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Environmental dynamics of red *Noctiluca scintillans* bloom in tropical coastal waters

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Abstract

An intense bloom of red *Noctiluca scintillans* (NS) occurred off Rushikulya estuarine region along east coast of India, an important site for mass nesting events of endangered Olive Ridley sea turtle. At its peak, densities of NS were 3.3 x 10^5 cells-l^{-1}, with low relative abundance of other phytoplankton. The peak bloom coincided with high abundance of gelatinous planktivores which may have facilitated bloom development by grazing on other zooplankton, particularly copepods. Ammonium concentrations increased by approximately 4-fold in the later stages of bloom, coincident with stable NS abundance and chlorophyll concentrations in the nano- and microplankton. This increase likely was attributable to release of intracellular ammonium accumulated through NS grazing. Dissolved oxygen concentrations decreased in sub-surface waters to near hypoxia. Micro-phytoplankton increasingly dominated chlorophyll-*a* biomass as the bloom declined, with diminishing picoplankton abundance likely the result of high predation by the ciliate *Mesodinium rubrum*.

Key Words: *Noctiluca scintillans*, bloom, chlorophyll, picoplankton, nutrient, Bay of Bengal

Introduction

Noctiluca scintillans ((Macartney) Kofoid&Swezy) [hereafter NS], a mainly heterotrophic dinoflagellate, often causes intensely colored red or green tides in coastal and offshore waters (D'Silva et al., 2012). Green strains of NS contain *Pedinomonas noctilucae* (a green alga) as an endosymbiont (Elbrachter and Qi, 1998; Sriwoon et al., 2008), which provides an added source of nutrition. In contrast, red NS strains are entirely heterotrophic. Blooms of red (non-chlorophyll containing) NS are observed globally in subtropical and temperate seas, whereas, the green NS blooms are generally restricted to western Pacific and Indian waters (Elbrachter and Qi, 1998; Saito and Furuya, 2006). In general both red and green NS feed voraciously on phytoplankton (especially diatoms) by phagotrophy, thereby shaping the size distribution and species composition of phytoplankton assemblages, some zooplankton, particularly copepods, and fish eggs (Elbrachter and Qi, 1998; Nakamura, 1998; Saito et al., 2006). Phytoplankton assemblages often are rich in diatoms at the onset of both red and green species of NS proliferation (Mohanty et al., 2007; Madhu et al., 2012) suggesting that they are a preferred prey, although NS also feed upon nanoplankton and picoplankton (Umani et al., 2004). When grazing on toxic phytoplankton, NS can transfer these toxins to higher trophic levels (Escalera et al., 2007). While zooplankton can graze on NS (Erkan et al., 2000), the collapse of NS blooms are more often the result of prey depletion (Kiorboe and Titelman, 1998; Nakamura, 1998). Ammonia excretion by NS species during grazing, and particularly the release of high intracellular ammonia pools upon cell death, can result in fish mortality and toxicity to other organisms (Aiyar, 1936; Okaichi and Nishio, 1976). The sudden collapse of these blooms also can generate hypoxic conditions in coastal regions (Naqvi et al., 1998). This broad range of negative environmental impacts is the reason why the ecophysiology of NS and their blooms are topics of active research.

Both red and green NS blooms are common in Indian coastal waters along both the eastern (Bay of Bengal) and western (Arabian Sea) shores, although they appear to be more frequent in the Arabian Sea than in the Bay of Bengal (Table 1 and references therein). Green NS blooms are most common in the Arabian Sea, except along Kerala coast where red NS recurrences are reported. Red and green NS blooms occur in the Bay of Bengal region, particularly off the Chennai coast and Rushikulya estuarine region (Table 1). The Rushikulya estuarine region, midway along the east coast of India, is recognized internationally as an eco-sensitive zone hosting mass nesting events of Olive Ridley sea turtles. The long-term data from time-series stations revealed significant variability in water quality parameters showing two local water types (Baliarsingh et al., 2015) along with a bi-modal distribution of chlorophyll-*a* (chl-*a*) at annual scales (Lotliker et al., 2015). Further, long-term satellite data analysis and previous reports on chl-*a* trend discerned comparatively high peak magnitude during the pre-south west monsoon that was more often associated with blooms (Sasamal et al., 2005). A large NS bloom was observed for the first time in this region during the summer 2005, which coincided with limited utilization of silicate in surface waters, and oxygen depletion of deep waters (Mohanty et al., 2007). Against this backdrop, a field campaign was conducted during the pre-monsoon period in 2014 to decipher the environmental dynamics of the bloom. We report here observations of a large NS bloom off the Rushikulya estuary during April 2014. These data contribute to our understanding of the causative linkages between physico-chemical conditions and the phytoplankton community composition during red NS blooms.

Materials and Methods

Study site

The present work was carried out in coastal waters off the Rushikulya estuary in the northwestern Bay of Bengal (Fig. 1). The tropical southwest (SW) monsoon in this region begins in June and July and ends in October, contributing an average annual rainfall of 1,210 mm (Mishra, 2001). Periodic pre-monsoon phytoplankton blooms associated with coastal upwelling is a prominent feature of the study area (Sasamal et al., 2005). The regional coastal currents are governed by the seasonal East India Coastal Current (EICC), monsoonal wind-driven surface currents, cyclonic regional eddy circulation, and local river discharge (Shetye et al., 1991; Vinayachandran and Mathew, 2003; Rao et al., 2007). This region has a long-term time-series of bio-optical and physico-chemical parameters under the SATellite Coastal and Oceanographic REsearch (SATCORE) programme coordinated by Indian National Centre for Ocean Information Services (INCOIS).

Methods

Five field surveys were carried out in the pre-monsoon period (April, 2014) at three stations (S1 to S3) and three depths (0, 10, 20 m) on April 13, 16, 20, 23, and 27 (Fig. 1). Level-3 Moderate Resolution Imaging Spectroradiometer - Aqua (MODISA) sea surface temperature (SST) data with 4km spatial resolution was obtained from the National Aeronautics and Space Administration's Goddard Space Flight Center. Light availability was measured using a Hyperspectral Radiometer (Satlantic™). Water samples collected for measurement of physico-chemical parameters and chl-*a* concentrations were frozen (-40ºC) until analysis. Water samples for the analysis of dissolved oxygen (DO) were fixed onboard with Winkler A and B solutions for further titrimetric analysis in the shore laboratory (Grasshoff et al., 1999). Salinity was measured by the Knudsen's titration method (Grasshoff et al., 1999), and total suspended matter (TSM) was quantified gravimetrically by filtering water samples through pre-weighed cellulose nitrate membrane filter papers (0.45µm) (Strickland and Parson, 1984). Water samples for nutrient analysis were collected using an acid-washed bucket (surface) and Niskin bottles (below surface) and stored in HDPE bottles under low temperature. The samples were filtered (<0.45 µm) in the laboratory on the day of collection and concentrations of nitrite (NO_2), nitrate (NO_3), ammonia (NH_4), phosphate (PO_4) and silicate (SiO_4) were measured using a UV-visible spectrophotometer (JASCO™, V-650) (Grasshoff et al., 1999). Ammonium concentrations were measured using an indophenol dye method (Riley and Chester 1971), taking care to correct for urea interference and to precondition the laboratory as ammonia free. The analytical precision of NO_2, NO_3, NH_4, PO_4 and SiO_4 were ±0.01, ±0.05, ±0.1, ±0.03 and ±0.03 µmol l^{-1} respectively.

