the west coast of India and northeastern India during southwest monsoon whereas southeastern India receives high rainfall during northeast monsoon (Perumal, 1993) due to masking effect of Western Ghats (Deepthy and Balakrishnan, 2005). During the Southwest monsoon, which accounts for three fourths of the total rainfall, almost all the Indian estuaries are completely filled with freshwater and therefore show no vertical salinity variation occurs. (Vijith et al., 2009; Acharyya et al., 2012; Sridevi et al., 2015). During no discharge period, when there is less (or negligible) influx of upstream riverine input, partial mixing pattern is exhibited (Vijith et al., 2009; Sridevi et al., 2015).

2.2 Sampling strategy, data collection and analysis

In order to examine phytoplankton abundance and their compositions in Indian estuaries, samples have been collected during no discharge period (10 January to 1 February, 2012) in 26 estuaries along the Indian coast (Fig. 1) using local mechanized boats. Three locations were (upper, middle, and lower region of the estuary) selected in each estuary for sampling to cover the entire salinity range. One sample was collected from each location per estuary for the biogeochemical and phytoplankton analysis. Samples were collected from most of the estuaries in three locations, but in some estuaries, samples were collected from either one or two locations. The maximum number of samples (n) in upper, middle and lower estuarine regions are 16, 17 and 18, respectively. For the convenience of

discussion, data pooled together from all estuaries and data were presented as an upper, middle, and lower estuary.

Conductivity-temperature-depth profiler (SBE 19 plus, Sea Bird Electronics, USA) was employed to measure the temperature, salinity, and depth. Nutrients, mainly dissolved inorganic nitrogen (sum of nitrite, nitrate, and ammonium), dissolved inorganic phosphorous and dissolved inorganic silicate, were measured using auto analyzer by following the methodology suggested by Grashoff et al. (1992). The precisions of the dissolved inorganic nitrogen, dissolved inorganic phosphorous and dissolved inorganic silicate were ± 0.02 , 0.02 and 0.01 $\mu\text{mol l}^{-1}$, respectively. Following Suzuki and Ishimaru (1990), about 500 mL of sample was filtered through a Glass Fiber (GF/F; 0.7 μm pore size; 47 mm diameter; Whatman) filter under gentle vacuum, and the phytoplankton biomass (in terms of chlorophyll a) retained on the filter was extracted to dimethyl formamide, and the extract's fluorescence was measured using a Varian Eclipse fluorescence photometer (Varian Electronics, USA). The weight difference of filter (0.2 μm polycarbonate filter (Millipore)) after passing 200–500 mL of water, from that of initial was used to estimate suspended particulate matter (SPM). The phytoplankton composition was analyzed by fixing the 1L of surface water sample with 0.5% Lugols iodine solution (Thronsen, 1978). After settling of phytoplankton samples for 24 h, the sample was concentrated to 10 ml by decanting upper water and 100 μL of this concentrate phytoplankton sample was observed under BX51 OLYMPUS microscope (Olympus, Japan) for composition of phytoplankton. 400x magnification was used to record the abundance of phytoplankton. Phytoplankton keys (Santra, 1993; Tomas, 1996 and Baker et al., 2012) were used for identification of phytoplankton. Horizontal towing using 200 μm mesh and a calibrated flow meter (Hydrobios, USA) mounted at the net mouth was used to collect the mesozooplankton samples and the volume of water filtered by the net is noted with the flow meter. During the larger sample volumes, splitting was carried using the Folsom plankton splitter. To determine zooplankton abundance, 25% of the aliquot was taken from the subsamples. Primer 5.2.8 software (Clarke and Warwick, 1994) is used to compute diversity (Shannon Wiener Diversity Index) and domination (Simpson's Dominance Index). Hierarchical cluster analysis dependent on the Bray–Curtis similarity index ($\sim 40\%$ similarity cut off) is used to describe the spatial variations among phytoplankton at various stations was performed by using Primer 5.2.8 software. The relationship among physicochemical and biological parameters was defined by correlation analysis (Spearman) and principal component analysis bundled in Statistica software.

3. Results and discussions

3.1. *Spatial variations in hydrographic properties in the Indian estuaries during no discharge period*

The overall range of tidal amplitudes in the Indian estuaries sampled was between 1.3 and 10.9 m. Haldia, Narmada and Mahisagar estuaries have a higher amplitude of tides (>2 m), while the rest of the estuaries are showing lower tidal amplitude (~ 2m) (Fig. 2). The variations in physical and biogeochemical properties are mainly controlled by semi diurnal tides.

3.1.1. Salinity and turbidity (SPM)

Existence of well mixed and unsteady state conditions in the Indian estuaries during peak discharge period were reported (Sarma et al., 2014; Sridevi et al., 2015; Bharati et al., 2019). Due to high magnitude of discharge, entire estuary is filled with freshwater with less spatial variability in salinity during discharge period (Sridevi et al., 2015). In contrast to peak discharge period, the salinity of estuarine waters was comparatively higher during the period of no discharge due to less rainfall, leading to drying of upstream river and closure of dam gates for preserving water for domestic and other commercial purposes. In addition, salinity showed significant spatial variability within the estuary during no discharge and it is mainly governed by tidal mixing. It was reported that salinity was one of the prominent key factors for influencing/distribution of biogeochemical properties such as nutrients, primary production, plankton metabolic rates, and plankton composition (Howarth et al., 2011). In order to understand the impact of variations in the biogeochemical properties of the estuary, study area was divided into upper (< 2), middle (2-15), and lower (15-34) estuarine regions with respect to salinity.

Temperature ranged between 21.4 and 32.0°C, did not show significant difference between upper to lower estuaries. Relatively warmer temperatures were observed in the upper (27.3°C) and middle estuaries (27.2°C) than lower estuaries (26.6°C) (Supplementary fig. 1). SPM ranged from 3.7 to 916 mg/l and relatively higher SPM values were observed in lower estuaries than upper and middle estuaries (Fig. 3). Combined action of local currents, wave action, mixing of surface sediment and their advection (Lucas, 2003) are the possible reasons for higher SPM in lower estuarine regions. The higher SPM was observed in Tapti and Sabarmathi estuaries, where the higher tidal amplitude occurs resulting in resuspension of surface sediments into the water column leading to higher concentration of SPM than other estuaries (Table 1). Positive relation is observed between SPM and salinity indicating tidal influence is enhancing through intrusion of seawater into the estuaries leading to resuspension of sediments (Supplementary Table 1).

3.1.2. Concentrations and ratios of nutrients

Gallegos (1992) stated that the conversion efficiency of nutrients into biomass and structuring effect on phytoplankton community depend upon both concentration and ratios of supplied nutrients. In the present study, dissolved inorganic nitrogen (DIN) concentrations ranged from 3.3 to 82.3, 2.7 to 27.6 and 1.5 to 59.8 μM in the upper, middle and lower estuaries, respectively (Fig. 3). A decreased trend was noticed in concentrations of DIN from upper to lower estuary (Fig. 3), except in Tapti, Narmada and Sabarmati (Table 1). Such high concentrations in the Tapti, Narmada and Sabarmati were due to discharge of sewages as high industrial activities are noticed on the bank of these estuaries. In addition to this, the tidal amplitude is also significantly high ($>7\text{m}$) that might lead to re-suspension of sediment resulting in increase in nutrient concentrations. Dissolved inorganic phosphorous (DIP) concentrations ranged from 1.2 to 9.8 μM with less variation within the estuary. Dissolved inorganic silicate (DISi) concentration ranged between 4.6 and 294.9 μM with relatively higher concentration in the upper estuary ($151.5 \pm 73.3 \mu\text{M}$) and middle ($84.4 \pm 62.5 \mu\text{M}$) than lower estuary ($66.9 \pm 52.4 \mu\text{M}$).

The N:P, Si:P and N:Si ratios were calculated to identify peculiarities in ecosystem dynamics and functioning with reference to nutrients (Bethoux et al. 2002). The nutrients ratios (N:Si:P) for optimal phytoplankton growth is 16:16:1 (Redfield 1963). N: P and N: Si ratios were always found below 16 and 1 in the Indian estuaries indicating that nitrogen is a limiting nutrient during no discharge period (Supplementary fig. 2). Previous studies in several Indian estuaries (Mandovi and Zuari (Ram et al., 2003), Hoogly (Mukhopadhyay et al., 2006), Cochin (Gupta et al., 2009) and Godavari estuaries (Sarma et al., 2010)) also noticed that nitrogen is a limiting nutrient during dry period. Si:P ratios were always lower than 16, is indicating that excess supply of phosphate to the estuary.

3.2. Variability in phytoplankton community structure in the Indian estuaries during no discharge period

3.2.1. Phytoplankton biomass and abundance

Relatively, higher phytoplankton biomass (represented by Chl-*a*) was observed in the upper (0.5-65.9 mg/m^3) and decreased towards middle (0.9-42.6 mg/m^3) and lower estuaries (0.4-22.5 mg/m^3) (Fig. 3). The lower concentrations of phytoplankton biomass in lower estuarine region was coincided with higher loads of SPM due to re-suspension of sediments, caused by tidal action, that declines light availability. Phytoplankton biomass $> 10 \text{ mg}/\text{m}^3$ was noticed in Cauvery, Krishna, Vellar and Ponniyaar estuaries due to high concentrations of DISi. Correlation analysis also showed that a significant positive relation between phytoplankton biomass and DISi (Supplementary Table 1).

Phytoplankton abundances varied between 0.2×10^5 and 55.2×10^5 cells/L in the Indian estuaries during no discharge period. The cell abundances varied from 0.7×10^5 to 40.2×10^5 cells/L, 0.2×10^5 to 55.2×10^5 cells/L and 0.3×10^5 to 14.1×10^5 cells/L in the upper, middle and lower estuary, respectively (Fig. 4). Relatively higher phytoplankton abundances was observed in upper and middle than lower estuarine region due to high SPM in the latter zone resulting from high tidal action (Fig. 4). No significant correlation was observed between SPM and phytoplankton abundance that may be due to grazing by zooplankton and also limitation of phytoplankton growth by nutrients. Phytoplankton did not seem to have a significant correlation with any of the variable factors as their growth and abundance is affected by the combined influence of several variables at a time (Supplementary Table 1).

Among the upper estuarine region estuaries, about 3 times higher phytoplankton abundances were observed of Nagavali, Penna, Ponnayaar and Vellar estuaries which consists of relatively lower SPM and higher concentrations of nutrients, than other estuaries where higher SPM and lower nutrients are noticed (Fig. 4). This study indicates that combination of nutrients and SPM controlled the variability in phytoplankton abundance in the upper estuarine region among Indian estuaries. A positive relation is observed between concentration of DISi and phytoplankton abundance ($r^2 = 0.4$; $n=13$; $p < 0.09$) in upper estuary while negative relation with SPM ($r^2 = 0.4$; $n = 15$; $p < 0.09$) further confirms their influence.

Higher phytoplankton abundance in the middle estuarine region was noticed in the Netravathi followed by Vellar estuaries compared to other Indian estuaries (Fig. 4). Comparatively, lower concentrations of SPM in Netravathi and higher concentrations of DIN in Vellar might be potential reason for such higher abundances. On the other hand, estuaries such as Bharatapuzha, Netravathi, Mandovi, Ponnayaar Rushikulya, CBW (Cochin backwaters) and Sabarmati estuaries displayed comparatively higher abundance in the lower estuarine region. These estuaries consist of lower SPM (except Ponnayaar) and higher phosphate concentrations (except Bharatapuzha and Netravathi). Salinity in all these estuaries were >20 indicating that concentrations of SPM, phosphate and salinity may be playing significant role on phytoplankton abundance in lower estuarine regions along the Indian estuaries. On the whole, higher phytoplankton abundances were mainly presented in upper estuarine region, it is about >26 Lakhs cells/L, where as lower abundances presented in lower estuarine region (Fig. 4)

3.2.2. Phytoplankton community structure

Nearly 100 phytoplankton species have been recorded belonging to six groups during no discharge period. In which, diatoms (31), dinoflagellates (8), green algae (40), blue-green algae (20), and chrysophytes (1) contributed during no discharge period in the Indian estuaries. The cell abundance of diatoms, dinoflagellates, green algae and blue-green algae ranged from 0.1×10^5 to 53.8×10^5 , 0 to 13.9×10^5 , 0 to 18.2×10^5 and 0 to 7.3×10^5 cells/L, respectively. Variation in terms of phytoplankton group dominance was observed along the salinity gradient in the Indian estuaries. Among the estuaries, *Dinobryon* sp. was found at only one station, upper estuarine region of Khali estuary, and these species contribution was also $< 0.1\%$. Diatoms are dominant group among the other groups and their contribution varied significantly within estuary and also among the Indian estuaries. For instance, in Ponnayaar, 99% of the phytoplankton abundance was contributed by diatoms in the upper estuary and has decreased to $\sim 25\%$ in the lower estuary (Fig. 5). In contrast, $\sim 40\%$ of phytoplankton abundance was contributed by diatoms in the upper estuary in Vaigai and CBW and it was increased to 70-80% in the lower estuary (Fig. 4). The least ($\sim 20\%$) contribution of diatoms were noticed in Ambalayaar, Mahisagar and Sabarmati in the upper estuarine region whereas Rushikulya, Vellar, Cauvery and Bharatapuzha in the middle and Krishna, Ponnayaar and Bharatapuzha in the lower estuary (Fig. 4). As a whole, the diatom group represented up to 60% of the phytoplankton community, with the green algae, blue-green algae and dinoflagellates making up rest of the community (Supplementary fig. 3). The diatom dominance decreased towards the upper estuarine region (lower salinities; 52%), where abundance of green algae and blue-green algae contributed significantly in the upper and middle estuary and their abundance decreased towards lower estuary. Contribution of dinoflagellates was high in the middle and lower estuarine region compared to upper estuary. Muylaert and Sabbe (1999) reported blue-green algae and green algae more tend to be in brackish water whereas dinoflagellates are more in the high saline water (Kies, 1997). Therefore salinity seems to be playing major role on distribution of different groups of phytoplankton in the Indian estuaries.

