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Phytoplankton associated with seasonal oxygen depletion in waters of the western continental shelf of India

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Abstract

We report here results of a time series study carried out to understand seasonal variability of phytoplankton in relation to changes in dissolved oxygen based on observations at the Candolim Time Series (CaTS) station located in coastal waters of Goa, Central West Coast of India. The water column remains well oxygenated during the non-southwest (SW) monsoon period (November-May). However, upwelling of water already depleted in dissolved oxygen during the SW monsoon, coupled with degradation of copious amounts of locally produced organic matter, leads to severe oxygen depletion including sulphate reduction beneath a thin surface layer during late summer-early autumn (August-October). The onset of oxygen-deficient conditions greatly alters the community structure of water-column phytoplankton. Pico-autotrophs and pennate diatoms were found to dominate the autotrophic biomass in such oxygen depleted waters.

Keywords: Phytoplankton, Coastal upwelling, Dissolved oxygen, Picoplankton, West coast of India

1. Introduction

Biological productivity in the Arabian Sea is regulated mainly by nutrient inputs from subsurface waters via upwelling in summer and convective mixing in winter (Banse and Mc Clain, 1986, Madhupratap et al., 1996; Barber et al., 2001). The fertilization of euphotic zone leads to high biological productivity during most parts of the year and widespread phytoplankton blooms during both summer and winter (Naqvi et al., 2003). This, in turn, supports high export flux of organic matter to deep sea (Haake et al., 1993; Ramaswamy and Nair, 1994; Rixen et al., 2005), which contributes to the development of one of the thickest and most intense oxygen minimum zones of the World oceans (Naqvi, 1987; Olson et al., 1993; Morrison et al., 1999).

In contrast to the perennial OMZs found in the open oceanic areas of the northern Indian Ocean, severe oxygen deficiency also occurs during summer upwelling along the western continental shelf of India, covering an area of 180,000 km² (Naqvi et al., 2006). The onset of the southwest monsoon (SWM) in June marks the beginning of upwelling along the SW coast of India (Sarma., 1967; Naqvi et al., 2000) which propagates northward and persists at least until October (Banse, 1959, 1984; Unnikrishnan and Antony, 1992). Upwelling brings up subsurface water having low O₂ content over the shelf. The upwelled water is however capped by a thin low-salinity layer, which is formed as a result of intense rainfall in the coastal zone. Degradation of organic matter in the relatively stagnated upwelled water and in the underlying sediments quickly removes the residual oxygen below the shallow pycnocline (Naqvi et al., 2006). The total areas of the continental shelf margin exposed to bottom waters having dissolved O₂ < 0.5 ml L⁻¹ and < 0.2 ml L⁻¹ are estimated to be 1.15 x 10⁶ and 0.76 x 10⁶ km², respectively; of these the contribution of the northern Indian ocean alone is roughly 59 and 63%, respectively (Helly and Levin, 2004). The prevalence of oxygen-deficient conditions in coastal upwelling regions, including the eastern Arabian Sea, leads to depletion of marine life in particularly benthic fauna (Carruthers et al., 1959; Levin et al., 2009).

Most of the studies on phytoplankton along the continental shelf of India including the study region have focused on spatial and temporal variability. For example, variability of phytoplankton distribution during the onset, peak and late phases of upwelling in the Arabian Sea has been reported previously by Habeebrehman et al. (2008) and Parab et al. (2006). However, a study of phytoplankton (especially pico-plankton) in relation to seasonal changes in oxygen content of water along the west coast of India is not known. This paper deals with shifts in community structure of phytoplankton along the central west coast of India in response to dissolved oxygen changes that occur on a magnitude rarely seen elsewhere along an open coast.

2. Methods

2.1 Study area

The study was carried out over a period of 2 years (2005-2006) at the Candolim Time Series (CaTS) site located approximately 11 km off Goa coast at 15°31'N, 73°39'E. The CaTS station (G5; station depth, 27m; sampling depths, 0, 9, 18 and 25 m) forms the offshore end of a coast-perpendicular transect that also includes four other stations G1(sampling depths,0 and 4m), G2(0 and 6m), G3(0, 6 and 12 m) and G4(0,6 and 15m) (Fig.1). These stations were visited on a monthly basis using a mechanized boat.However, no sampling could be carried out during peak SW monsoon (June-July) due to non-availability of a suitable vessel that could withstand the stormy weather. Nevertheless, peak anoxic conditions usually develop toward the end of the SW monsoon, a period well-covered by our observations.During this period, whenever possible, observations were extended well beyond the CaTS section - to the shelf break - using NIO's coastal research vessels *Sagar Sukti* and *RVSindhu Sankalp*.

As described below, a suite of physico-chemical and biological measurements were made in order to understand the dynamics of phytoplankton communities in response to changes in the dissolved oxygen field over the annual cycle. All biological chemical measurements were made by collecting samples from one Niskin sampler so that conclusion drawn from analyses are reasonable.

2.2. Sample collection and analyses

Water samples were collected using a Niskin samplers (cap.5L)mounted on a hydrowire and fitted with reversing thermometers to record *in situ* water temperature. The water was sub-sampled for analysis of salinity, dissolved oxygen, chlorophylla and phytoplankton.

Vertical profiles of temperature, and salinity were also obtained using a portable Conductivity-Temperature-Depth (CTD) System (Sea Bird, SBE 25).Salinity in discrete samples was determined using an AUTOSAL salinometer. Dissolved oxygen (DO) in seawater was determined by the Winkler method as described by Grasshoff et al. (1983)and concentrations are represented in ml l⁻¹ (1ml l⁻¹=44.64 µM). Annual variations of these data have been explained elsewhere (see Naqvi et al., 2010); therefore,only the biology data are explained in detail here.

For estimation of total phytoplankton biomass (chlorophyll *a*), a known volume of water (0.25L) was filtered through a Whatman GF/F filter paper (47 mm diameter, 0.7 µm pore size) under low vacuum. For size-fractionated chlorophyll measurements, a known volume of sample (5L) was passed serially through bolting silk mesh of different pore size filters (200, 60, 20 and 5 µm) by

means of gravity filtration and finally through GF/F filter paper (0.7 μm). Size fractionated chl *a* data are clustered in accordance to the size classes as pico- (<5-0.7 μm), nano- (<20-5 μm) and micro- (>20 μm) plankton for convenience. Pigments were extracted in 10 ml 90% acetone in the dark for 24 hrs in a refrigerator. A Turner Designs fluorometer (10-AU) was used for measuring fluorescence. For qualitative analysis of phytoplankton, 250 ml of water sample was fixed with 2% acid Lugol's iodine and preserved in 3% buffered formalin. For enumerating and speciation of phytoplankton cells (>5 μm), sub-samples (50 ml) were enumerated under an inverted microscope (40X /100X magnification) following the method of Utermöhl (1958). Empty frustules of diatoms were not considered in total counts. Phytoplankton having numerical abundance of more than 2% are designated as major forms in this study.