Size-fractionated chlorophyll-*a* (chl-*a*) concentrations were collected by sequential filtration; 20 µm (for microplankton), 2 µm (for nanoplankton) and 0.2 µm (for picoplankton) (Brewin et al., 2014); concentrations were measured spectrophotometrically after 24 h extraction in 90% acetone at -4°C (Strickland and Parson, 1984). Water samples were collected from the surface in pre-cleaned plastic bottles for phytoplankton identification and enumeration and preserved with 1% Lugol's iodine-2% neutral formalin until analyzed (Hotzel and Croome, 1999). Phytoplankton were counted in the preserved samples using an inverted microscope (Labomed; Model: Lx 400) and standard identification keys (Tomas, 1997).

Results

Phytoplankton community composition

Our investigation began shortly after the initiation of a red NS bloom, where the coastal water was observed having a prominent brown to dull-red discolouration (Fig. 2). Taxonomic analysis confirmed the presence of red NS ranging in abundance from 0.15 - 3.3 x 10^5 cells l^{-1}. This observed maximum abundance was the second highest NS cell concentration reported along the Indian east coast, compared to the highest reported for a NS bloom in the Gulf of Mannar at 1.4 x 10^6 cells l^{-1} (Table 1). Total phytoplankton abundance varied by an order of magnitude, from 3.4 x 10^5 cells l^{-1} (St. 2, April 13) to 2.3 x 10^4 cells l^{-1} (St. 1, April 27), over the 12 d of observation. The phytoplankton community comprised primarily three major groups; diatoms (30 species), dinoflagellates (6 species), and unidentified picoplankton. Cell abundance and percentages of identified phytoplankton groups are presented in Table 2.

The phytoplankton community was dominated by NS over the early stage of the field survey (April 13, 16 and 20), which represented the peak phase of the NS bloom. During this time, NS ranged between 95.7% (April 13) and 79.3% (April 20) of the total cell abundance, which decreased during the declining phase of the bloom to 20.4 % (April 23) and 6.7 % (April 27) (Fig. 3). The decline in NS abundance coincided with increasing diversity of diatom species, presumably related in part to decreased predation. During the peak NS phase, *Thalassiosira* spp. was the dominant genus, a known prey species for red NS (Sahayak et al., 2005), along with fewer numbers of *Rhizosolenia castracanei* and *Thalassiothrix frauenfeldii* (Table 2). The declining NS abundance during the later stages of the NS bloom was accompanied by an increased presence of *Thalassiothrix frauenfeldii* and *Leptocylindrus danicus*. Low species diversity and abundance of other phytoplankton were observed during the bloom. These species included *Alexandrium* spp., *Ceratium furca, Ceratium tripos, Dinophysis caudata, Gonyaulax* spp., as well as the cyanobacterium *Trichodesmium erythraeum* (Table 2).

Size fractionated phytoplankton biomass

Total chl-*a* varied between 0.8 and 12.3 mg.m^{-3} during the bloom period, with picoplankton accounting for the majority of this chl-*a* biomass (49.5-66.1%) followed by nanoplankton (22.3-33.3%; Fig. 4). Microplankton composed the smallest proportion of total chl-*a* biomass (11.5-18.5%), consistent with a high level of predation by red NS. With the decline of the NS bloom the chl-*a* size distribution reversed—the proportion of total chl-*a* comprising microplankton (mainly diatoms) increased relative to pico and nanoplankton biomass (Fig. 3) although the total chl-*a* concentrations still were low (Fig. 4).

Environmental parameters

The monthly sea surface temperature (SST) from MODIS-Aqua varied between 26 to 29°C during the pre-bloom period (March) and the early stage of the NS bloom before *in situ* sampling (early April), but increased to 27 to 31°C during the mid to late bloom phase (late April; Fig. 5). Salinity remained high during the study, between 34.19 to 34.78 with an overall mean of 34.38 ± 0.14 (Fig. 4), presenting a stable environment for red NS cell division and population growth (Miyaguchi et al., 2006), and confirming that the Rushikulya estuary had little impact on NS bloom development during this pre-monsoon period. During the study period, TSM ranged from 4.66 - 20.70 mg l^{-1} (Fig. 4), the majority of which was cellular biomass and detritus with higher values coinciding with the peak phase of the bloom.

The concentrations of dissolved oxygen ranged from 2.14 to 5.78 mg.l^{-1} over the course of the survey (Fig. 4), decreasing during the decline of the NS bloom and from surface to deep waters. This decrease in DO can be ascribed to high respiration and decomposition of sinking detrital NS (Venugopal et al., 1979; Sahayak et al., 2005; Rabalais et al., 2010). Light availability was high during the study period, even with the high abundance of NS, with the base of the photic zone measured at ~ 20 m.

Nitrate concentrations decreased from 7.04 µmol l^{-1} on the first sampling date to 0.83 µmol l^{-1} at the end of the bloom, while NO_2 decreased from 0.81 to 0.02 µmol l^{-1} over the same period (Fig. 4). There were no consistent patterns in nitrogen profiles, with concentrations at times marginally higher in surface waters and sometimes in bottom waters. Ammonium concentrations increased from a low of 0.17 µmol l^{-1} on April 13 to 4.26 µmol l^{-1} on April 27 (Fig. 4). Concentrations of NH_4 increased slightly with depth, presumably reflecting either direct excretion by red NS (Drits et al., 2013), or regeneration from detrital degradation.

Phosphorus concentrations were highest (3.20 µmol l^{-1}) at the beginning of the survey, and decreased by an order of magnitude (0.32 µmol l^{-1}) by the end (Fig. 4). The maximum PO_4 concentration coincided with peak of the bloom. Elevated phosphorus concentrations became disproportionately depleted relative to N as the bloom progressed, likely due to preferential regeneration of N over P due to grazing and bacterial activity. In contrast to NO_3 and PO_4, SiO_4 concentrations were variable (2.98 to 6.65 µmol l^{-1}) but did not become depleted during the survey (Fig. 4). Indeed, SiO_4 concentrations may have increased slightly in the latter stages of the bloom. SiO_4 concentrations increased with depth in a number of instances, but this pattern was not uniform for all sampling periods and sites.