3.3. Impacts of salinity gradients on phytoplankton community structure during no discharge period

In estuaries where salinity often variable due to tides and river runoff, salinity is one of the key parameters along with nutrients for regulation of phytoplankton abundance and species assemblages. Bharathi et al. (2018a) found considerable changes in diversity indices and community structure of phytoplankton with respect to salinity gradients in the coastal Bay of Bengal during discharge period. In order to understand the influence of salinity changes on phytoplankton community, present data were pooled into three groups, upper, middle and lower estuary; dendrograms were drawn based on phytoplankton abundance.

3.3.1. Upper estuarine region (Low saline waters)

The dendrogram in the upper estuarine region (low saline) is divided into two major groups (group A and B) at 40% level (Fig. 6). These groups were mainly formed with reference to concentration of SPM and nutrients (Table 2). The estuaries grouped in group (A) were composed of higher phytoplankton abundance coincided with relatively lower SPM (11.6 mg/l; except Sabarmati) and higher concentrations of nutrients. These estuaries receive significant amount of domestic and industrial pollution than other estuaries, resulting in higher concentrations of nutrients and promoting higher phytoplankton abundances than other Indian estuaries. Diatoms, such as *Thalassiosira* spp. and *Paralia* spp., contributed significantly to Group A as they have opportunistic nature and grow in severe polluted region (Harding et al., 2004). Group B was divided into two sub groups B1 and B2 under 50% level due to concentrations of DIN (82.3 μ M and 15.2 μ M, respectively) and SPM (3.7 and 34.8 mg/l, respectively). Group B1 consists of only one estuary, Mahisagar, which is dominated with *Chroococcus* spp. (blue-green algae) due to heavy loads of sewage disposal, which favored the growth of pollution indicating algae. The estuary receives high pollutants which are indicated by the highest concentration of DIN (Table 2). Group B2 mainly consists of a mixture of algae and mainly dominated by *Melosira* spp., *Navicula* spp., *Nitzschia* spp., *Thalassiosira* spp. and *Chlorella* spp. B2 group has lower phytoplankton abundance due to higher SPM as evident by the inverse correlation between SPM and phytoplankton abundance ($r^2=0.8$; $p<0.01$) in estuaries viz. Mahanadi, Vamsadhara, CBW, Bharatapuzha, Netravathi, Kali and Narmada. Moreover two taxa (*Navicula* spp. and *Nitzschia* spp.) have been identified during no discharge period, indicating their euryhaline and eurythermal nature. In upper estuarine region, diatoms and green algae are the dominant phytoplankton groups. Green algae may be out competed than other phytoplankton groups under non-limited nutrient conditions and freshwater ecosystems (Jensen et al., 1994).

In upper estuarine region, lower diversity indices values are coincided with lower phytoplankton abundance, where as higher diversity indices values are coincided with higher phytoplankton abundance, except Penna and Mahisagar where exceptionally high phytoplankton abundance coincided with lower diversity indices values. Pollution stress reduces the number of algal species but increases the dominance (Manna et al., 2012). It was evidenced for Mahisagar, which was having high DIN concentrations as this estuary receives higher rate of industrial pollution, displayed low diversity with high abundance of blue-green algae.

3.3.2. Middle estuarine region (Brackish waters)

The dendrogram in the middle estuarine region (brackish water) is divided into two groups with 40% similarity (Fig. 6). Between these two groups, significant variations were not observed in the environmental parameters except Si:P, which is higher in the group A (24.5; n=8) than group B (11.6; n=8) and meso zooplankton abundances is lower in the group A (235; n=4) than group B (371; n=6) (Table 2). Due to high residence time of water during no discharge period, zooplankton grazing plays significant role on controlling phytoplankton abundances in the estuarine ecosystem (Venkataramana et al., 2017; Bharathi et al., 2018). In middle estuarine region, diatoms and blue-green algae are the dominant phytoplankton groups. A higher abundance of blue green algae occurred in the middle estuarine region rather than the upper and lower estuarine regions, which could be attributed to lower DIN concentrations (than upper estuarine region) and decreased tidal effect (from lower estuarine region). Mostly colonial blue-green algae were observed, as they can store nitrogen and utilize under low N:P conditions (Rocha et al., 2002). Moreover, longer residence time of estuarine ecosystem promotes the occurrence of blue-green algae during no discharge period in middle estuarine region.

Higher values of diversity indices are coincided with higher phytoplankton abundances in middle estuarine region except Bharatapuzha estuary. Highest percentage of dinoflagellates were noticed only at Bharatapuzha in middle estuarine region, where it contributed ~70% to the phytoplankton abundance. No significant differences were found in the Bharatapuzha compared to other estuaries, except higher phosphate concentration than nitrate. Lower elemental ratio of N:P, which is resulted from excess phosphate discharge than nitrate might have supported to increase dominance of dinoflagellates followed by diatoms. Bharathi et al. (2019) also reported that dinoflagellate dominance due to variations in elemental ration of N:P in Indian estuaries along southwest coast of India.

3.3.3. Lower estuarine region (high saline waters)

In lower estuarine region at 40% similarity, dendograms formed two groups (Fig. 6). These groups were mainly formed with reference to concentrations SPM, composition of nutrients and meso zooplankton abundance (Table 2). For instance, meso zooplankton abundance was almost double in group A (546 organisms/m³; except Krishna estuary) than group B (304 organisms/m³) resulting in higher grazing pressure on phytoplankton in the former than latter group. Phytoplankton abundance exhibited inverse correlation with SPM ($r^2 = 0.7$; n=10; $p < 0.05$) indicating that higher turbidity limits the light availability for phytoplankton growth. Diatoms are predominant phytoplankton group in most of the estuaries in lower estuarine region during no discharge period. Salinity has a direct influence on

the distribution of diatoms, which supports the predominance the group than other group (Redekar and Wagh, 2000). Moreover, the disappearance of green algae and the drop in phytoplankton abundance from upper to lower estuaries may be governed by decrease in salinity and increasing grazing pressure.

Lower diversity was recorded in estuaries, such as Tapti and Narmada, where lower phytoplankton abundances are observed due to higher amplitude of tides resulting in re-suspension of sediments. Higher dominance and lower diversity were observed in estuaries like Krishna and Bharatapuzha (high dominance of *Aphanotheca* spp. in Krishna and *Peridinium* spp. in Bharatapuzha) due to variations in nutrient concentrations and their elemental ratios.

3.4. *Factors controlling phytoplankton community along Indian estuaries during no discharge period*

The factors controlling phytoplankton distribution in estuarine ecosystems is myriad and it is probable that no single factor is responsible (Rochelle-Newall et al., 2011). Anthropogenic stressors play fundamental role in shaping phytoplankton structure (Paerl et al., 2010) and influences phytoplankton diversity (Ptacnik et al., 2008). In order to understand the factors controlling the phytoplankton community structure along the Indian estuaries, principal component analysis was performed (Fig. 7). Factors 1 and 2 explained ~60% (41% and 15% individually) of the total variance, and revealed a strong positive loading of SPM, salinity and grazers (zooplankton), and a strong negative loading of phytoplankton. This indicates that the phytoplankton growth is controlled by decrease in light penetration to the water column due to increase in SPM load, and zooplankton grazing. The close association between nutrients (mainly DIP and DISi) and phytoplankton abundance indicates that availability of nutrient supported higher phytoplankton abundances and diversity, particularly in upper estuarine region. Decline in phytoplankton abundances and diversity from upper to lower estuary was caused by increase in salinity, SPM and grazers abundance. The positive correlation between salinity and zooplankton abundance revealed that increase in salinity seems to accelerate the zooplankton growth.

Estuaries contain surplus amount of nutrients in Indian estuaries, hence, there is no scarcity in availability of nutrients and Indian estuaries act as a strong source of nutrients to the adjacent coastal waters (Krishna et al., 2016). For instance, DISi concentrations were mostly above 2 μM in all Indian estuaries resulting in dominant diatom growth. Though upstream river brings some amount of nutrients to the estuary, regenerated nutrients in the water column and exchanges at the groundwater and sediment water interface are important sources of nutrients to Indian estuaries during no discharge period (Sarma et al., 2010). Therefore, the abundance and diversity of the phytoplankton in the Indian estuaries are mainly controlled by light availability due to turbidity and zooplankton grazers.

3.5. Phytoplankton succession along environmental gradients during no discharge period

Freshwater and marine species experience severe osmotic stress for salinity gradients and salinity act as a lethal barrier for phytoplankton species (Kies, 1997). From upper to lower estuary, different groups and taxa of phytoplankton are adapted to certain salinity range (Kies, 1997). In addition to this, phytoplankton growth rates vary significantly due to water column height, turbidity, nutrient concentrations and grazing pressure (Lucas et al., 1999a; 1999b). Upper estuarine region composed of diatoms followed by green algae, where as blue-green algae replaced with green algae in middle estuarine region. Because of their stenohaline nature, most of the green algae was limited to upper estuarine region (Fig. 8). Lower N:P ratios in middle estuarine region compared with upper and lower estuarine region, resulting from higher concentrations of DIP (lower DIN) due to desorption of DIP from sediments due to increase in salinity and pH, tend to be more favorable to blue-green algae abundance in middle estuarine region. Diatoms are most dominant and abundant group in lower estuarine region along the Indian estuaries during no discharge period. Even though, higher silicate concentrations were found in the upper estuarine region, diatoms abundance was not significantly higher in the upper than lower estuary. It is because most marine diatoms have lower demand for silicate than fresh water diatom species (Paasche, 1980; Sommer, 1988; Conley et al., 1989).

The list of dominating species in the Indian estuaries during no discharge period were presented in Table 3. Upper estuarine region exhibited the greatest diversity owing to the presence of major algal categories like the diatoms in addition to the green algae and blue-green algae (Supplementary fig. 4). While middle estuarine region shows low diversity due to few dominant species of short stress-tolerant, euryoecious, short lived organisms, which occurs in high numbers and mostly competition occurs between intraspecific organisms than interspecific organisms (McLusky and Elliott, 2004). It is still unknown which factors play a primary role in shaping the patterns of natural biological diversity that allow more species to be either facilitated or excluded from communities as a result of environmental fluctuations. (McLusky and Elliott, 2004). *Navicula* spp. and *Nitzschia* spp. have been identified during the entire study period, indicating their euryhaline and eurythermal nature. These euryhaline species able to regulate their intracellular osmotic pressure and grow at different salinity conditions (Flameling and Kromkamp, 1994; Orive et al., 1998; Erdmann and Hagemann, 2001; Roubex et al., 2008) (Fig. 9). In upper estuarine region, phytoplankton made a highly significant contribution of heterogeneity particularly by diatoms. Middle and lower estuarine region (include all groups in clusters) was mainly dominated by *Thalassiosira* spp. Particularly at high saline regions, the dominance of single taxa (*Thalassiosira* spp.) was more common. Cloern and Dufford (2005) noticed dominance of *Thalassiosira* spp. is confined to near coastal domains in San Francisco Bay. Due to lack

of osmo-regulatory mechanism, green algae highly abundant and restricted to lower salinity ranges (Fig 8). During no discharge period, green algae predominated and occupied 40% followed by diatoms (32%) in entire estuary. The dominance order of green algae in present study is *Desmodesmus* spp.> *Scenedesmus* spp.> *Chlorella* spp.> *Coelastrum* spp.> *Closterium* spp.> *Franceia* spp.> *Eudorina* spp.> *Monoraphidium* spp.> *Tetraspora* spp. Majority of the pennales appeared in freshwater zone while reverse is the case for the centrales. The order of dominance of the diatoms is: *Thalassiosira* spp.> *Navicula* spp.> *Nitzschia* spp.> *Achnanthes* spp. Members of the blue-green algae made up to 19% of the total phytoplankton and representative genera include *Aphanotheca* spp., *Chroococcus* spp., *Merismopedia* spp., *Aphanocapsa* spp., *Snowella* spp., *Nostoc* spp. and the dinoflagellates accounted for 8.5% of the taxa and next to the blue-green algae in proportions. The representative genera include *Peridinium* spp. The chrysophyta contributed less than one per cent and represented by *Dinobryon* spp.