Primary productivity (PP; $\text{mg C m}^{-3} \text{ d}^{-1}$) measurements were carried out in situ by collecting water samples from three depths [near surface (~1m), 18m and near bottom (26m)]. At each depth, three light bottles and one dark bottle (ca. 300ml) were deployed for 12 h (dawn to dusk, 12 h being considered as a day) by adding one ampoule of $\text{NaH}^{14}\text{CO}_3$ (specific activity of 185kBq). Uptake of ^{14}C was measured by filtering 100 mL of sample from each bottle through glass fiber/F (GF/F) filters (25 mm diameter, 0.7 μm pore size; Whatman); filters were transferred into scintillation vials and exposed to HCl (0.5 N) fumes in a closed container overnight. Five milliliters of liquid scintillation cocktail (Sisco Research Laboratory, Mumbai, India) were added to each vial and assayed for radioactivity in a scintillation counter (Wallac 1409 DSA, Perkin Elmer, Waltham, Massachusetts, USA). PP rate was calculated and expressed as $\text{mg C m}^{-3} \text{ d}^{-1}$ [UNESCO, 1994].

2.3. Statistical analysis

The data were evaluated by multivariate techniques using PRIMER software package (version 5.2.6, PRIMER-E (Clarke and Warwick, 2001)). Biodiversity indices were calculated using Margalef's species richness (d), Shannon–Wiener diversity (H') and Pielou's evenness (J'). Bray–Curtis similarity matrix was produced on the square root transformed numerical abundance data of phytoplankton. Cluster analysis (group average) was conducted using similarity matrix to produce dendograms.

3. Results

3.1. Field study

Climatological data (see Naqvi et al., 2006a) show that the water column in the study region experiences large changes in the oxygen field on a seasonal basis with oxygen deficient conditions prevailing at the beginning that intensifies towards the end of the SW monsoon, whereas the water

column remains well oxygenated during other periods. During the study period as reported previously (Naqvi et al., 2006; Pratihary et al., 2014), O₂ deficiency (hypoxic/suboxic/anoxic) was recorded 9m below surface; near bottom water were completely anoxic during October 2006 (H₂S; 0.8μM). Since stns G1 (inner shelf), G2, G3, G4 and G5 (outer shelf) along the transect are located within 10kms, data from these stations was put together based on levels of dissolved oxygen and is designated as oxic (DO>2ml l⁻¹), hypoxic (<2ml l⁻¹), suboxic (<0.2ml l⁻¹) and anoxic (~ 0 ml l⁻¹). Phytoplankton distributions for each of these categories are described below. Variations in physico-chemical and biological parameters are summarized in Table 1a.

Nutrient chemistry from the study site well established and is been described previously (Naqvi et al., 2006; Pratihary et al., 2014). With the onset of the SW monsoon a reducing condition that develops near bottom results accumulation of oxidized nitrogen (NO₃⁻) which is reduced to NO₂⁻ (to molecular nitrogen) but get enriched in NH₄⁺ during the late monsoon (Table 1b) when oxygen concentration falls to near zero and leads to the formation of hydrogen sulphide.

3.2. Oxic

As stated above, the water column remains generally well oxygenated from December to April ranging from 6.67 to 3.13 ml l⁻¹ (mean±SD=4.09±0.97). The lowest DO was recorded in April 2006 at 19m at sta. G5 while the highest was measured at surface at sta. G1 in January 2005. The water temperature varied between 26.95 and 29.19 (27.86±0.90), with the highest and the lowest values in the month of May 2005 (sta. G1, surface) and December 2005 (sta G5, 25m) respectively. The amplitude of salinity change was relatively small ranged between 34.98 and 35.79 (35.24 ± 0.35, Table 1). Phytoplankton biomass (Chl *a*) ranged from 0.68 to 16.02 mg m⁻³ (4.46 ± 4.46). Size fractionation analysis showed that pico-autotrophs (<5-0.7μm) on an average accounted for 51% of the total algal biomass while, nano- (<20-5 μm) and micro- (>20 μm) phytoplankton contributed 6 and 43%, respectively, to the biomass (Fig.2).

A total of 96 phytoplankton species were found in the study region considering all seasons. Most of them occurred under oxic conditions (66 species belonging to 41 genera, including 47 species of diatoms and 16 species of dinoflagellates and others belong to silicoflagellates and prasinophytes). The list of species is given in Table 2. Phytoplankton abundance ranged from 4 x 10⁴ to 5.5x10⁵ (avg. 1.2x10⁵ ± 1.5x10⁵) cells l⁻¹. In general, diatoms remained the predominant group accounting for >95% of all phytoplankton counts at all stations except during a bloom of prasinophytes that occurred at stn. G1 in January 2005. Diatoms, were largely dominated by the centric forms (e.g. *Chaetoceros curvisetus*, *Chaetoceros* spp., *Leptocylindrus minimus*, *Skeletonema costatum*,

Thalassiosira spp) while pennates included *Cocconeis* spp., *Navicula* spp, *Pseudo-nitzschia* spp. and *Thalassionema nitzschoides*. Amongst dinoflagellates, *Heterocapsa* spp., *Gyrodinium* spp., *Gymnodinium* spp., *Prorocentrum dentatum*, *Scrippsiella trochoidea* and *Protoperdinium* spp. were commonly seen. *Dictyocha* spp was the only representative of silicoflagellate in oxic waters. Phytoplankton species diversity index and evenness in oxic condition were found to be low (2.77 and 0.66, respectively) as compared to other oxygen conditions (see below; Table 3). This was due to the occurrence of blooms such as prasinophytes (abundance $\sim 2.8 \times 10^5$ cells l^{-1} , $\sim 52\%$ of the total phytoplankton community) and dinoflagellates (2.5×10^5 cells l^{-1} , 45% of the total phytoplankton community) such as *Scrippsiella trochoidea*, *Prorocentrum dentatum*, *Heterocapsa* sp., *Gyrodinium* spp. and *Gymnodinium* sp.