Discussion

Community structure and NS bloom dynamics

The Rushikulya estuarine region is a sensitive ecological zone hosting one of the few remaining mass nesting sites of Olive Ridley sea turtles, an endangered species that has declined dramatically in numbers over the last decade (Abreu-Grobois and Plotkin, 2008; Barik et al., 2014). There is an interest in better understanding the factors and signals of environmental quality in these waters. However, while all NS blooms do not necessarily cause negative environmental effects, some green NS blooms have been linked to anthropogenic inputs (Gomes et al. 2014), thus their linkage to degraded water quality deserves further study. In the bloom event described here, NS overwhelmingly dominated the plankton assemblage, with maximum cell densities of 3.3 x 10^5 cells-l^{-1} during the study period. This study was initiated after notification by local fishermen of its appearance, and as a consequence, there are no data to define the pre-bloom conditions, although qualitative observations confirmed that diatom abundances indeed were high prior to the NS bloom (data not shown), consistent with patterns of past observations in the study area (Panigrahy and Gouda, 1990). Diatoms are a preferred prey of red NS, and blooms of red NS often occur after diatom blooms (Turkoglu et al., 2013), however we cannot determine the specific conditions that triggered rapid growth of NS.

It is recognized that red NS prey sizes span from microzooplankton to bacteria (Umani et al., 2004), so the dynamics of change in phytoplankton size distribution provides a signal of the ecological interactions during the bloom. Lower abundances of microplankton and nanoplankton abundance were observed during the height of the NS bloom from 14-20 April. This was consistent with expected high predation rates on these size classes, and suggests that they had, and likely still were supporting NS growth. Although red NS are reported to prey upon bacteria (Umani et al., 2004), the proportion of picoplankton chl-*a* biomass increased during the peak NS phase. Either picoplankton growth rates exceeded NS predation rates— nutrient uptake rates of picoplankton exceed those of nano- and micro-phytoplankton—or the growth rates of nano- and microphytoplankton were sufficient to support high NS abundance. However, the overall low SiO_4 concentrations during peak bloom period would have negatively impacted diatom growth.

Picoplankton (<2 µm) and nanoplankton (2-20 µm) generally comprise ~60 to 98% of chlorophyll standing stock in oligotrophic conditions (Glover et al., 1985; Hopcroft and Roff, 1990), as was the case during the active phase of the NS bloom. The microphytoplankton (20-100 µm) contributed to 5-39% of total chlorophyll biomass during active phase of bloom, which increased to 43-73% during decline phase. In contrast, pico- and nano-phytoplankton biomass collapsed during the declining phase of the NS bloom (April 23-27), resulting in microphytoplankton dominating the autotrophic biomass during this later stage. The rapid decline in picophytoplankton abundance coincided with a sharp increase in abundance of the ciliate *Mesodinium rubrum* (~ 10^3 cells ml^{-1}; Fig. 2i), a grazer known to feed upon picoplankton (Stoecker and Evans, 1985; Bernard and Rassoulzadegan, 1990). The reasons for the decrease in nanophytoplankton are less clear.

Phytoplankton community structure, representing micro-plankton, revealed a total number of 29 diatoms and six dinoflagellates during the present study (Table 2). Although diatoms contributed comparatively less to total phytoplankton abundance during active phase of the bloom, species richness during both peak and decline phase signified the ecological adaptation of these species against the grazing pressure during NS bloom. No such significant change in species richness was observed in dinoflagellates (excluding NS) during either phase of the bloom.

Asterionellopsis glacialis, *Thallssiosira* spp., *Rhizosolenia styliformis*, *Rhizosolenia alata*, *Lauderia annulata* and *Rhizosoelnia catracanei* were dominant diatoms during the peak phase of the NS bloom. Diatomic species *viz*. *Coscinodiscus radiatus*, *Lauderia annulata*, *Rhizosolenia alata*, *Thalassiothrix frauenfeldii* and *Thalassiothrix longissima* were observed to dominate the diatom community during decline phase of the NS bloom. Among dinoflagallates, *Alexandrium* spp. and *Gonyaulax* spp. were observed as dominant dinoflagellates (excluding NS) during the peak phase of the NS bloom. *Dinophysis caudata* and *Gonyaulax* spp. dominated the dinoflagellates (excluding NS) during decline phase of the NS bloom. During the declining phase of the NS bloom, diatoms again accounted for a larger proportion of chlorophyll biomass, together with photosynthetic dinoflagellates. Mohanty et al. (2007) also reported a reduction in micro-phytoplankton diversity during a NS bloom, reporting the presence of only nine species of dinoflagellates, 19 species of diatoms, and one species of cyanobacteria (*Trichodesmium erythraeum*). The most abundant dinoflagellates, second to NS, were *Ceratium furca*, *Ceratium tripos*, *Dinophysis caudata* and *Prorocentrum micans*, while the most abundant diatoms included *Chaetoceros saffinis*, *Coscinodiscus radiatus*, *Coscinodiscus asteromphalus*, *Nitzschia longissima*, *Nitzschia sigma*, *Asterionellopsis glacialis*, *Thalassiothrix longissima* and *Rhizosolenia alata.* As with the 2014 NS bloom, it is not clear whether these phytoplankton represented preferred prey species for NS, or were those remaining after selective feeding on others. Padmakumar et al. (2010) also observed that red NS and diatoms (representing 14 genera) composed 56.2% and 43.8%, respectively, of the total phytoplankton biomass during a NS bloom off Kochi on the southwestern Indian coast. Although the species composition of potential prey varied among NS blooms, there was a general trend of reduced phytoplankton species diversity with the development of NS blooms.

The nutrient dynamics over the course of the bloom provide additional insight to the factors contributing to the decline of NS. The increase in NH_4 midway through the bloom phase is consistent which could be attributed to the release of intracellular NH_4 by NS , but it is the magnitude and change in nutrient ratios that provide more insight. The N:P ratios were very low (≤ 5) during the early bloom phase increasing to a maximum of 8.3 near the peak of the NS bloom (Fig. 7). These values are far below expected Redfield values (16:1) and signify either previous P-rich cultural eutrophication in the study area or enhanced denitrification in coastal bottom waters or sediments in and up current of the study region. Indeed, dissolved oxygen levels were uniformly low and at the threshold for the expression of denitrification genes in bacteria (Ward, 1996).