3.6. Variability in phytoplankton abundance during discharge and no discharge periods

The variability in phytoplankton community structure in Indian estuaries during discharge period was explained in detail in Bharathi and Sarma (2019), however, it is explained in brief here. Despite high nutrient levels, the lowest phytoplankton abundance were noticed in high discharge estuaries, while highest phytoplankton abundance were noticed in moderate and low discharge estuaries due to longer residence time with brackish salinity conditions and low SPM in the latter estuaries. The phytoplankton community response is consistent throughout the estuary during peak discharge period. Unlike peak discharge period, when variations within estuary (upper estuary to lower estuary) are much lower than the variations among estuaries, contrary to that can be noticed during no discharge period. In comparison to the discharge period, high abundances were observed in most of the estuaries during no discharge period, particularly in Haldia, Baitarani, Mahanadi, Godavari, Tapti, Sabarmati, and Narmada, which received high discharge during the discharge period (Supplementary fig. 5). During discharge period in addition to SPM limited photic depth, low flushing time and decreased water column stability did not favour phytoplankton growth. Reduced river discharge and increased tidal force can promote a stratified, stable, and clearer water column, which can support high phytoplankton abundances during the no discharge period (Acharya et al. 2012). In present study, high phytoplankton diversity noticed in discharge period than no discharge period in most of the estuaries (Supplementary fig. 6). Changes in species composition reflecting species preferences for different salinity ranges, as well as phytoplankton from fresh water sources could be reason for this (Qasim et al., 1972; Devassy and Goes, 1988; Krishna Kumari et al., 2002).

4. Summary and conclusions

The summary of the physico-chemical conditions along salinity gradients and biological responses during no discharge period in the Indian estuaries are given in Figure 9. Salinity exhibited significant variations from upper to lower estuary due to saline water intrusion by tides. Nutrients showed decreased from upper to lower estuary, and their concentrations are above the limiting levels for phytoplankton along Indian estuaries during no discharge period. Lower phytoplankton abundances are coincided with higher SPM load in lower estuarine region due to tidal activity resulting in re-suspension of sediments and it is higher in macro than micro tidal estuaries. Zooplankton abundance is controlling phytoplankton abundance in the middle and lower estuarine regions when SPM load is low. Zooplankton showed their higher abundances in high saline zones associating with high contribution of diatoms. Though high phytoplankton abundance was presented in low saline regions, decreasing trend was noticed in zooplankton abundances from lower estuarine region to upper estuarine region. It may be due to less preference of freshwater algae for grazing by zooplankton as they are colonial and unpalatable in nature.

The upper estuarine regions of certain estuaries such as Nagavali, Vellar, Sabarmati, Penna and Ponnayaar show high abundance because these estuaries receive significant amount of domestic and industrial effluents that promote high phytoplankton abundance. Phytoplankton composition significantly varied with respect to salinity gradients. Green algae and diatoms dominated in the upper estuary, diatoms and blue-green algae were abundant in the middle estuary and diatoms alone were prominent in the lower estuarine region. In addition to green algae, diatoms are also displayed high heterogeneity, for instance, *Melosira* spp., *Thalassiosira* spp., *Navicula* spp. and *Nitzschia* spp. are dominant in upper estuarine region, while *Thalassiosira* spp. is mainly dominated in the middle and lower estuarine regions. At high salinity regions, species diversity generally becomes low as high salinities are lethal for many phytoplankton. Compared to upper estuarine region, high dominance was found in the estuarine region due to mesohaline conditions are conducive for high growth of the dominant species. This study suggests that, in addition to salinity gradients, tidal influence and anthropogenic activities also influenced significantly on the phytoplankton community structure due to modifications in SPM, nutrients composition and grazers abundance. The negligible discharge and dominance of sea water for longer time, whether natural (monsoon variability related) or artificial (dam construction on rivers or inter-linking rivers), may cause eutrophication consequently alters the health of Indian estuaries. In addition to health of the estuaries, considerable modification may occur in phytoplankton functional groups and diversity and it may have significant impact on secondary and tertiary producers. This hypothesis must be tested in further using observations, remote sensing sensor

data and modeling. Long-term time-series observations are highly essential to understand possible modification in the future due to inter-linking rivers and new dams proposed over the Indian rivers.

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Table 1 Variations in physico-chemical and biological parameters in Indian estuaries during no discharge period.

		Temperature	Salinity	SPM	DIN	DIP	DISi	Chl-a
Upper Estuary	Mahanadi	25.3	2.3	12.0	5.0	3.5	53.2	4.6
	Nagavali	23.6	0.2	5.0	9.7	9.8	118.5	5.7
	Vamsadhara	27.4	1.2	12.3	3.8	5.2	249.6	2.9
	Penna	27.2	0.5	7.0	40.7	7.5	89.4	2.4
	Ponnayaar	28.9	0.5	7.3	3.5	4.4	201.5	15.9
	Vellar	28.6	2.2	27.0	25.0	5.0	256.4	65.9
	Ambalayaar	27.3	2.0	27.0	7.7	3.1	144.8	0.9
	Vaigai	29.6	0.2	65.0	10.4	3.5	157.2	3.9
	CBW	30.4	0.3	62.7	22.0	2.6	69.8	
	Bharatapuzha	32.0	0.4	14.7	3.3	4.8	105.7	
	Netravathi	31.1	0.6	4.7	4.9	3.9	96.1	1.7
	Kali	26.2	0.7	62.7	51.3		151.3	
	Zuari	27.0	0.6	68.7	11.0	6.5	57.6	1.0
	Narmada	23.0	0.2	18.0	32.9	5.0	230.0	0.5
	Sabarmati	25.4			39.0	7.0	165.7	8.7
Mahisagar	21.7	0.0	3.7	82.3	4.6	277.1		
Middle estuary	Haldia	22.1	4.2	78.0	27.6	4.9	59.0	8.6
	Subarnarekha	23.2	4.4	25.5	6.8	4.1	57.5	9.7
	Baitarani	22.9	10.7	35.5	15.4	3.2	45.8	4.6
	Mahanadi	25.0	3.7	9.7	4.5		47.3	4.7
	Rushikulya	26.4	17.3	27.7	9.2	7.1	44.3	1.6
	Godavari	26.7	7.2	30.0		2.0	70.0	
	Krishna	26.2	10.1	55.0	4.6	1.7		42.6
	Penna	27.6	8.4	17.0	11.4	4.0	79.2	3.3
	Vellar	29.5	3.4	32.0	25.3	5.4	294.9	12.2
	Cauvery	27.8	6.3	25.0	8.5	6.3	131.4	23.4
	Vaigai	28.9	9.6	59.0	4.7		129.4	6.8
	CBW	29.9	11.3	20.0	6.1	2.9	68.5	2.1
	Chalakudi	31.2	3.3	21.3	3.9	2.8	60.9	
	Bharatapuzha	31.4	13.7	22.0	3.2	6.1	75.3	
	Netravathi	29.3	5.9	12.7	2.7	2.5	94.3	1.6
Zuari	28.1	14.6	20.0	12.5	6.0	39.1	0.9	
Mandovi	28.2	8.4	7.3	16.0		54.1		
Lower estuary	Baitarani	23.0	21.9	82.0	7.6	2.6	18.0	1.1
	Mahanadi	24.7	15.6	24.7	6.6	8.5	4.6	3.7
	Rushikulya	26.3	21.6	26.3	4.5		49.9	2.9
	Vamsadhara	26.1	28.1	29.7	5.5	7.3	25.1	1.8
	Godavari	25.7	29.1	47.0		1.2	15.0	

Krishna	25.2	26.5	95.0	13.3	2.3	33.9	3.6
Ponnayaar	28.0	16.0	184.0		7.0	199.5	22.5
Vellar	28.9	22.9	92.0	11.5	4.3	69.6	16.5
Cauvery	27.3	27.6	132.0	8.5	6.3	131.4	3.6
Vaigai	30.2	20.9	85.0	13.9	2.9	125.6	2.8
CBW	29.6	23.5	78.0	4.9	2.2	34.6	0.4
Chalakudi	29.9	32.0	12.0	3.7	3.2	53.3	
Bharatapuzha	30.9	23.6	44.7	1.5	3.6	57.9	
Netravathi	29.2	33.7	60.7	5.0	2.7	37.9	
Mandovi	26.6	30.2	51.3	6.4		25.7	0.5
Tapti	23.2	26.7	916.0	41.6	7.5	125.5	
Narmada	23.2	14.7		45.9	7.5	108.2	
Sabarmati	21.4	26.9	334.0	59.8	6.3	88.8	

Table 2 Variations in hydrographic properties, environmental variables and phytoplankton composition in Indian estuaries during no discharge period. Groups (First column) are made from cluster analysis (figure 6).

Salinity	Groups	SPM (mg/l)	NO ₃ (μM)	PO ₄ (μM)	SiO ₄ (μM)	Si:P	Abundance (Cells/l)	Abundant group	Genus example	Zooplankton (org.m ³)
Upper estuary <2	A	11.6	23.6	6.7	166.3	29.1	27.2 x 10 ⁵	Diatoms	<i>Thalassiosira</i> <i>Paralia</i>	91
	B	3.7	82.3	4.6	277	60.2	7.5 x 10 ⁵	Blue-green algae	<i>Chroococcus</i>	ND
	C	34.8	15.8	4.2	131.5	31.5	2.2 x 10 ⁵	Diatoms and Green algae	<i>Nitzschia</i> <i>Melosira</i> <i>Thalassiosira</i> <i>Chlorella</i> <i>Navicula</i>	48
Middle estuary 2-15	A	27.7	11.6	4.0	98.6	27.9	15.3 x 10 ⁵	Diatoms	<i>Thalassiosira</i> <i>Navicula</i>	235
	B	30.7	9.1	4.5	70.3	14.0	1.4 x 10 ⁵	Diatoms and Blue-green algae	<i>Thalassiosira</i> <i>Nostoc</i>	371
Lower estuary >15	A	151.5	15.8	4.9	64.5	15.1	1.2 x 10 ⁵	Diatoms	<i>Thalassiosira</i>	476
	B	111.3	13.7	4.4	70.6	17.6	9.3 x 10 ⁵	Diatoms	<i>Thalassiosira</i>	304

Table 3 List of dominant phytoplankton species in upper, middle and lower regions along the Indian estuaries during no discharge period.