3.3. Hypoxic

During the SW monsoon, subsurface waters became hypoxic. Waters with DO falling within this range (0.24-1.56 ml^{-1} ; 0.64 ± 0.39 , Table 1) were relatively cool (22.14-26.62°C; mean+SD=24.16 \pm 1.41). The salinity of such waters varied widely from 22.10 to 35.87 (34.07 ± 4.49). The low salinity values arise from intense rainfall during the SW monsoon and were confined close to sea surface. The upwelled cold, nutrient-rich waters well within the photic zone supported high phytoplankton biomass (1.47-7.60 mg Chl *a* m^{-3} ; 4.19 ± 2.19). Interestingly, the highest chlorophyll concentrations were encountered in near bottom waters at stns. G3 and G5 in September 2005. Maximal contribution (74%) to the total chlorophyll came from pico-autotrophs ($< 5-0.7 \mu m$) with the shares of nano- ($< 20-5 \mu m$) and micro- ($> 20 \mu m$) fractions being 6.7% and 18.7%, respectively (Fig. 2). Total phytoplankton abundance in hypoxic waters ranged from 1.8×10^4 to 1.3×10^5 ($5.9 \times 10^4 \pm 4.1 \times 10^4$) cells l^{-1} , consisting of 68 species (56 species of diatoms and 12 species of dinoflagellates) belonging to 36 genera (Table 2). Species diversity and evenness were relatively higher than in oxic water (Table 3). Under hypoxic condition, major diatom species present were *Thalassiosira subtilis*, *Skeletonema costatum*, *Leptocylindrus minimus*, *Cheateoceros* spp., *Rhizosolenia setigera* (centric forms); *Thalassionema nitzschoides*, *Thalassiothrix* spp., *Pseudo-nitzschia* spp., *Asterionellopsis glacialis*, *Navicula transitrans* var. *derasa* f. *delicatula* and other *Navicula* spp. (pennate forms). The endemic species of hypoxic environment are shown in the dendrogram (see below). Interestingly, some of the diatoms (*Planktonella sol*, *Triceratium* spp., *Raphoneis*, *Cocconeis* spp., *Amphora* spp., *Melosira borealis*) and dinoflagellates (*Dinophysis acuminata*, *Heterocapsa* sp., *Polykrikos* and *Pyrophacus horologium*) that were present in oxic waters were absent in hypoxic water. The dinoflagellates numbered between 100 and 500 cells l^{-1} and accounted for $< 5\%$ of the total

phytoplankton in hypoxic water. Of these *Prorocentrum dentatum*, *Gymnodinium spp.*, *Gyrodinium spp.*, *Ceratium furca*, *Noctiluca scintillans* and *Protoberidinium*spp. were commonly recorded.

3.4. Suboxic

The suboxic condition prevailed during August-October with the recorded DO concentrations ranging between 0.03 and 0.13 ml l⁻¹ (0.08 ± 0.033). These concentrations are very close to the detection limit of the Winkler procedure. The suboxic water had low temperatures, ranging from 22.52 to 25.23°C with a mean (±SD) of 23.63 ± 0.93°C reflecting their deeper, offshore origin, while the salinity varied from 32 to 36 (34.3 ± 1.5), the lower values ostensibly caused by some mixing with the fresher surface layer. Phytoplankton biomass varied between 0.38 and 8.51 mg Chl *a* m⁻³ (3.04±2.61) (Table 1). The lowest chlorophyll concentration was recorded in August 2005 at stn. G5 (19m) whereas the highest concentration also came from subsurface (stn. G5, bottom) in September 2005. The size-fractionated chlorophyll data showed larger biomass in the pico- fraction (66%) than in the nano-(8.8%) and micro-(24.7%) fractions (Fig. 2). Overall, phytoplankton density ranged from 6.4x10³ to 7.2x10⁴ (3.4 ± 2.2 x10⁴) cells l⁻¹ belonging to 52 species (47 species of diatoms and 5 species of dinoflagellates). The dominant species associated with suboxic waters were *Thalassiosera subtilis*, *Leptocylindrus minimus*, *Chaetoceros spp.*, *Skeletonema costatum*, *Rhizosolenia spp.*, *Guinardia striata* (centric diatoms), and *Pseudo-nitzschia spp.*, *Thalassionema nitzschoides*, *Thalassiothrix spp.*, *Asterionellopsis glacialis* and *Navicula transitrans var. derasa f. delicatula* (pennates) (Table 2). A species of *Gyrodinium* was the only abundant dinoflagellate found in suboxic waters (density >100 cells l⁻¹). Other less abundant diatoms and dinoflagellates were *Hemiaulus sinensis*, *Rhizosolenia setigera*, *Pleurosigma elongatum*, *Actinoptichus undulates*, *Coscinodiscus radiatus*, *Corethron hystrix*, *Cocconeis sp.*, *Ditylum sol*, *Ditylum brightwelli*, *Dactyliosolen sp.*, *Eucampia zodiacus* (diatoms) and *Ceratium fusus*, *Gonyaulax sp.*, *Protoberidinium* and *Scrippsiella trochoidea* (dinoflagellates). Nevertheless, phytoplankton diversity and evenness in suboxic waters were comparable to those in hypoxic waters (Table 3).

3.5. Anoxic

In the fall intermonsoon phase, particularly in October 2006, near-bottom waters often became completely anoxic and were characterized by low temperatures (23.3 - 23.6; 23.5±0.14°C) and high salinity (mean 35.48) (Table 1). Chlorophyll *a* varied between 1.11 and 3.84 (2.58±1.38) mg Chl *a* m⁻³, with the pico-autotrophs constituting about 68% of the total phytoplankton biomass (Fig. 2). Even at undetectable levels of dissolved oxygen, some algal forms were present, and their abundance varied between 5.6x10³ and 8.2x10⁴ (3.8 ± 3.9 x10⁴) cells l⁻¹.