Silicate concentrations were low (~0.4 µM) during the NS bloom phase but increased slightly (~6 µM) in the declining phase, while P concentrations decreased rapidly at first and then slower but consistently through both bloom phases (Fig. 4). As a consequence, Si:P ratios were ≤5 during the active phase of the NS bloom (Fig. 7), which at these low nutrient concentrations suggests that diatom growth would have been Si-limited (Paul et al., 2008). As the NS bloom entered in decline phase the small increase in Si concentrations, perhaps due to greater sediment regeneration (e.g., Montani et al., 1998) associated with sinking NS biomass, would have partially alleviated this limitation. In any case, the increased Si availability would help explain the observed floristic shift to diatoms (Fig. 3).

Predator-prey dynamics of the bloom

The peak of the red NS bloom coincided with a high abundance of swarming gelatinous zooplankton (Fig. 2). These planktivores are known to strongly graze on copepods, and their increasing presence would have relieved copepod grazing pressure on diatoms and other phytoplankton (Pitt et al., 2007; Wollrab and Diehl, 2015). Thus the jellyfish presence may have helped establish favorable conditions for initiation of the NS bloom. However, other studies report that jellyfish and salps feed upon green NS (Matondkar et al., 2012), indicating the complexity of intra-trophic dynamics among grazers. In addition to causing a shift in planktonic communities from dominance by diatoms and copepods at the lower trophic level, NS can alter trophic interactions via carbon transfer to salps and jellyfish (Gomes et al., 2014). It is possible though that the predation rates on NS were low as NS is considered to be a poor energy source due to its low carbon and high ammonia content (Okaichi and Nishio, 1976; Kiørboe and Titelman, 1998). However, ammonium concentrations increased in the later stages of the red NS bloom concurrent with decreases in NO_3. Chlorophyll concentrations in the nano- and microplankton remained relatively low and stable from April 13-20, as did NS abundance (as a percentage), while ammonium concentrations increased approximately 4-fold over this time frame. This increase likely is attributable to the release of intracellular ammonium accumulated through NS grazing, rather than bacterial degradation of phytoplankton biomass given that diatom biomass did not decline substantially. These grazer-grazer interactions play a key role in understanding food web dynamics that regulate the initiation, development and decline of NS blooms.

Environmental controls and consequences of the NS bloom

The initiation of red NS blooms is the result of a complex interaction among currents, wind, nutrients, and prey (Huang and QI, 1997; Smayda, 1997; Dela-Cruz et al., 2003, Harrison et al., 2011). Low riverine inputs were also confirmed by uniformly high salinity measurements during the bloom. This also suggests that the driving factors for the NS bloom and associated predator/prey interactions were in-situ conditions rather than riverine in origin.

Previous studies related to red NS bloom in this area reported lower SSTs during peak bloom stages compared to pre and post bloom periods (Mohanty et al., 2007). In contrast, in the present study, lower SSTs were observed prior to and during the decline of the bloom with increasing SST observed during the active phase of the bloom (Fig 4). Huang and QI (1997) reported proliferation of red NS in Dapeng Bay, South China Sea, associated with low SST, which is consistent with indications that stable temperature (and relatively low runoff) preceded the proliferation of NS.

The higher rates of respiration and enhanced carbon export with large NS blooms often leads to low oxygen concentrations in and below the photic zone (Naqvi et al., 1998; Sahayak et al., 2005), consistent with the findings in the present study. Dissolved oxygen concentrations were depleted substantially in both surface and sub-surface waters, very close to the upper boundary (2 mg L^{-1}) for hypoxia (Fig. 4). At these low levels of dissolved oxygen, some disruption of benthic and demersal communities are expected, leading to sublethal and avoidance effects for fish and other species (Davis, 1975). Indeed, anecdotal information from local fishermen suggested that fish were avoiding the area. Low oxygen conditions associated with a red NS bloom off Kochi, Arabian Sea, caused mortality of fish (Naqvi et al., 1998). Hypoxic conditions associated with a recent green NS bloom off Mangalore in the Arabian Sea led to fish evasion of the affected area, and fishermen reported that fishing activity was poor during the NS bloom

(Sulochanan et al., 2014). Dissolved oxygen values in the upper 20 m ranged from ~2-6 mg L^{-1}, in most cases substantially less than the ~6.5-8 mg L^{-1} measured during April in non-bloom years (Baliarsingh et al., 2015). Although data are sparse for the period immediately preceding the NS bloom, there were no indications of low oxygen conditions before the bloom, as supported by anecdotal reports from local fishermen. Although high NH_4 concentrations also can become toxic to coastal fisheries (Padmakumar et al., 2010), the concentrations measured during the present study are well below this threshold.

Recent work suggests that hypoxic or low-oxygen concentrations may facilitate the photosynthetic rates of *Pedinomonas noctilucae*, the endosymbiont of green NS strains, implying that hypoxia may provide a competitive advantage (Gomes et al., 2014). However, red NS strains lack these photosynthetic endosymbionts, and there are no clear mechanisms as to why hypoxic conditions might favor NS competitive success, meaning that it is more likely that hypoxia in these waters was a consequence of, rather than trigger of, NS bloom development.

Conclusions

An ecosystem disruptive NS bloom occurred in coastal waters of the northwestern Bay of Bengal prior to the onset of the southwest monsoon, generating lowered oxygen concentrations within the photic zone, increased NH_4 concentrations, and anecdotal evidence of fish avoidance in the region. Salinity was uniformly high during the bloom, indicating that this event was triggered by in-situ conditions rather than riverine inputs. Although diatoms were abundant before the bloom (unpublished data), they were a small proportion of the picoplankton-dominated phytoplankton assemblage during the bloom. This change is consistent with the expected grazing of red NS on nano- and microplankton. Co-occurrence of gelatinous planktivors at the early stages of the NS bloom likely facilitated the NS growth by feeding on their copepod competitors. Nutrient concentrations were low during the bloom, consistent with both the picoplankton dominance of the assemblage. Collapse of the red NS bloom likely occurred when availability of diatom prey declined. Diatom and photosynthetic dinoflagellates emerged as an increasing proportion of chlorophyll biomass as the NS bloom declined. A small increase in Si concentrations may have contributed to this community shift, but more importantly there was a sharp decrease in picoplankton biomass. This decline was coincident with increasing grazing pressure from the ciliate *M. rubrum,* which became abundant in the declining phase of the NS bloom. These findings show how recurrent NS blooms can disrupt ecosystem balance in Indian coastal waters, and provide insights into the trophic interactions that support the initiation, development and decline of NS blooms.

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Figure legends

Fig. 1 Study site in northwestern Bay of Bengal (inset) with sampling sites shown as S1, S2 and S3. [Inset: Study site relative toknown occurrences of red *Noctiluca scintillans* (red dots), green *N. scintillans* (green dots), and *N. scintillans* blooms with no color reported (black dots)

Fig. 2 Discoloration of water and floating bloom off the Rushikulya estuary (photographed on 13-16 April 2014; a-e), swarming jellyfish off the Rushikulya estuary (f-h), microscopic images of *Mesodinium rubrum* (40x magnification; i), microscopic images of *Noctiluca scintillans* (4x magnification; j-l).