Estuary		Dominant species (>10%)
Upper estuary	Mahanadi	<i>Thalassiosira</i> spp., <i>Eudorina</i> spp.
	Vamsudhara	<i>Thalassiosira</i> spp., <i>Nitzschia</i> spp.
	Nagavali	<i>Thalassiosira</i> spp., <i>Amphora</i> spp., <i>Navicula</i> spp., <i>Chlorella</i> spp., <i>Scenedesmus</i> spp.
	Penna	<i>Acnantes</i> spp.
	Ponnair	<i>Paralia</i> spp., <i>Acnantes</i> spp., <i>Synedra</i> spp.
	Vellar	<i>Leptocylindrus</i> spp., <i>Thalassiosira</i> spp., <i>Desmodesmus</i> spp., <i>Scenedesmus</i> spp.
	Ambuliyar	<i>Thalassiosira</i> spp., <i>Peridinium</i> spp., <i>Chlorella</i> spp., <i>Desmodesmus</i> spp.
	Vaigai	<i>Thalassiosira</i> spp., <i>Navicula</i> spp., <i>Aphanocapsa</i> spp., <i>Scenedesmus</i> spp., <i>Merismopedia</i> spp.
	CBW	<i>Melosira</i> spp., <i>Aphanocapsa</i> spp.
	Bharatkulya	<i>Navicula</i> spp., <i>Nitzschia</i> spp., <i>Peridinium</i> spp., <i>Gloeocapsa</i> spp.
	Nethravathi	<i>Melosira</i> spp., <i>Synedra</i> spp.
	Khali	<i>Acnantes</i> spp., <i>Navicula</i> spp., <i>Desmodesmus</i> spp., <i>Franceia</i> spp., <i>Scenedesmus</i> spp.
	Zuari	<i>Coscinodiscus</i> spp. <i>Thalassiosira</i> spp.
	Narmada	<i>Leptocylindrus</i> spp., <i>Nitzschia</i> spp., <i>Chlorella</i> spp., <i>Desmodesmus</i> spp.
	Mahisagar	<i>Chroococcus</i> spp.
Sabarmathi	<i>Closterium</i> spp.	
Middle estuary	Haldia	<i>Thalassiosira</i> spp., <i>Snowella</i> spp.
	Subernalekha	<i>Coscinodiscus</i> spp., <i>Thalassiosira</i> spp., <i>Peridinium</i> spp., <i>Chlorella</i> spp.
	Baitarani	<i>Melosira</i> spp., <i>Thalassiosira</i> spp., <i>Snowella</i> spp.
	Mahanadi	<i>Thalassiosira</i> spp., <i>Acnantes</i> spp., <i>Navicula</i> spp., <i>Franceia</i> spp.
	Rushikulya	<i>Cyclotella</i> spp., <i>Eudorina</i> spp., <i>Aphanocapsa</i> spp., <i>Nostoc</i> spp.
	Godavari	<i>Navicula</i> spp., <i>Peridinium</i> spp., <i>Merismopedia</i> spp.
	Krishna	<i>Thalassiosira</i> spp., <i>Acnantes</i> spp., <i>Gloeotheca</i> spp., <i>Pelagloea</i> spp.
	Penna	<i>Thalassiosira</i> spp., <i>Nitzschia</i> spp.
	Vellar	<i>Chodatella</i> spp., <i>Merismopedia</i> spp.
	Cauvery	<i>Golenkinia</i> spp., <i>Gloeocapsa</i> spp., <i>Holopedium</i> spp.
	Vaigai	<i>Thalassiosira</i> spp.
	CBW	<i>Navicula</i> spp., <i>Merismopedia</i> spp.
	Chalakudi	<i>Thalassiosira</i> spp., <i>Carteria</i> spp., <i>Chlorella</i> spp., <i>Anabaena</i> spp.
	Bharatkulya	<i>Thalassiosira</i> spp., <i>Peridinium</i> spp., <i>Docidium</i> spp.
	Nethravati	<i>Paralia</i> spp., <i>Thalassiosira</i> spp., <i>Navicula</i> spp.
Mandovi	<i>Coscinodiscus</i> spp., <i>Thalassiosira</i> spp., <i>Gloeotheca</i> spp.	
Zuari	<i>Thalassiosira</i> spp.	
Lower	Baitarani	<i>Thalassiosira</i> spp., <i>Nitzschia</i> spp.
	Mahanadi	<i>Thalassiosira</i> spp.
	Rushikulya	<i>Thalassiosira</i> spp., <i>Nitzschia</i> spp.
	Vamsudhara	<i>Thalassiosira</i> spp., <i>Tetraedon</i> spp.

Godavari	<i>Chaetoceros</i> spp., <i>Thalassiosira</i> spp., <i>Navicula</i> spp., <i>Nitzschia</i> spp.
Krishna	<i>Aphanotheca</i> spp.
Ponnayar	<i>Thalassiosira</i> spp., <i>Scenedesmus</i> spp.
Vellar	<i>Thalassiosira</i> spp., <i>Navicula</i> spp., <i>Scripsiella</i> spp.
Cauvery	<i>Helicotheca</i> spp., <i>Thalassiosira</i> spp., <i>Peridinium</i> spp., <i>Trochisia</i> spp.
Vaigai	<i>Thalassiosira</i> spp., <i>Navicula</i> spp., <i>Peridinium</i> spp., <i>Merismopedia</i> spp.
CBW	<i>Thalassiosira</i> spp., <i>Thalassionema</i> spp.
Chalakudi	<i>Thalassiosira</i> spp.
Bharatkulay	<i>Peridinium</i> spp.
Nethravati	<i>Thalassiosira</i> spp., <i>Nitzschia</i> spp., <i>Thalassiothrix</i> spp.
Mondovi	<i>Thalassiosira</i> spp.
Tapati	<i>Thalassiosira</i> spp., <i>Nitzschia</i> spp.
Narmada	<i>Thalassiosira</i> spp., <i>Navicula</i> spp.
Sabarmati	<i>Thalassiosira</i> spp., <i>Amphiprora</i> spp., <i>Nitzschia</i> spp.

Figure Legend

Fig. 1 Map showing estuaries sampled in this study. Map also showing upper estuary, middle estuary and lower estuary regions in different symbols.

Fig. 2 Variability in tidal height in the Indian estuaries

Fig. 3 Variability in dissolved inorganic nutrients (DIN, DIP, DISi), SPM, salinity and phytoplankton biomass in upper, middle and lower regions along the Indian estuaries during no discharge period. (Number of samples (n) for DIN is 16, 16, and 16, DIP is 15, 14, and 16, DISi is 16, 17, and 18, salinity is 15, 17, and 18, SPM is 15, 17, and 17, and Chl-a is 12, 13, and 11 in upper, middle, and lower estuarine regions, respectively).

Fig. 4 (a) Map is showing distribution of phytoplankton abundance in different estuaries in upper, middle and lower regions along the Indian estuaries during no discharge period. (b) Variability in phytoplankton abundance in upper (n=16), middle (n=17) and lower (n=18) regions along the Indian estuaries during no discharge period. (C) Frequency distribution of phytoplankton abundance in upper, middle and lower regions along the Indian estuaries during no discharge period.

Fig. 5 Variability in phytoplankton groups composition in Indian estuaries upper, middle and lower regions in Indian estuaries during no discharge period

Fig. 6 Dendrogram is showing similarity of estuaries in terms of phytoplankton abundance during no discharge period in (a) Upper estuarine region (b) Middle estuarine region and (c) Lower estuarine region

Fig. 7 PCA biplot for environmental and biological variables along Indian estuaries during no discharge period. Parameters represented in short forms. Those are Diversity (Div.), DISi, DIP, DIN, phytoplankton abundance (Phy.), diatoms (Dia.), green algae (Gre.), blue-green algae (Blu.), zooplankton abundance (Zoo.), SPM, and salinity (Sal.). U, M and L letters are representing upper, middle and lower estuaries

Fig. 8 Salinity ranges of each phytoplankton and the levels at which they were present during no discharge period. Blue colour bars are representing diatoms, red colour for dinoflagellates, green colour for green algae and purple colour for blue-green algae.

Fig. 9 Schematic diagrams showing different physical, chemical conditions and biological responses in upper, middle and lower regions along the Indian estuaries during no discharge period. Size of the pie chart is representing variations in phytoplankton abundance.

Fig. 1 Map showing estuaries sampled in this study. Map also showing upper estuary, middle estuary and lower estuary regions in different symbols.