Some of the dominant diatom species found in anoxic waters were *Thalassiosira subtilis*, *Melosira* spp., *Leptocylindrus minimus*, *Rhizosolenia setigera* and *Actinoptichus undulates* (centric diatoms); and *Thalassionema nitzschoides*, *Pseudo-nitzschia* spp., *Thalassiothrix* sp., *Navicula transitrans* var. *derasa*, *N. transitrans* var. *derasa* f. *delicatula*, *Pleurosigma angulatum*, *Pleurosigma elongatum*, *Pleurosigma* spp. (pennate diatoms). The contribution of pennate diatoms to the total abundance was three fold higher than that of centric forms. Interestingly, these forms were with distinct chloroplast inside their cells (Plate1). Composition-wise the latter forms were more diverse. Interestingly, the dinoflagellate community was virtually absent except for *Gyrodinium* species (Table2). Species diversity in anoxic waters was also not much different from that in the oxic environment (Table3). Overall, as the DO concentrations decline, phytoplankton abundances and their standing stocks also exhibit marked decreases (Fig.3).

Cluster analysis of phytoplankton composition at 60% similarity showed 5 distinct clusters (Fig. 4). Clusters A and C contain species that thrive exclusively in oxic and hypoxic waters, respectively. Clusters B and D include species that can tolerate a wide range of oxygen levels (from oxic to suboxic) although they are distinctly separate in terms of their abundance. Cluster B mainly comprises the mixotrophic group while Cluster D contains mostly the autotrophic forms. Finally, Cluster E includes cosmopolitan species present throughout the year irrespective of the oxygen level.

4. Discussion

The study area situated along the central west coast of India experiences large changes in hydrography and circulation which, in turn, experience the development of seasonally contrasting biogeochemical regimes including the prevalence of wide-spread and very severe oxygen deficiency during late summer and early autumn. The results obtained in the present study are consistent with well-established trend of variability of physico-chemical parameters. Interestingly, we observed large shifts in the abundance and composition of phytoplankton that can be related to changes in ambient DO concentrations.

The establishment of the SW monsoon circulation makes a profound impact on the chemistry of waters over the western Indian continental shelf. The upwelled water is initially hypoxic and rich in macronutrients (nitrate and phosphate). However, the DO in this water gets consumed (at times fully) quickly, making the environment reducing. Under these conditions, nitrate is converted to elemental nitrogen by heterotrophic bacteria. This process (denitrification) restricts the availability of bioavailable nitrogen. However, once sulphidic conditions develop in near-bottom water, which normally happens over the inner shelf in September-October, nitrogen released from the decaying

organic matter accumulates as ammonium (Naqvi et al., 2000, 2006). This progression from hypoxic to suboxic/anoxic conditions with time is expected to affect the growth and composition of both phytoplankton. Changes in quantity and quality of nutrients are also known to influence phytoplankton composition (Hutchings et al., 1995). It is known that large diatoms often predominate in upwelling systems (Malone, 1980; Habeebrehman et al., 2008). These diatoms usually use nitrate. In our study region, however, the above-mentioned shift from nitrate as the dominant form of fixed nitrogen during the early stages of upwelling to ammonium, when the subsurface waters become fully anoxic toward the end of the upwelling period, is expected to affect the phytoplankton composition. Moreover, completely anoxia may not be suitable for their growth despite the availability of macronutrients (Naqvi et al., 2010). Our size-fractionated Chl *a* data show that during the NE monsoon (December-March) and spring intermonsoon periods (April-May), when oxic conditions prevail throughout the water column, microplankton account for roughly 50% of the total biomass (Fig. 2), thereby playing a key role in food web dynamics. Unfortunately, we do not have any data from early and mid-monsoon phases (June-July) when nitrate supply is high and oxygen-deficiency is not so severe, but the work of Habeebrehman et al. (2008) from the southeastern Arabian Sea shows high abundance of diatoms such as *Skeletonema costatum*, *Rhizosolenia setigera* and *R. alata* during this period (it may be noted that the oxygen-deficiency is also less severe in this area as compared to our area of observations). Likewise, *Pseudo-nitzschia delicatissima*, *Rhizosolenia styliformis*, among other diatoms, have been found to be characteristic species in the Somali upwelling zone (Smith and Codispoti, 1980). Pigment measurements also showed that next to Chl *a*, fucoxanthin, the marker pigment of diatoms is usually the most abundant phytoplankton pigment in the Arabian Sea during the SW monsoon (Latasa and Bidagare, 1998; Roy et al., 2006). In a more recent study of pigments at the CaTS location, Roy (2010) found that as the nitrate gets consumed, presumably by both autotrophs (and heterotrophs), the dominance of diatoms and dinoflagellates decreases, and the contribution of small green flagellates and cyanobacteria increases. In conformity with this finding, our results show that in the oxygen deficient waters (hypoxic-anoxic) cells larger than 5 μm in size contributed only 30% to the phytoplankton biomass (Chl *a*) with the bulk (70%) of the biomass occurring in the smaller size range (0.7-5 μm) (Fig. 2). Flow cytometry and HPLC pigment (not presented here) data suggest the dominance of *Synechococcus* in low oxygen waters. However, there are times when the anoxic near-bottom waters have high Chl *a* content, which may be because of sinking of large active cells from the surface and their preservation in anoxic waters (Plate 1). This was evident through ^{14}C based in-situ primary productivity (PP) measurements [see Gauns et al. (2005) for detailed methodology], which showed

sharp decrease in PP rates at subsurface depth when intense low oxygen condition prevails in the month of September (Fig.5a). Concomitant increase in oxygen concentration in the water column (in October), also resulted increase in PP rates (Fig.5b). Preservation of active cells in subsurface low oxygen water could contribute enormously to export production that could in turn lead to further enhancement of reducing condition along the open coast of eastern Arabian Sea.

Overall, the available data suggest a clear shift in autotrophic community and in PP rates in oxygen deficient waters which seems to be dominated by picoplankton rather than microplankton, mostly diatoms, which account for the bulk of phytoplankton biomass in oxic waters.

Some diatoms have been found to be present throughout the year irrespective of the oxygen level viz. *Leptocylindrus minimus*, *Thalassiosira* spp., *Skeletonema costatum*, *Thalassionema nitzschoides*, *Pseudo-nitzschia* spp. and *Navicula* spp. These species belong to distinct cluster (see dendrogram Fig.4). Intriguingly, in anoxic waters the contribution of large pennate diatoms was found to be quite sizable in the present study. How the plankton cope with such low DO levels is something of a mystery. A study by Kamp et al. (2011) revealed that benthic diatoms can accumulate large amounts of nitrate and respire it anaerobically via dissimilatory nitrate reduction to ammonia (DNRA) during dark or anoxic conditions. Whether such a respiratory pathway also exists in the pelagic diatom community still remains to be demonstrated. Or, is it that hypoxia tolerance and threshold values are species- and stage-specific (Miller et al., 2002) resulting dominance of pennate diatoms in low oxygen condition in contrast to centric diatoms. Although the impact of hypoxia on benthic communities has been studied intensively, less is known about its effect on pelagic communities in coastal ecosystems.