Fig. 3 The relative abundance of diatoms, *Noctiluca scintillans* (NS) and other dinoflagellates (OD) to total phytoplankton abundance (upper row) and the relative contributions of picoplankton, nanoplankton (nano) and microplankton (micro) to the total size fractionated chlorophyll-*a* (lower row) on13, 16, 20, 23, and 27 April 2014

Fig.4 Vertical distribution of hydrobiological parameters at different stations (S1-S3, see Figure 1 for locations) and observation days (13, 16, 20, 23, and 27 April 2014).Fractionated chlorophyll concentrations (mg-m^{-3}) are shown for picoplankton (Chl_*a*_pico), nanoplankton (Chl_*a*_nano), and microplankton (Chl_*a*_micro). Phytoplankton abundance is shown as 10^{4}cells-l^{-1}. Total suspended matter (TSM) and dissolved oxygen (DO)concentrations are shown in mg-l^{-1}. Salinity is shown in practical salinity units (psu) and nutrients (NO_2, NO_3, NH_4, PO_4, SiO_4) are in µmol-l^{-1}.

Fig. 5 Variability in Sea Surface Temperature (SST) retrieved from the MODIS-Aqua satellite in April 2014.

Fig. 6 Molar ratios of macronutrients [Nitrate (N) to Phosphate (P) and Silicate (S) to Phosphate (P)] in surface seawater from 13-27 April. Blue oval outline denotes significant silicate limiting conditions and red oval outline denotes significant nitrogen limiting conditions.

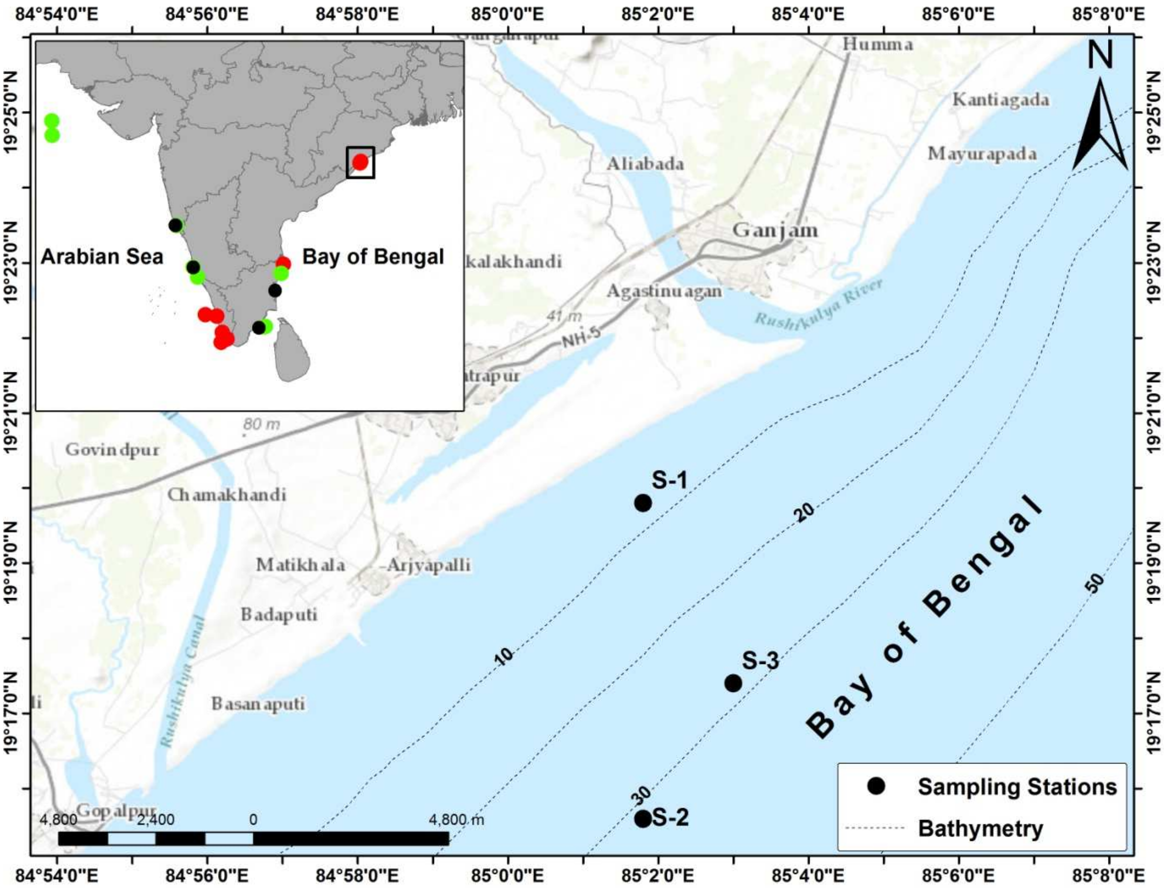
84°54'0"E
84°56'0"E
84°58'0"E
85°0'0"E
85°2'0"E
85°4'0"E
85°6'0"E
85°8'0"E
19°25'0"N
19°23'0"N
19°21'0"N
19°19'0"N
19°17'0"N
Arabian Sea
Bay of Bengal
Humma
Kantiagada
Mayurapada
Aliabada
Ganjam
Agastinuagan
Rushikulya River
NH-5
41 m
80 m
Govindpur
Chamakhandi
Matikhala
Arjyapalli
Badaputi
Basanaputi
Rushikulya Canal
Gopalpur
S-1
S-2
S-3
10
20
30
50
Bay of Bengal
N
4,800
2,400
0
4,800 m
Sampling Stations
Bathymetry