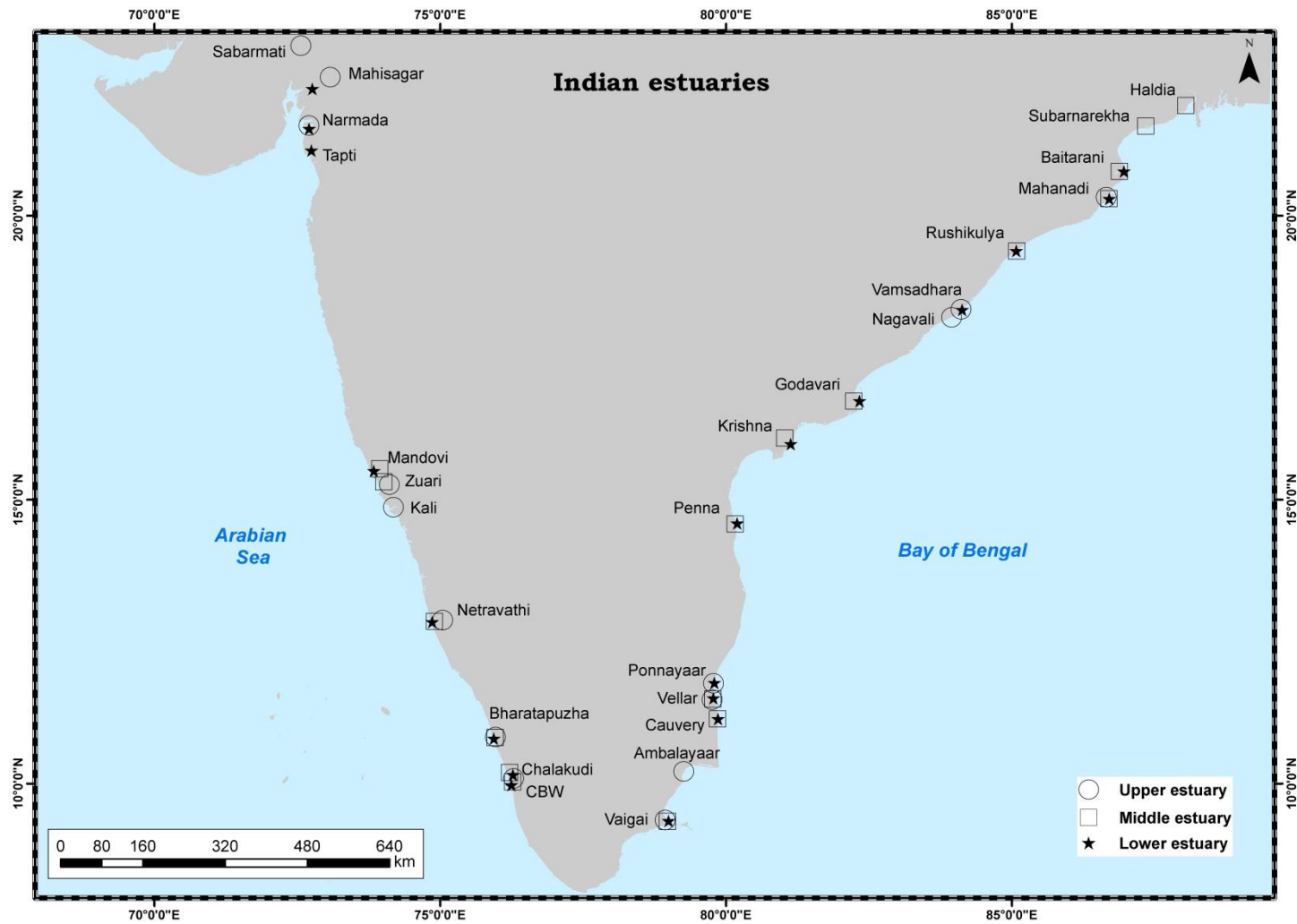


Fig. 2 Variability in tidal height in the Indian estuaries

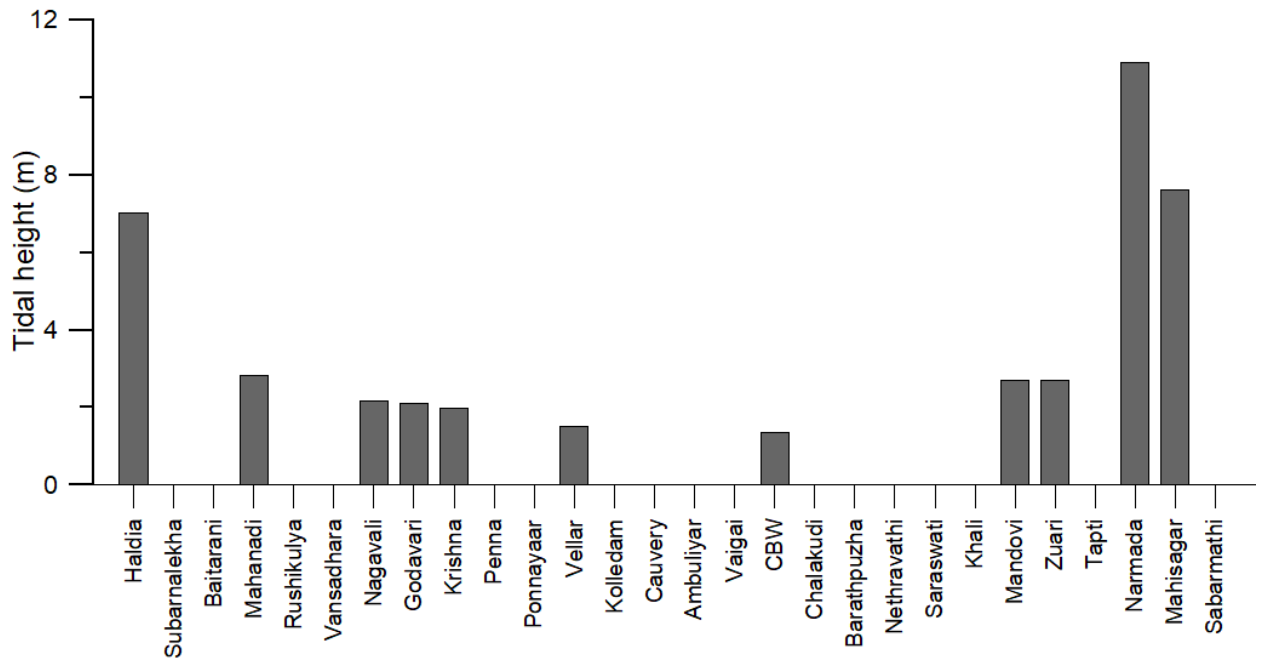


Fig. 3 Variability in dissolved inorganic nutrients (DIN, DIP, DISi), SPM, salinity and phytoplankton biomass in upper, middle and lower regions along the Indian estuaries during no discharge period. (Number of samples (n) for DIN is 16, 16, and 16, DIP is 15, 14, and 16, DISi is 16, 17, and 18, salinity is 15, 17, and 18, SPM is 15, 17, and 17, and Chl-a is 12, 13, and 11 in upper, middle, and lower estuarine regions, respectively)

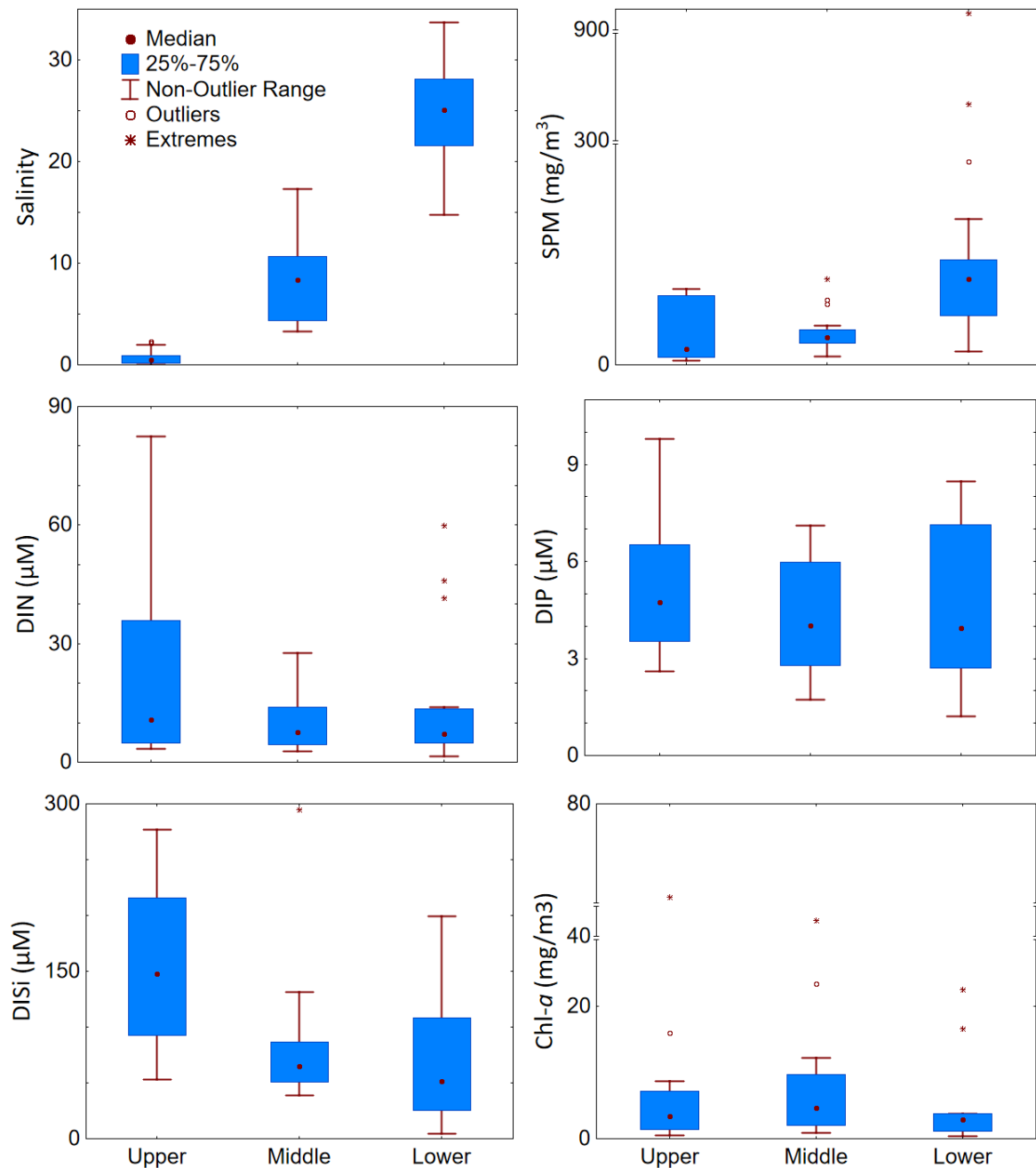


Fig. 4 (a) Map is showing distribution of phytoplankton abundance in different estuaries in upper, middle and lower regions along the Indian estuaries during no discharge period. (b) Variability in phytoplankton abundance in **upper (n=16)**, **middle (n=17)** and **lower (n=18)** regions along the Indian estuaries during no discharge period. (C) Frequency distribution of phytoplankton abundance in upper, middle and lower regions along the Indian estuaries during no discharge period.

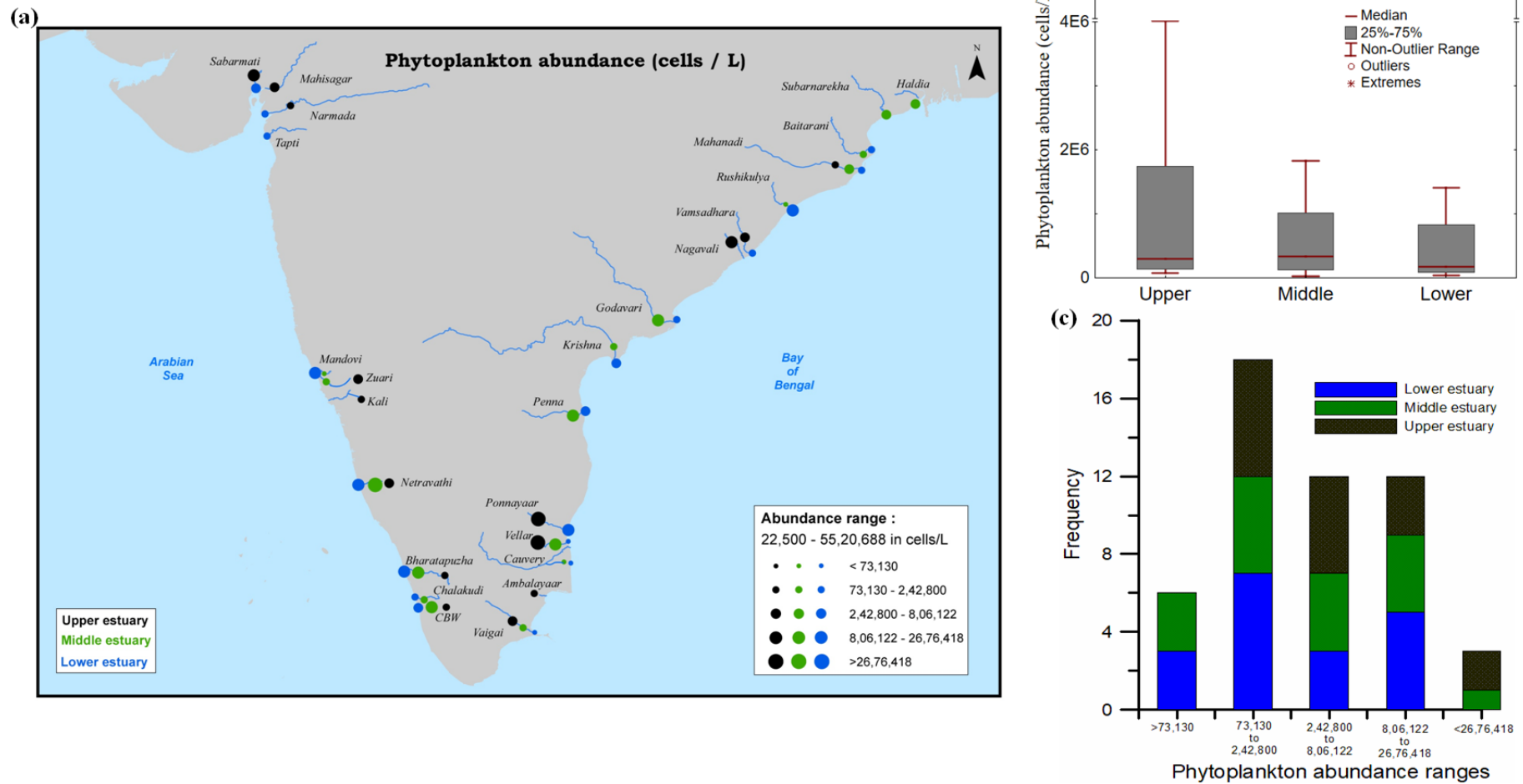


Fig. 5 Variability in phytoplankton groups composition in Indian estuaries upper, middle and lower regions in Indian estuaries during no discharge period

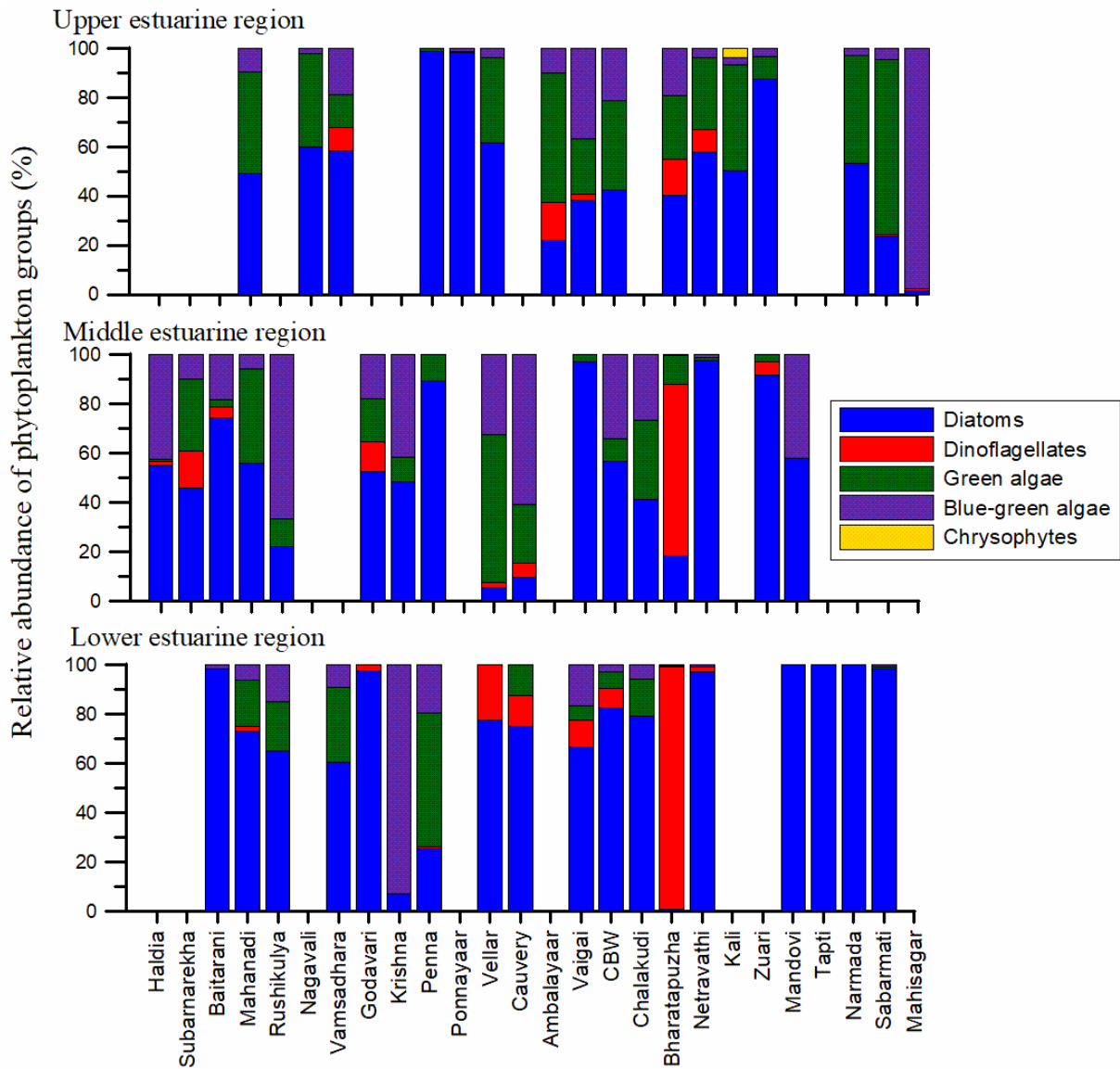


Fig. 6 Dendrogram is showing similarity of estuaries in terms of phytoplankton abundance during no discharge period in (a) Upper estuarine region (b) Middle estuarine region and (c) Lower estuarine region