In brief, during late south west monsoon one of the largest low-oxygen zone develops naturally every year over the continental shelf of India having upwelled water with oxygen concentration $<0.5 \text{ ml l}^{-1}$ occupying an area of $\sim 180,000 \text{ km}^2$ [Naqvi et al., 2000], an order of magnitude bigger than the famous “dead zone” in the Gulf of Mexico [Rabalais et al., 2002]. Globally, low oxygen condition is known to have severe impacts on the coastal marine environment and marine life particularly biodiversity losses. Further, the effects of low oxygen (hypoxia) zones are forecast to increase due to global warming /coastal eutrophication threatening aquatic ecosystems and are generally underestimated. And, the present study is an attempt showing that the low oxygen condition is detrimental to phytoplankton living in an aquatic system.

5. Conclusions

Seasonally reversing circulation along the west coast of India results in the prevalence of contrasting biogeochemical conditions in winter and summer, including widespread and severe oxygen deficiency in sub-pycnocline waters during the latter season. These conditions profoundly influence the dynamics of phytoplankton. While microplakton (mostly diatoms but also dinoflagellates) constitute the major part of the phytoplankton biomass in oxic waters, pico-autotrophs, and to a smaller extent, pennate diatoms are found to be predominant in oxygen deficient waters. The mechanism of survival of these organisms in very low oxygen environments is fully unknown and should be investigated in future.

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Legends to Table

Table 1a. Variations of chlorophyll *a* (chl *a*; mg m⁻³), phytoplankton abundance (phyto; cells l⁻¹), and temperature (temp; °C) and salinity for different categories of oxygen deficiency.

Table 1b: Variations of nutrients during non-monsoon (February) and monsoon (August & September) period at station G5

Table 2. Phytoplankton composition and abundance for different categories of oxygen deficiency.

Table 3. Species diversity indices for phytoplankton for different categories of oxygen deficiency : number of species (S); total individuals (N); species richness (d); Pielou's evenness (J'); species diversity H'(loge) at the CaTS site.

Legends to Figures

Fig.1. Map showing study area and stations (G1-G5, closed circles) that form the CaTS transect.

Fig.2. Size- fractionated Chl *a* distribution representing abundance of of pico (<10-0.7µm); nano (<20-10 µm); and micro plankton (>20 µm) in the study area under (A) oxic; (B) hypoxic; (C) suboxic and (D) anoxic conditions for the years 2005-2006.

Fig.3. Average variations in abundance of phytoplankton and biomass (Chl *a*) from oxic to anoxic conditions.

Fig.4 Dendrogram based on Bray-Curtis similarity showing average linkage cluster analysis for phytoplankton taxa in oxic , hypoxic , suboxic and anoxic waters.

Fig.5.Diagrams for Primary Productivity (PP, mg C m⁻³ d⁻¹), Chlorophyll *a* (mg m⁻³), Phytoplankton density (Phyto; no. x 10⁵ l⁻¹) and dissolved oxygen (DO; ml l⁻¹; 1ml l⁻¹=44.64 µM) at Sta G5 in coastal waters of Goa, central west coast of India Sea, in (a) September 2005 and (b) October 2005.

Table 1a

Variations of chlorophyll *a* (chl *a*; mg m⁻³), phytoplankton abundance (phyto; cells l⁻¹), and temperature (temp; °C) and salinity for different categories of oxygen deficiency.

	Parameters	Minimum	Maximum	Average	Standard deviation
OXIC	temp	26.95	29.19	27.86	0.901
	salinity	34.98	35.79	35.24	0.35
	oxygen	3.13	6.67	4.089	0.966
	chl a	0.68	16.02	4.455	4.457
	phyto	40000	553333	120766	156219
HYPOXIC	temp	22.14	26.62	24.16	1.41
	salinity	22.1	35.87	34.06	4.49
	oxygen	0.24	1.56	0.64	0.39
	chl a	1.47	7.6	4.185	2.185
	phyto	18204	135150	54319	41069
SUBOXIC	temp	22.52	25.23	23.629	0.93
	salinity	31.98	36	34.35	1.53
	oxygen	0.03	0.13	0.081	0.033
	chl a	0.38	8.51	3.036	2.613
	phyto	6429	72660	34246	22865
ANOXIC	temp	23.29	23.55	23.45	0.14
	salinity	35.2	35.67	35.48	0.24
	oxygen				
	chl a	1.11	3.84	2.583	1.378
	phyto	5600	82187	38319	39492

Table 1b:

Variations of nutrients during non-monsoon (February) and monsoon (August & September) period at stn G5

	28-Feb-05				
Depth(m)	NO3(μM)	NO2(μM)	NH4(μM)	PO4(μM)	SIO4(μM)
0	0.04	0.03	0.51	0.04	8.44
9	0.00	1.18	0.78	0.03	8.45
19	1.01	0.77	1.61	0.26	11.60
28	1.22	0.04	1.40	0.20	7.35
	22-Aug-05				
0	0	0.05	0.72	1	22.62
9	10.3	0.68	1.66	1.31	11.4
19	20.13	0.25	0.49	1.55	7.84
28	10.32	3.76	1.57	1.65	26.88
	05-Sep-05				
0	0.13	0	0.15	1.23	17.08
9	1.04	0.2	3.27	1.78	24.32

Table 2

Phytoplankton composition and abundance for different categories of oxygen deficiency.