Figure 1

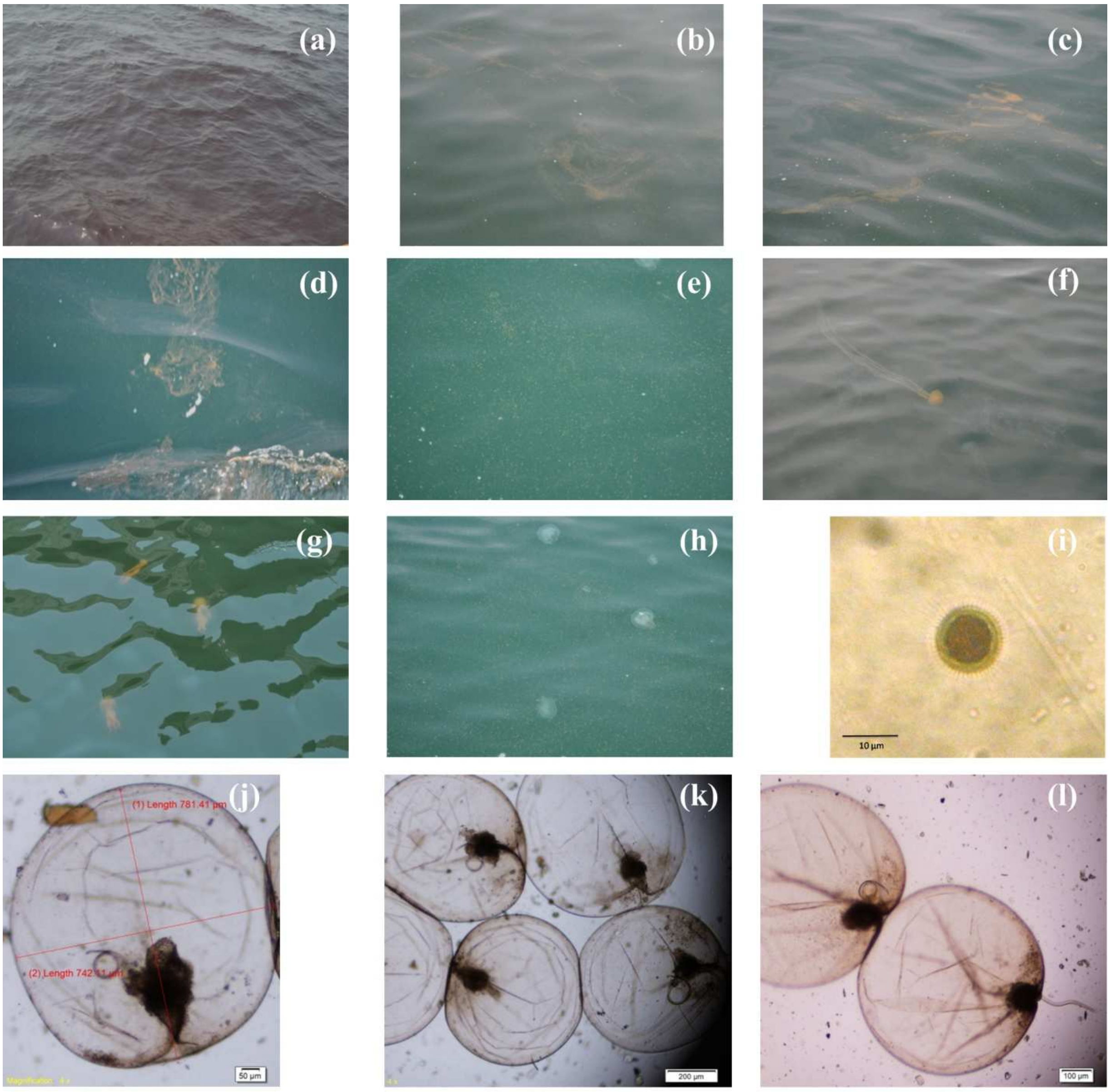
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
10 µm
(j)
(1) Length 781.41 µm
(2) Length 742.11 µm
50 µm
Magnification 4 x
(k)
200 µm
(l)
100 µm

Figure 2

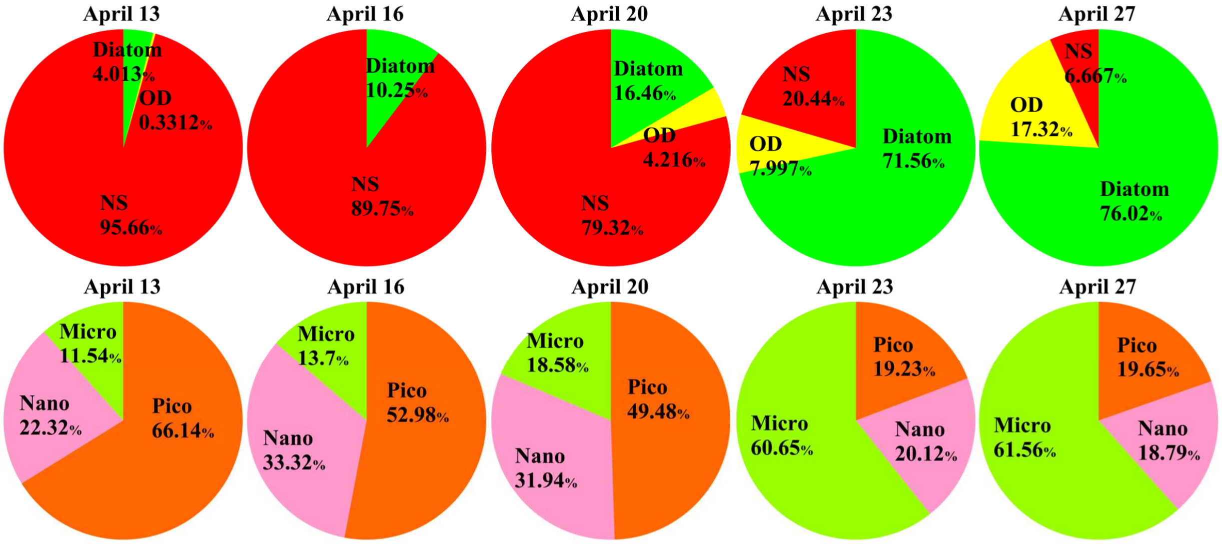
April 13
Diatom 4.013%
OD 0.3312%
NS 95.66%
April 16
Diatom 10.25%
NS 89.75%
April 20
Diatom 16.46%
OD 4.216%
NS 79.32%
April 23
NS 20.44%
OD 7.997%
Diatom 71.56%
April 27
NS 6.667%
OD 17.32%
Diatom 76.02%
April 13
Micro 11.54%
Nano 22.32%
Pico 66.14%
April 16
Micro 13.7%
Nano 33.32%
Pico 52.98%
April 20
Micro 18.58%
Nano 31.94%
Pico 49.48%
April 23
Pico 19.23%
Micro 60.65%
Nano 20.12%
April 27
Pico 19.65%
Micro 61.56%
Nano 18.79%