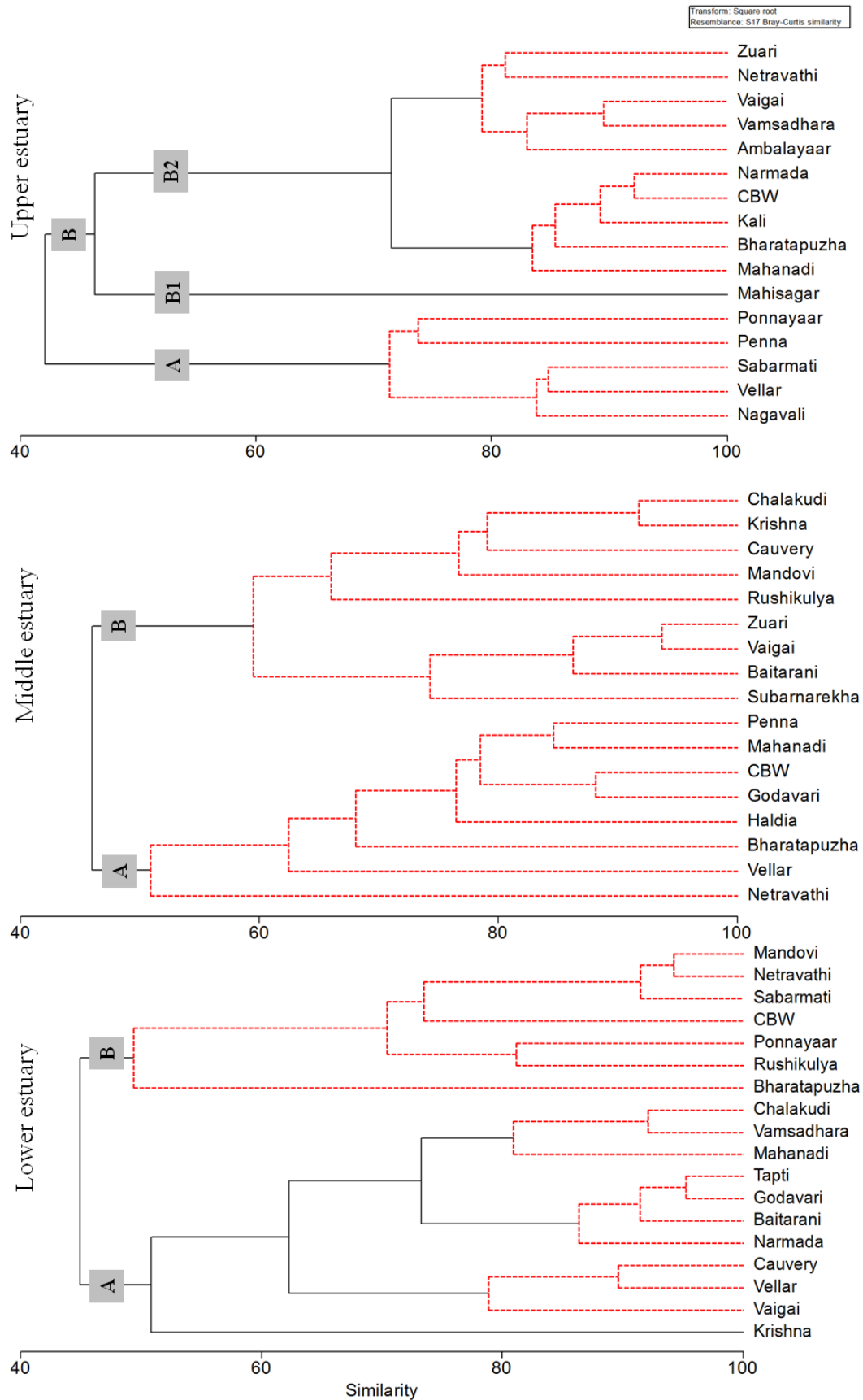


Fig. 7 PCA biplot for environmental and biological variables along Indian estuaries during no discharge period. Parameters represented in short forms. Those are Diversity (Div.), DISi, DIP, DIN, phytoplankton abundance (Phy.), diatoms (Dia.), green algae (Gre.), blue-green algae (Blu.), zooplankton abundance (Zoo.), SPM, and salinity (Sal.). U, M and L letters are representing upper, middle and lower estuaries

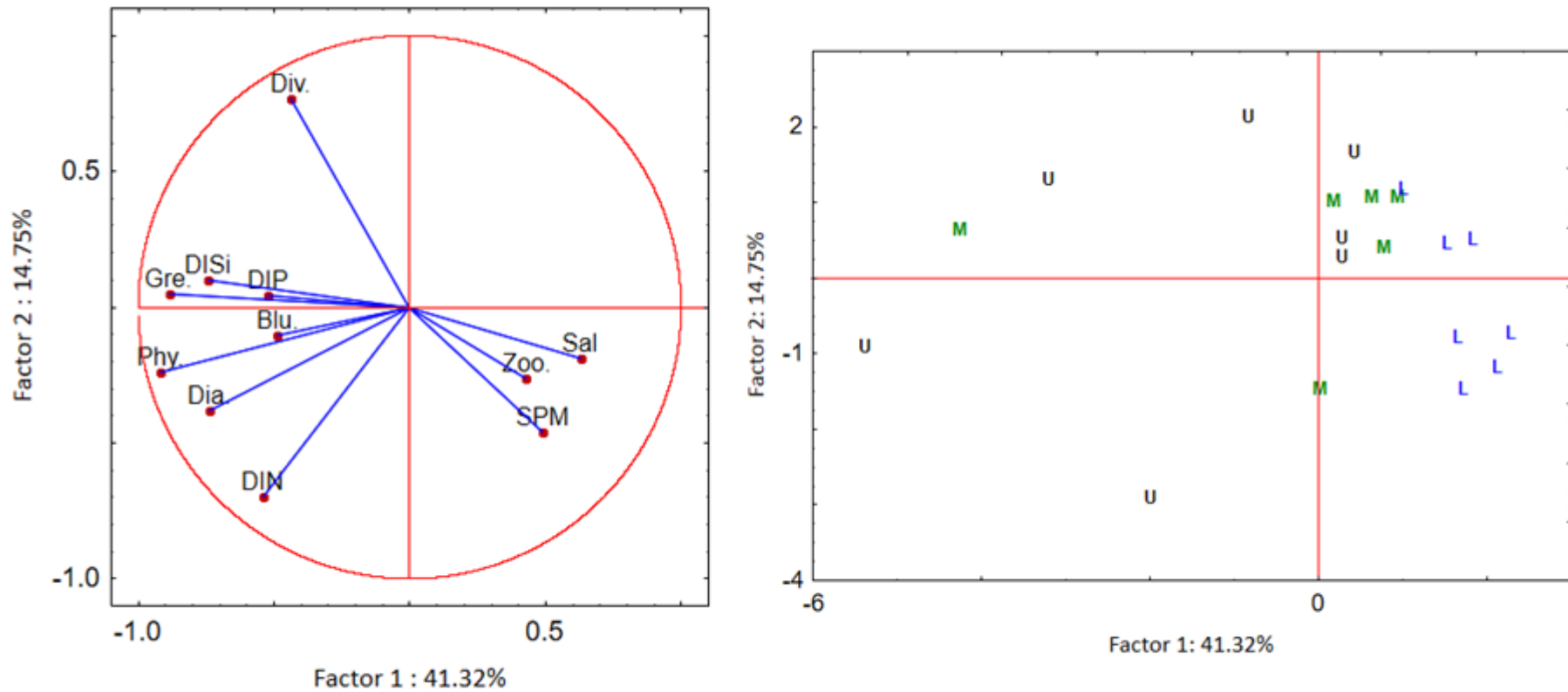


Fig. 8 Salinity ranges of each phytoplankton and the levels at which they were present during no discharge period. Blue colour bars are representing diatoms, red colour for dinoflagellates, green colour for green algae and purple colour for blue-green algae.