	OXIC	HYPOXIC	SUBOXIC	ANOXIC
Phytoplankton cell L ⁻¹	120766	54319	34246	38319
DIATOM (centric)				
<i>Actinoptychus undulatus</i>		3	1	3
<i>Bellerochea horologicalis</i>		2		
<i>Bacteriastrum hyalinum</i>		1		
<i>Coscinodiscus marginatus</i>	2	2		
<i>Coscinodiscus radiatus</i>		1	2	
<i>Coscinodiscus spp.</i>	2	2	2	2
<i>Corethron hystrix</i>	1	2	1	
<i>Chaetoceros affinis</i>	1	3		
<i>Chaetoceros lorenzianus</i>	3	2	2	
<i>Chaetoceros curvisetus</i>	6	3		
<i>Chaetoceros decipiens</i>	2			
<i>Chaetoceros spp.</i>	6	4	5	
<i>Cyclotella spp</i>		1	1	
<i>Ditylum sol</i>	2	1	2	
<i>Ditylum brightwellii</i>	2		1	
<i>Dactyliosolen spp</i>		2	2	
<i>Eucampia cornuta</i>	2	2		
<i>Eucampia zodiacus</i>	2	2	2	2
<i>Guinardia striata</i>	4	3	3	2
<i>Guinardia delicatula</i>			1	
<i>Guinardia flaccida</i>			2	
<i>Hemiaulus hauckii</i>	2	1		
<i>Hemiaulus membranaceus</i>		2		
<i>Hemiaulus sinensis</i>		2	3	
<i>Hemiaulus sp</i>		1		
<i>Lauderia sp</i>	2	3		
<i>Leptocylindrus minimus</i>	4	5	5	4
<i>Leptocylindrus danicus</i>	2	2	2	
<i>Odontella mobiliensis</i>	2	1	1	
<i>Odontella sinensis</i>	2	2	2	1
<i>Melosira borreri</i>	2			
<i>Melosira sulcata</i>		1		
<i>Melosira sp</i>	2			3
<i>Planktoniella sol</i>	2			
<i>Rhizosolenia alata</i>		1	2	
<i>Rhizosolenia crassispina</i>				2
<i>Rhizosolenia imbricata var shrubsolei</i>		3		
<i>Rhizosolenia setigera</i>	2	4	2	4

<i>Rhizosolenia stolterforthii</i>		2	2	
<i>Rhizosolenia syliformis</i>		3	2	1
<i>Rhizosolenia spp.</i>	3	2	3	
<i>Schroederella spp</i>		1		
<i>Skeletonema costatum</i>	6	6	5	3
<i>Streptotheca tamesis</i>	3		1	
<i>Thalassiosira subtilis</i>	4	6	6	5
<i>Thalassiosira spp</i>	4	1	2	4
<i>Triceratium sp</i>	1			
DIATOM (pennate)				
<i>Amphiphora spp</i>	1			
<i>Asterionellopsis glacialis</i>	2	4	4	
<i>Cocconeis spp.</i>	4		1	
<i>Meuniera membranacea</i>		2		3
<i>Fragilaria oceanica</i>			2	
<i>Navicula transitrans var.derasa</i>	1	2	2	4
<i>N. transitrans var.derasa f. delicatula</i>	1	5	5	5
<i>Navicula vanhoeffenii</i>		3		
<i>Navicula spp.</i>	4	4	3	3
<i>Nitzschia closterium</i>	1	3	2	
<i>Nitzschia longissima</i>		2		1
<i>Nitzschia sp</i>	2	2	1	2
<i>Pleurosigma directum</i>	2	2	2	2
<i>Pleurosigma angulatum</i>	2	3	2	4
<i>Pleurosigma elongatum</i>	1	3	3	5
<i>Pleurosigma normanii</i>	1			
<i>Pleurosigma spp.</i>	2	3	3	4
<i>Pseudo-nitzschia spp</i>	4	4	4	5
<i>Pseudo-nitzschia seriata</i>	3	3	2	
<i>Gyrosigma balticum</i>		1	2	3
<i>Raphoneis sp</i>	1			
<i>Synedra sp</i>			1	2
<i>Thalassionema nitzschioides</i>	6	6	4	6
<i>Thalassionema frauenfeldii</i>	2	3	2	
<i>Thalassiothrix spp</i>		5	4	4
DINOFLAGELLATES				
<i>Amphidinium spp.</i>	3	1		
<i>Ceratium furca</i>	2	2		
<i>Ceratium fusus</i>		1	1	
<i>Ceratium kofoidii</i>	1			
<i>Dinophysis acuminata</i>	2			
<i>Gonyaulax spp</i>			1	
<i>Gymnodium spp.</i>	4	2		
<i>Gyrodinium spp</i>	4	2	2	1

<i>Heterocapsa spp</i>	5			
<i>Noctiluca miliaris</i>		2		
<i>Prorocentrum micans</i>	2	1		
<i>Prorocentrum dentatum</i>	5	4		
<i>Prorocentrum gracile</i>	3			
<i>Protoperidinium steinii</i>	2	1		
<i>Protoperidinium pentagonum</i>		1		
<i>Protoperidinium depressum</i>	2	1		
<i>Protoperidinium spp.</i>	2	1	1	
<i>Pyrophacus horologium</i>	1			
<i>Polykrikos spp</i>	1			
<i>Scrippsiella trochoidea</i>	6		1	
SILICOFLAGELLATE				
<i>Dictyocha fibula</i>	2			
<i>Dictyocha speculum</i>				1
<i>Ebria tripartita</i>	1			
PRASINOPHYCEAE				
Bloom-Prasinophytes	6			

Note: Range represented as following digits 5 -100= 1; 100-500= 2; 500-1000= 3; 1000-2500= 4; 2500-5000= 5; >5000= 6 cell countsL⁻¹

Table 3

Species diversity indices for phytoplankton for different categories of oxygen deficiency : number of species (S); total individuals (N); species richness (d); Pielou's evenness (J'); species diversity H'(loge) at the CaTS site.

Oxygen level	S	N	d	J'	H'
Oxic	66	120766	5.55	0.66	2.77
Hypoxic	68	54319	6.15	0.77	3.26
Suboxic	52	34246	4.88	0.79	3.11
Anoxic	30	38319	2.75	0.81	2.76