Figure 3

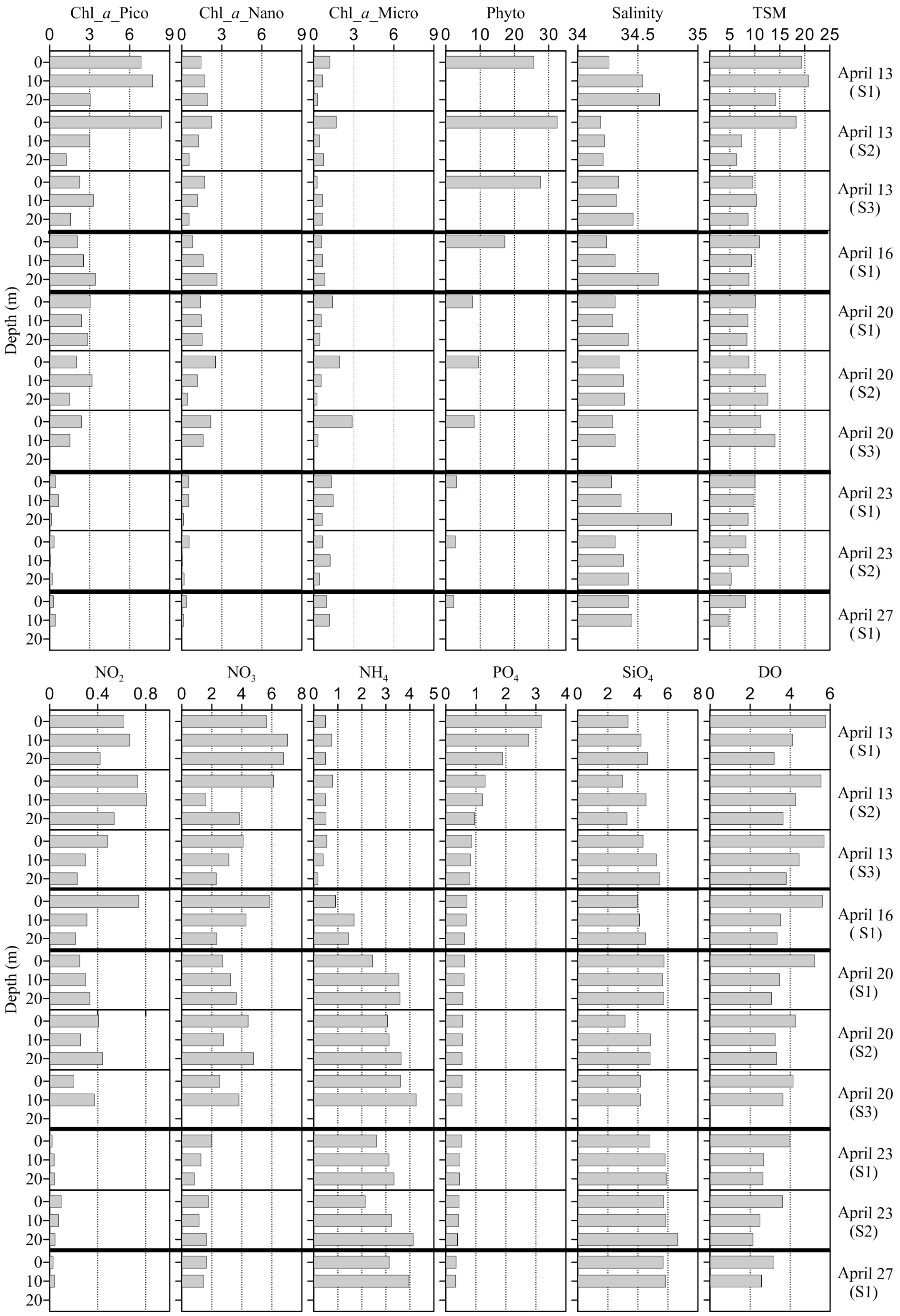
Chl_a_Pico
0 3 6 9
Chl_a_Nano
0 3 6 9
Chl_a_Micro
0 3 6 9
Phyto
0 10 20 30
Salinity
34 34.5 35
TSM
5 10 15 20 25
Depth (m)
0
10
20
April 13 (S1)
April 13 (S2)
April 13 (S3)
April 16 (S1)
April 20 (S1)
April 20 (S2)
April 20 (S3)
April 23 (S1)
April 23 (S2)
April 27 (S1)
NO2
0 0.4 0.8
NO3
0 2 4 6 8
NH4
0 1 2 3 4 5
PO4
0 1 2 3 4
SiO4
0 2 4 6 8
DO
0 2 4 6
Depth (m)
April 13 (S1)
April 13 (S2)
April 13 (S3)
April 16 (S1)
April 20 (S1)
April 20 (S2)
April 20 (S3)
April 23 (S1)
April 23 (S2)
April 27 (S1)

Figure 4

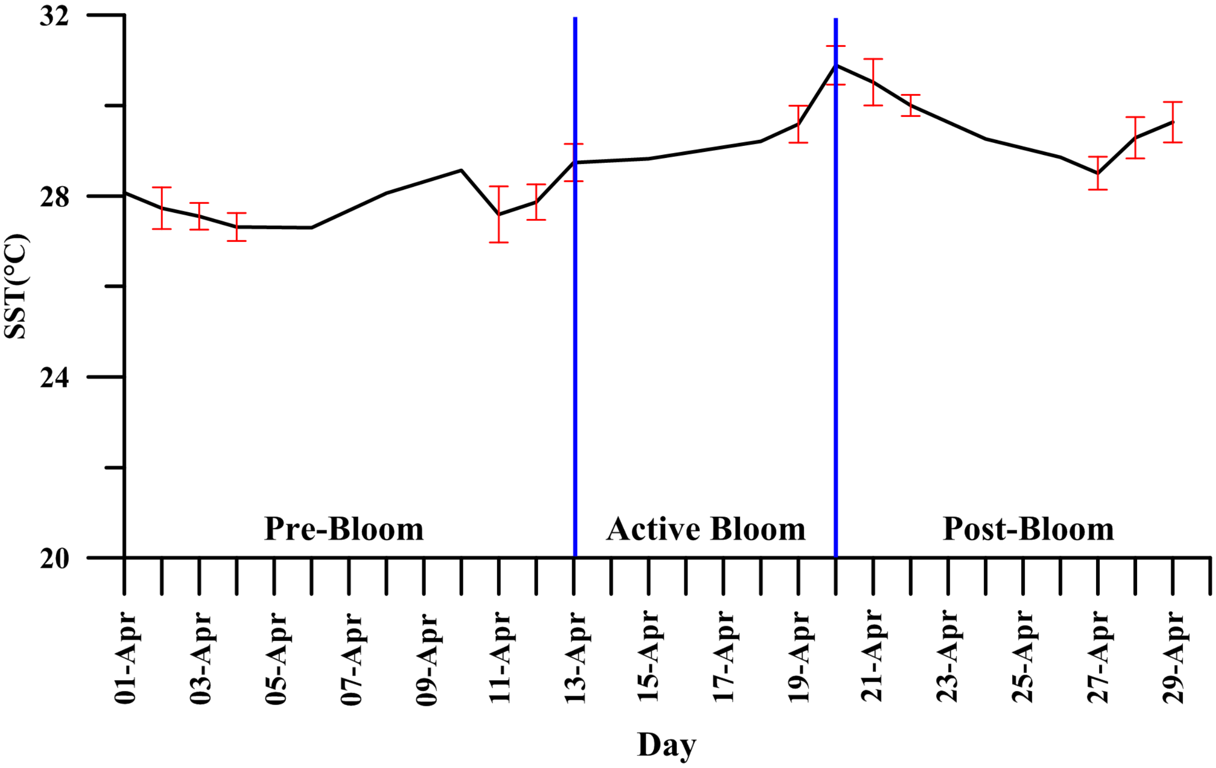
32
28
24
20
SST(°C)
Pre-Bloom
Active Bloom
Post-Bloom
01-Apr
03-Apr
05-Apr
07-Apr
09-Apr
11-Apr
13-Apr
15-Apr
17-Apr
19-Apr
21-Apr
23-Apr
25-Apr
27-Apr
29-Apr
Day