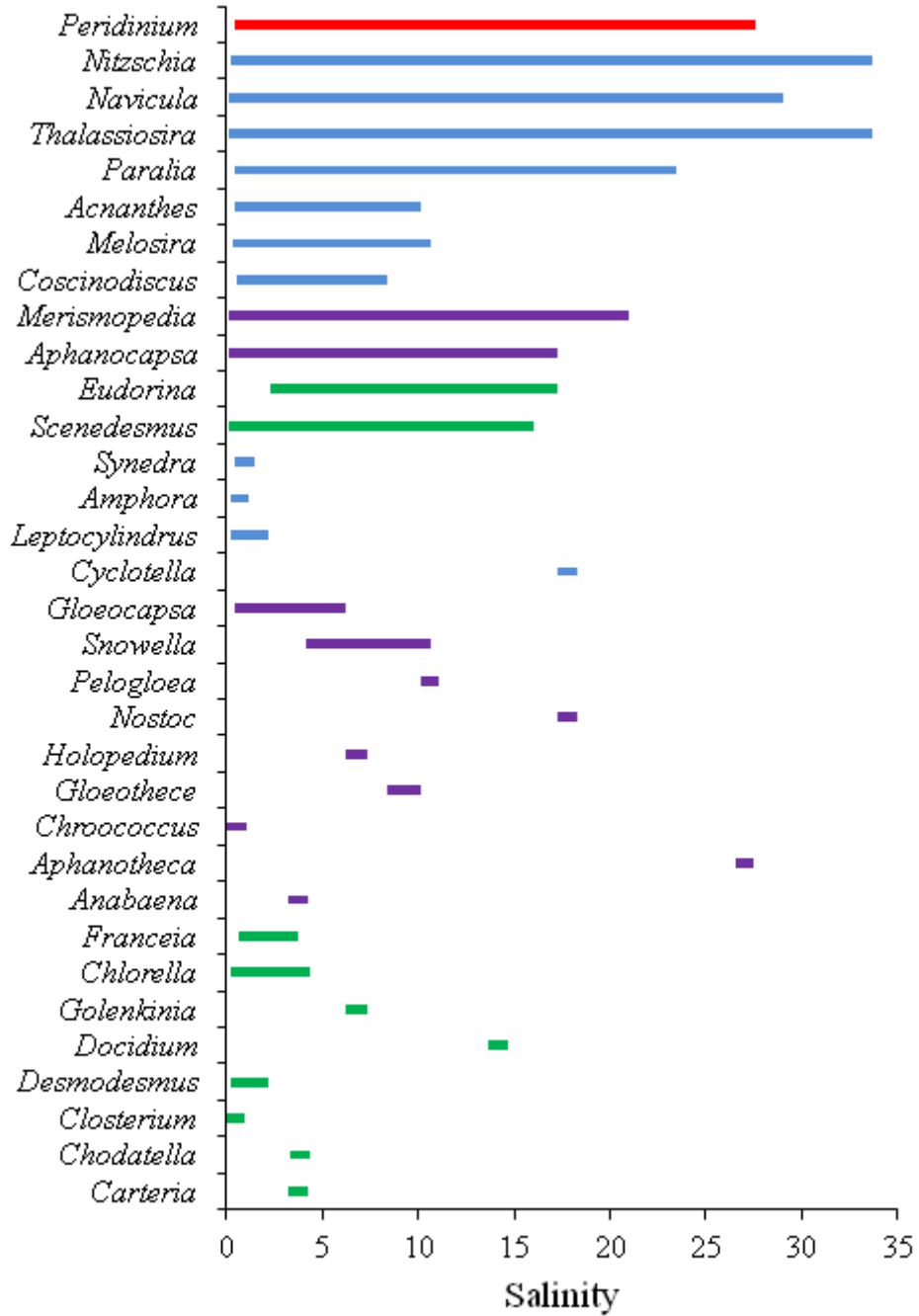
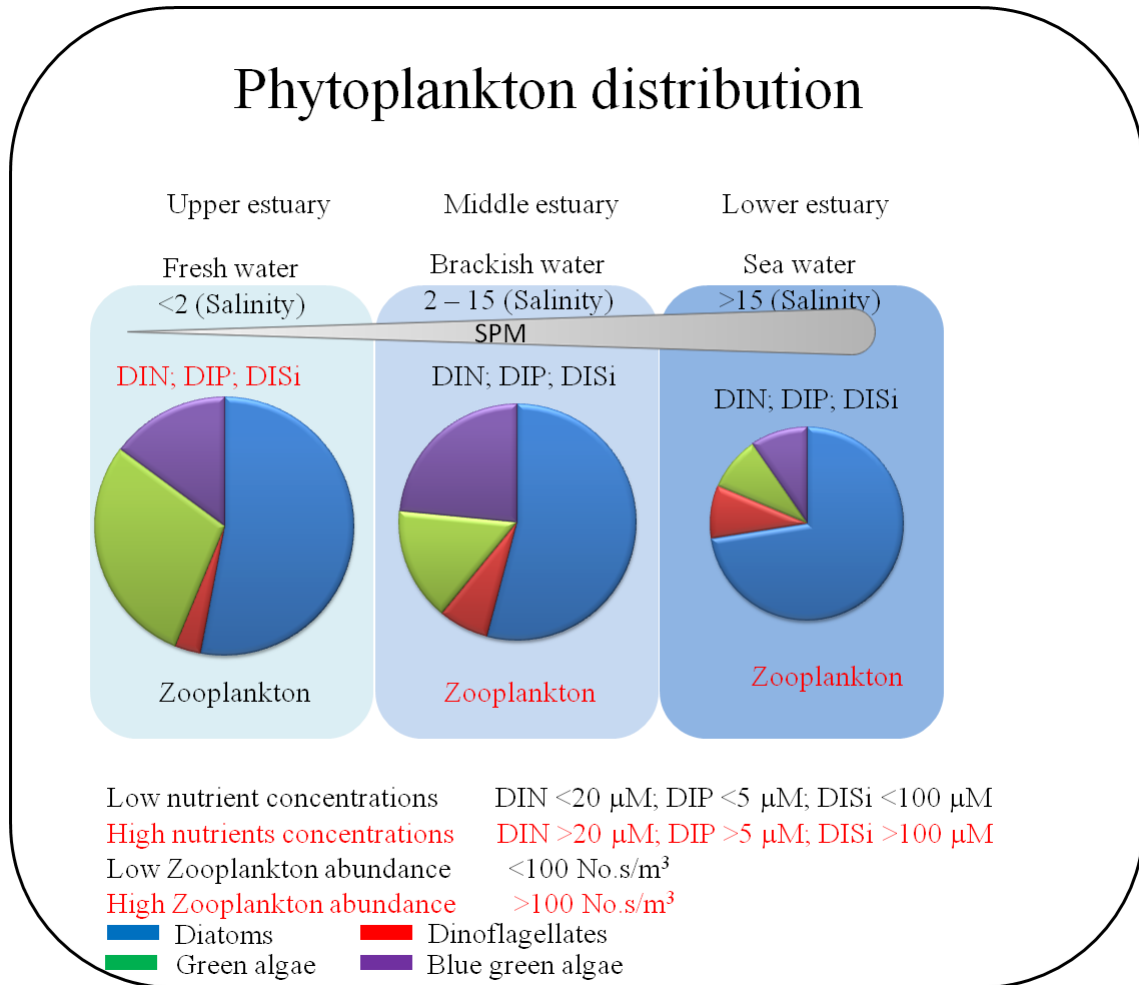


Fig. 9 Schematic diagrams showing different physical, chemical conditions and biological responses in upper, middle and lower regions along the Indian estuaries during no discharge period. Size of the pie chart is representing variations in phytoplankton abundance.



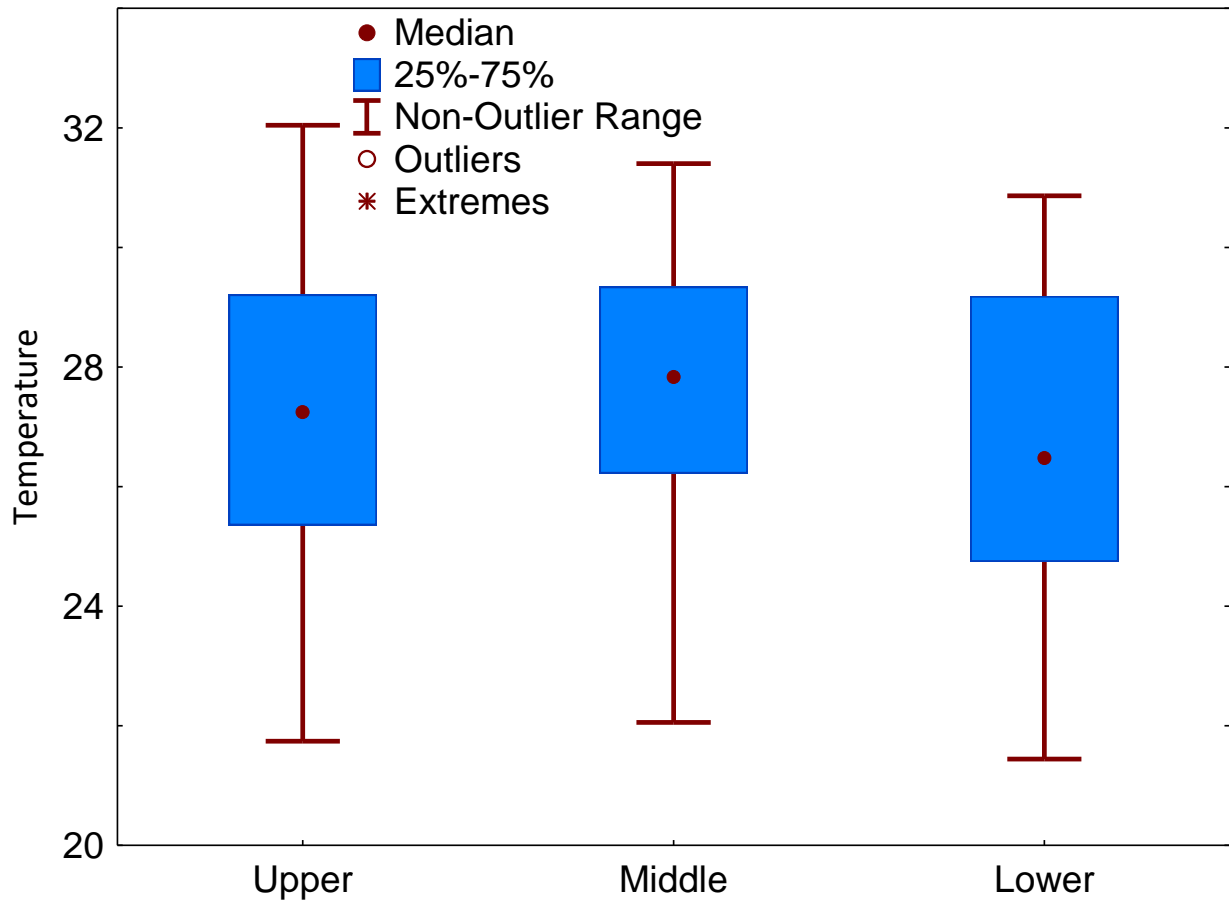
Supplementary Tables

Supplementary Table 1 Rank correlation matrix (Spearman's) of phytoplankton biomass and abundance with physical and chemical parameters along Indian estuaries during no discharge period. Numbers red in colour are indicating significant correlation ($p < 0.05$)

	Salinity	SPM	NO ₃	NH ₄	DIN	DIP	DISi	Chl a	Diatoms	Green	Blue-g	Diversity
Salinity	1.0											
SPM (mg/m ³)	0.5	1.0										
NO ₃	-0.3	0.1	1.0									
NH ₄	-0.1	0.4	0.0	1.0								
DIN (μM)	-0.2	0.3	0.9	0.3	1.0							
DIP (μM)	-0.1	-0.1	0.4	0.1	0.4	1.0						
DISi (μM)	-0.6	-0.1	0.2	0.3	0.3	0.3	1.0					
Phytoplankton Biomass (Chl a, mg/m ³)	-0.2	0.1	0.0	0.3	0.1	0.1	0.4	1.0				
Diatoms	-0.1	-0.2	0.1	-0.1	-0.1	0.1	0.0	0.0	1.0			
Green algae	-0.5	-0.3	0.0	0.1	-0.2	0.1	0.3	0.2	0.4	1.0		
Blue-green algae	-0.4	-0.2	0.0	0.0	-0.1	-0.2	0.3	0.4	0.1	0.5	1.0	
Phytoplankton abundance	-0.2	-0.2	0.1	-0.1	-0.1	0.0	0.2	0.2	0.8	0.5	0.4	
Diversity	-0.4	-0.2	0.0	0.0	-0.1	-0.1	0.2	0.2	0.2	0.8	0.5	1.0
Zooplankton abundance (org.m ³)	0.4	0.3	0.0	-0.2	0.0	-0.3	-0.1	-0.2	-0.1	-0.4	-0.2	-0.4

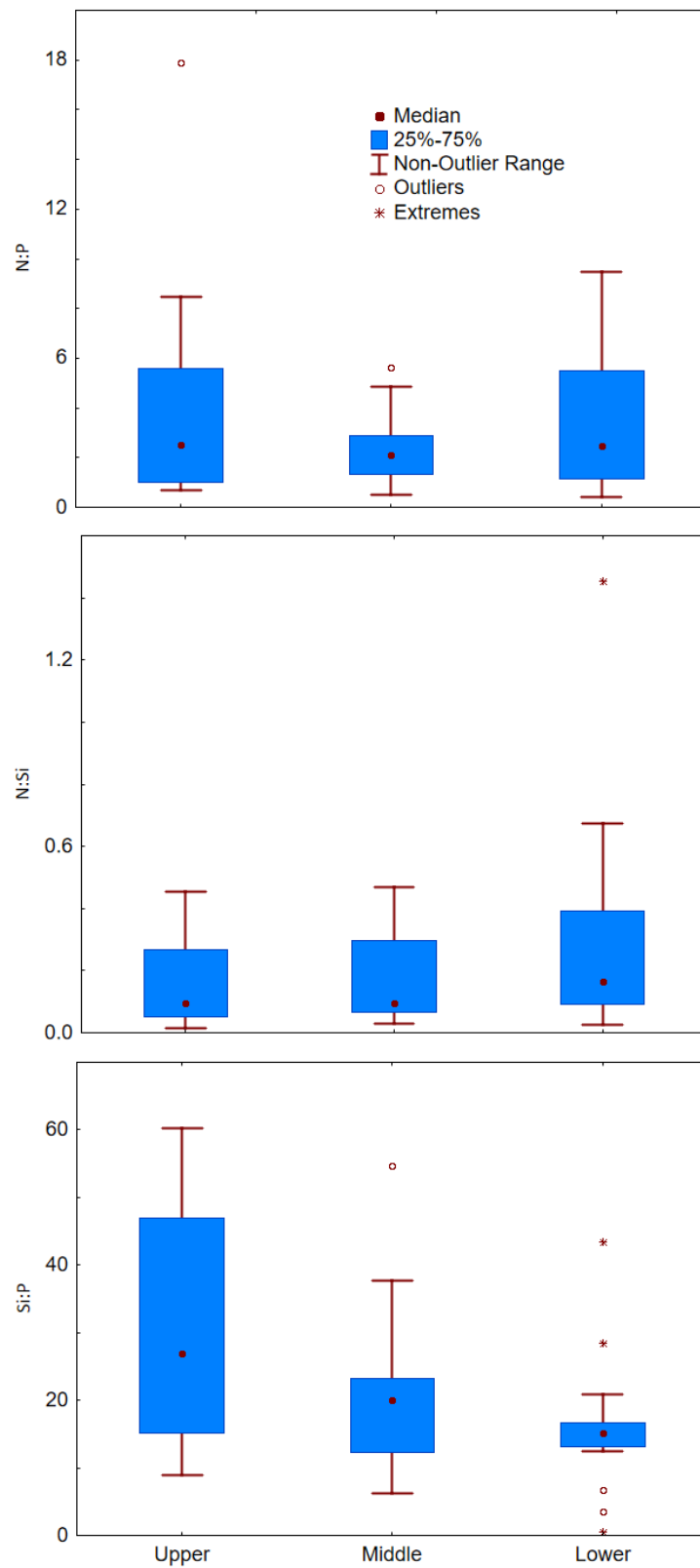
Supplementary Figures

Supplementary Fig. 1 Temperature variations in upper (n=16), middle (n=17) and lower (n=18) regions in the Indian estuaries during no discharge period