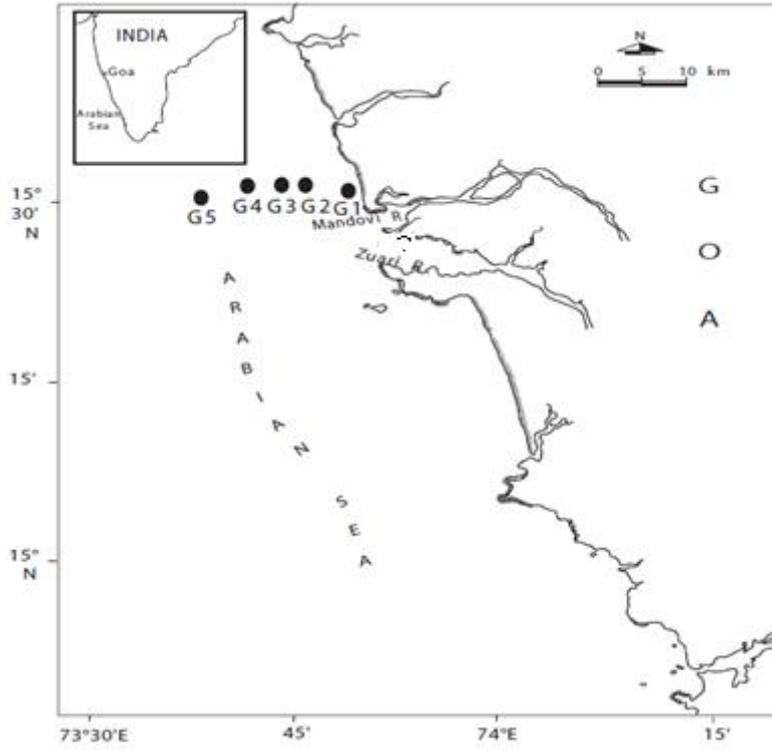


Fig.1. Map showing study area and stations (G1-G5, closed circles) that form the CaTS transect.

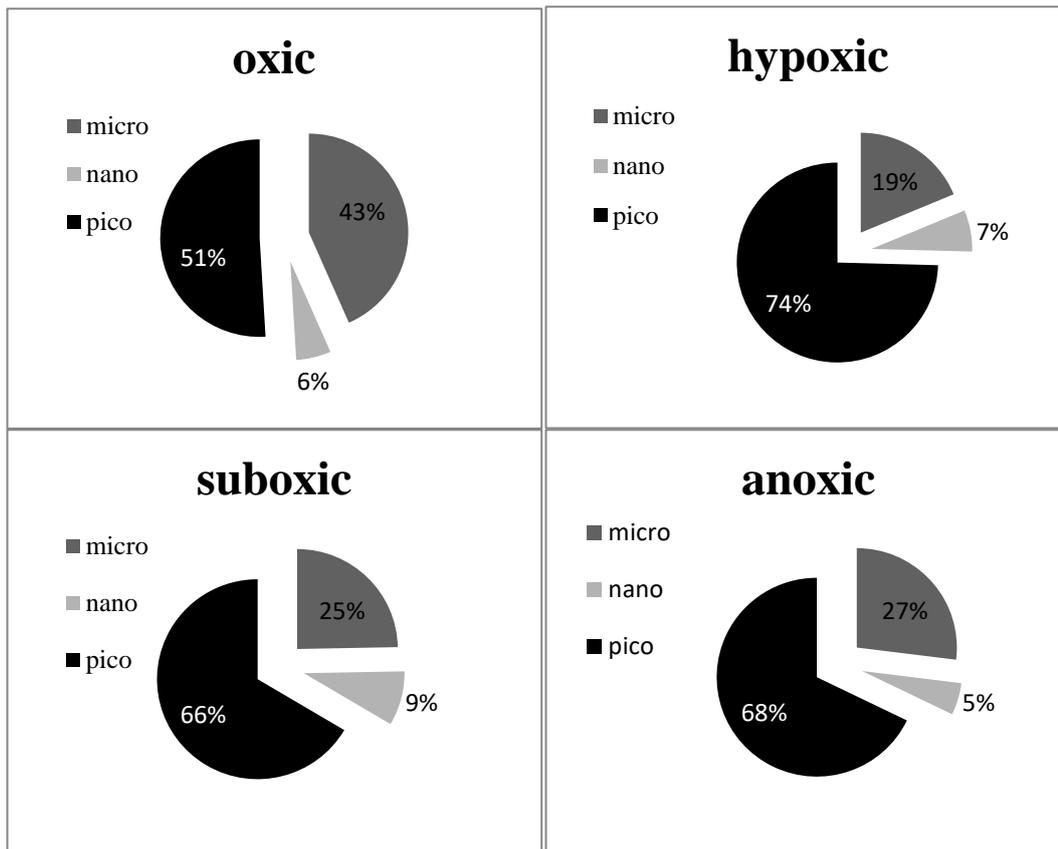


Fig.2. Size- fractionated Chl *a* distribution representing abundance of of pico (<5-0.7 μ m); nano (<20-5 μ m); and micro plankton (>20 μ m) in the study area under (A) oxic; (B) hypoxic; (C) suboxic and (D) anoxic conditions for the years 2005-2006.

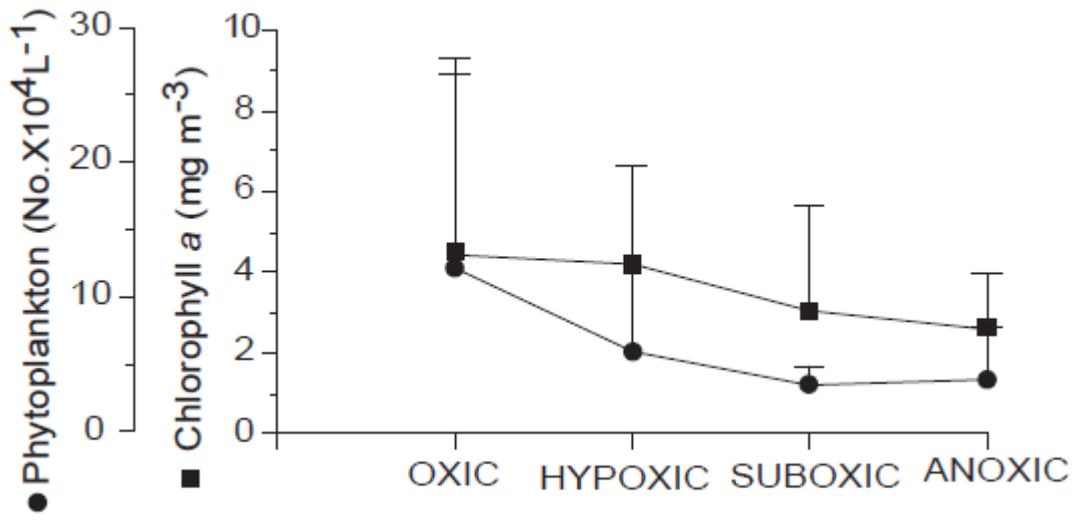


Fig.3. Average variations in abundance of phytoplankton and biomass (Chl *a*) from oxic to anoxic conditions.