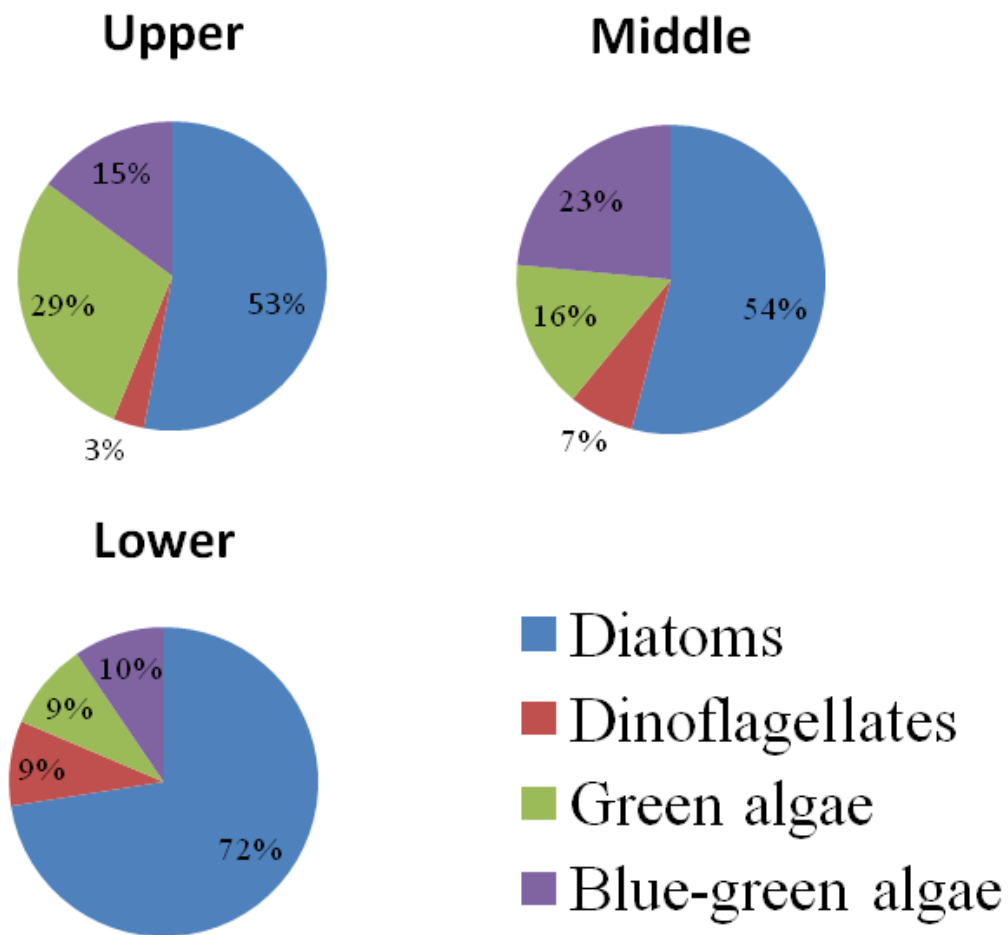


Supplementary Fig. 2 Variations of nutrient ratio's (N:P, N:Si and Si:P) in upper, middle and lower regions in Indian estuaries during no discharge period. (Number of samples (n) for N:P

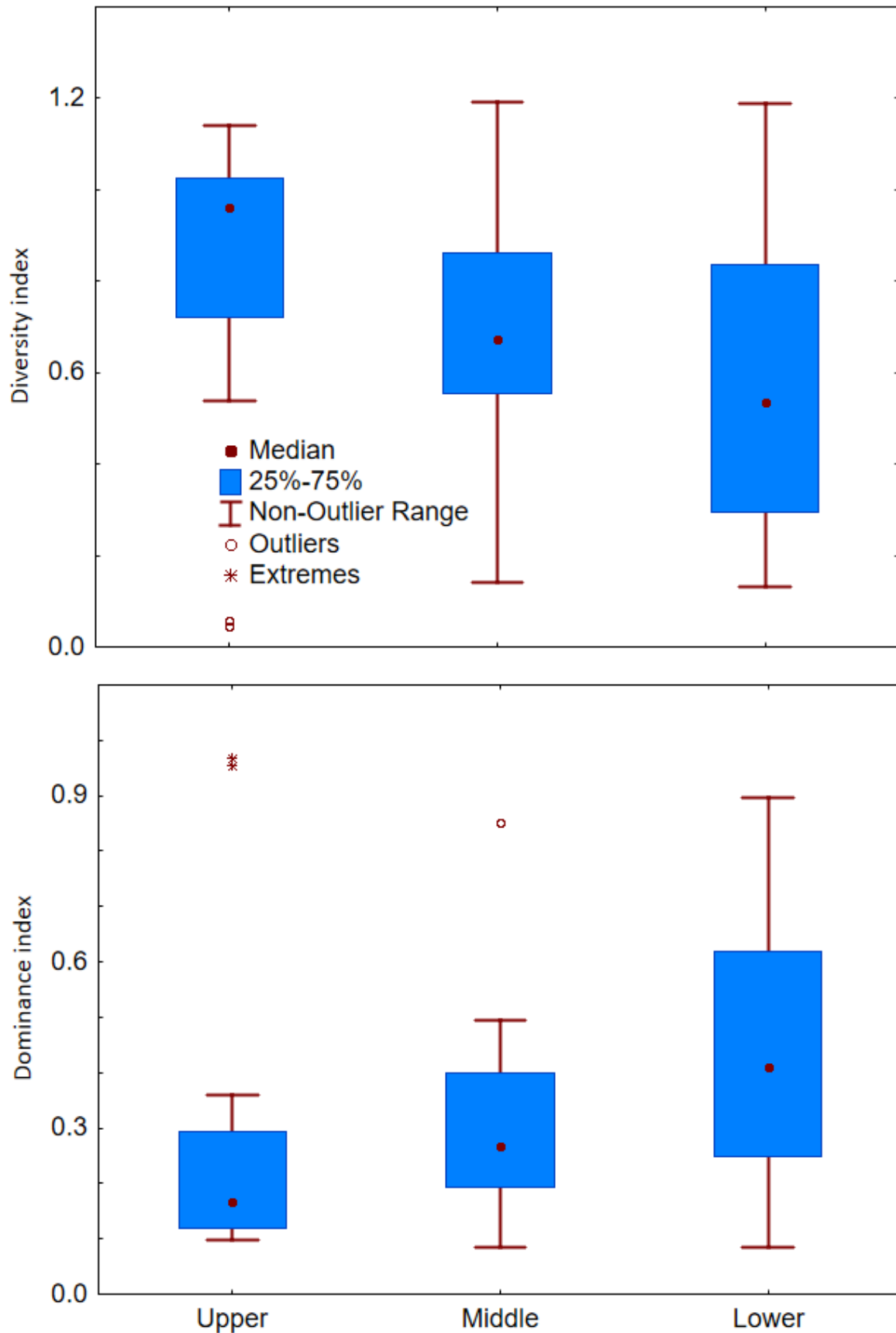
is 15, 13, and 14, Si:P is 15, 13, and 16, and N:Si is 16, 15, and 16 in upper, middle, and lower estuarine regions, respectively).



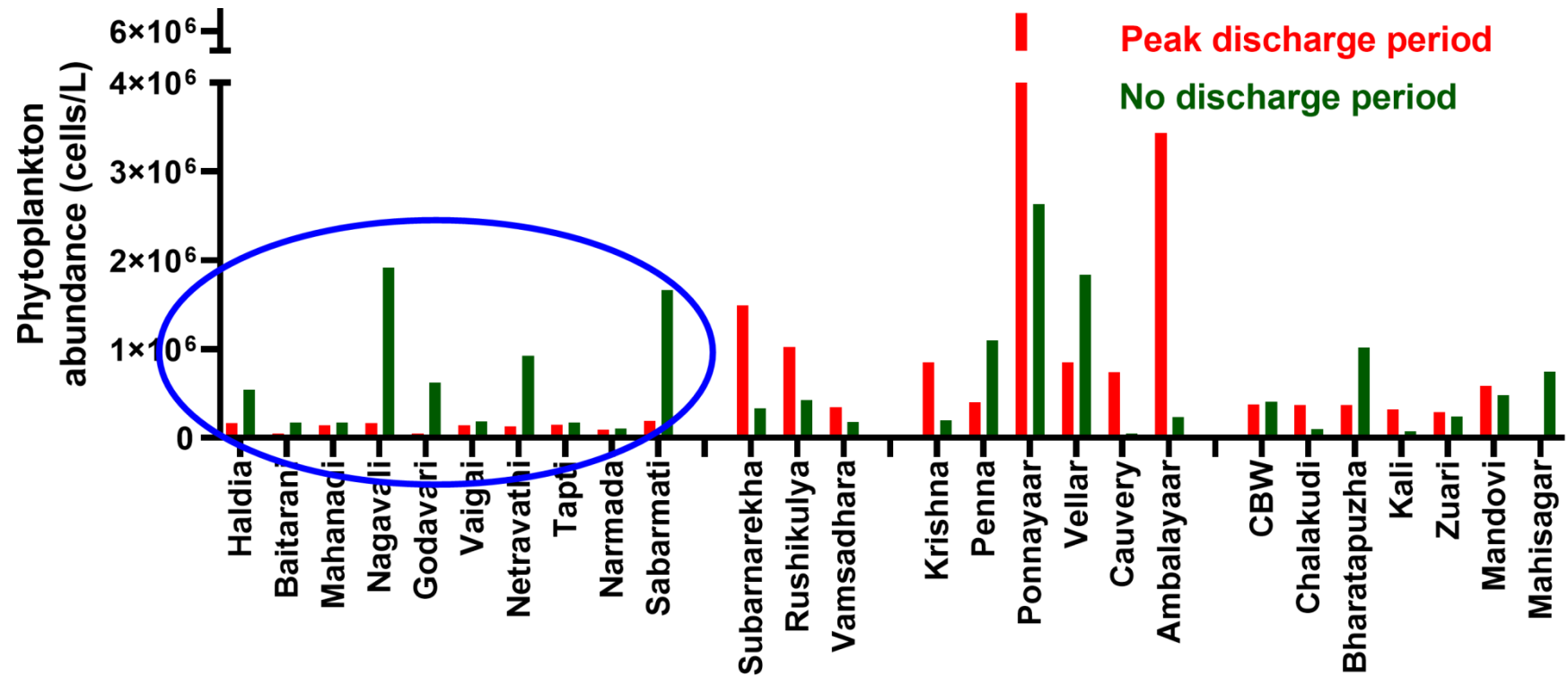
Supplementary Fig. 3 variability of phytoplankton groups in upper, middle and lower estuarine regions during no discharge period



Supplementary Fig. 4 Diversity and dominance indices in **upper** (n=16), **middle** (n=17) and **lower** (n=18) regions in Indian estuaries during no discharge period



Supplementary Fig. 5 Variability in phytoplankton abundance in Indian estuaries during peak discharge and no discharge periods. Estuaries in circle indicating that receiving high river discharge during peak discharge period except Nagavali and Vaigai.



Supplementary Fig. 6 Variability in phytoplankton diversity indices in Indian estuaries during peak discharge and no discharge period. Box and whisker plot inside the square is indicating total variability of diversity index during peak (n=25) and no discharge (n=26) periods.