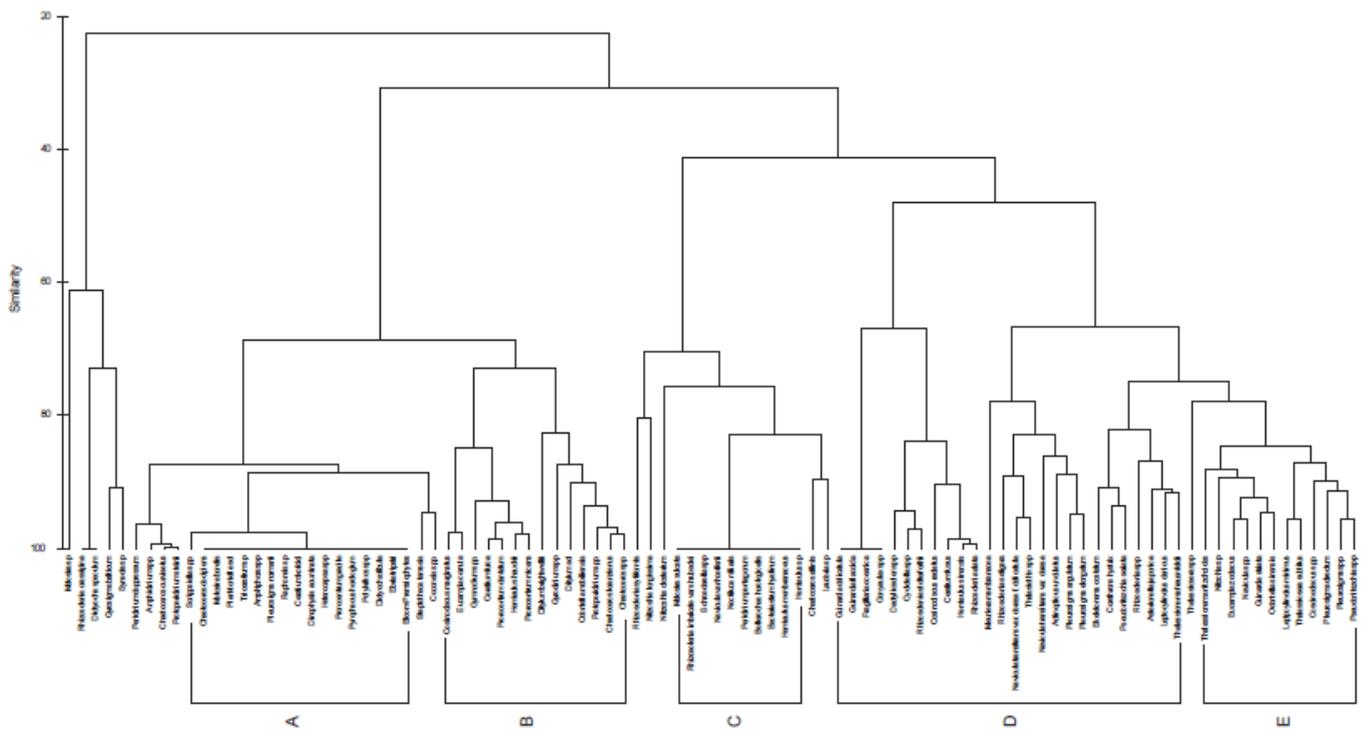


Fig.4. Dendrogram based on Bray-Curtis similarity showing average linkage cluster analysis for phytoplankton taxa in oxic , hypoxic , suboxic and anoxic waters.

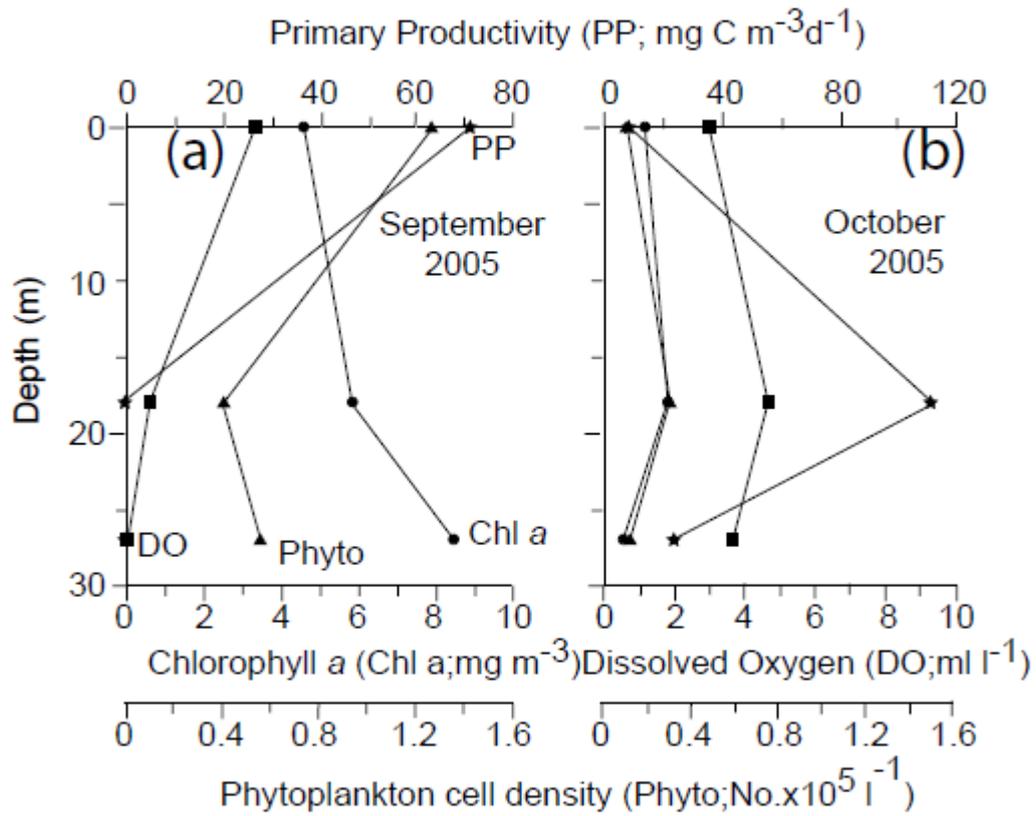


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Plate 1. Microphotographs of some of the diatoms showing *chlorophyll bearing* active cells associated with subsurface low oxygen coastal waters of Goa, central west coast of India.