Figure 5

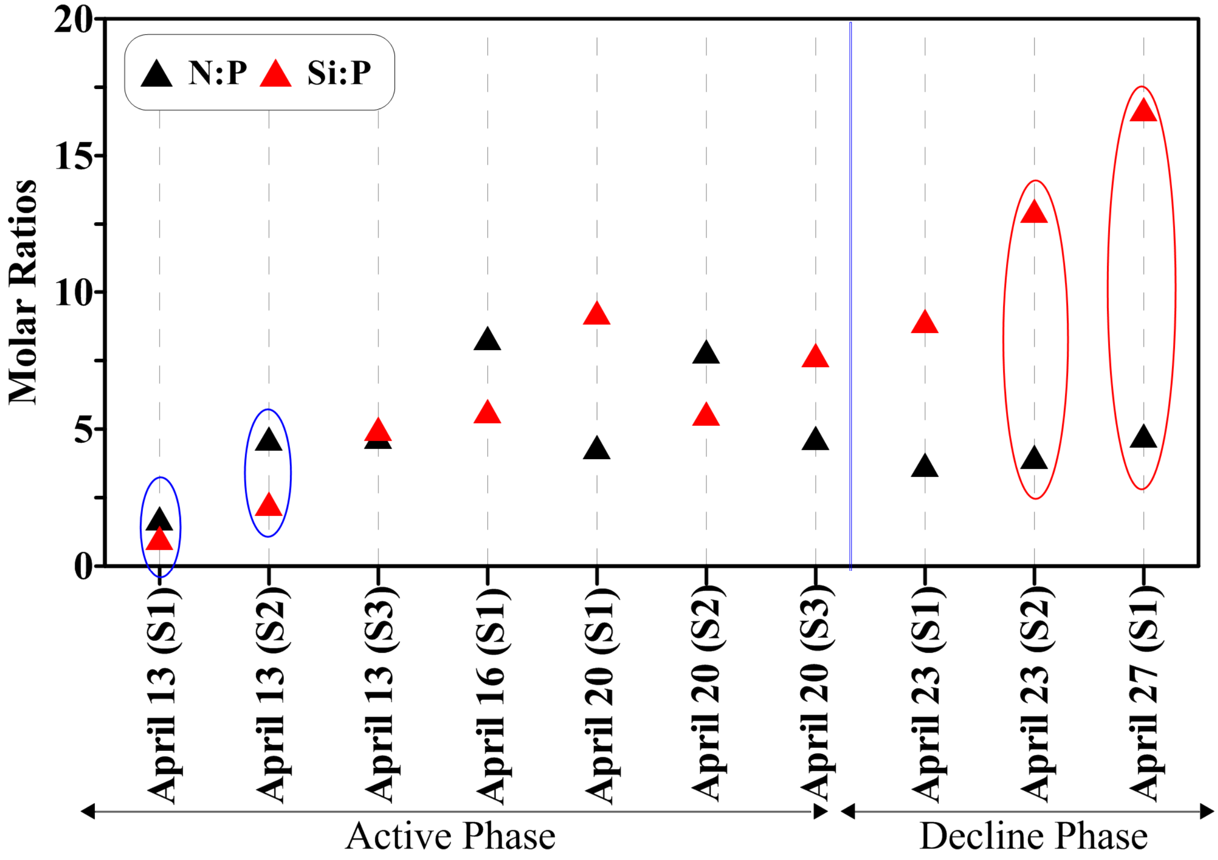
20
15
10
5
0
Molar Ratios
▲ N:P ▲ Si:P
April 13 (S1)
April 13 (S2)
April 13 (S3)
April 16 (S1)
April 20 (S1)
April 20 (S2)
April 20 (S3)
April 23 (S1)
April 23 (S2)
April 27 (S1)
Active Phase
Decline Phase

Figure 6

Table 1.Records of *Noctiluca scintillans* (also known as *Noctiluca miliaris*) blooms and their impacts in Indian waters [updated from D'Silva *et al.* (2012)]

Region	Date	Maximum Abundance (cells l^{-1})	Chl-*a* (mg m^{-3})	Observation	Reference
East coast of India(red *Noctiluca scintillans*)					
Off Rushikulya estuary, South Odisha coast	Apr 2014	32.87x 10^4	12.3	Brown to dull-red discolouration of seawater. Lack of fish in the area	Present study
Rushikulya river, South Odisha coast	5 Apr2005	2.38 x 10^5		Red discolouration of seawater, O_2 depletion	Mohanty et al. (2007)
Madras, Tamil Nadu	June 1935			Pink colouration of seawater; fish mortality	Aiyar (1936)
East coast of India(green *Noctiluca scintillans*)					
Gulf of Mannar	2 –12Oct 2008	13.5 x 10^5	116	Deep-green colouration of seawater; coral bleaching due to O_2 depletion; death of fish & other sea animals	Gopakumar et al. (2009)
Minnie bay, Port Blair, Andamans	20 Dec 2002	0.2 x 10^5	32.7	Green colouration of seawater	Dharani et al. (2004)
Port Blair Bay, Andamans	June–July 2000	2.3 x10^4	17.6	Green colouration of seawater	Eashwar et al. (2001)
Palk Bay, Mandapam, Tamil Nadu	Apr–July 1952			Green *Noctiluca*	Raghu Prasad (1953; 1958)
Kalpakkam, Tamil Nadu	11–17 Oct 1988	0.4 x 10^5	28	Green *Noctiluca*	Sargunam and Rao (1989)
East coast of India (no color reported)					
Mandapam and Keelakarai, South east coast of India	July to Dec 2008				Anantharaman et al. (2010)
Vellar Estuary, Tamil Nadu	Aug 1966, Aug 1967,	2.9 x 10^6			Santha Joseph (1975)

	May 1968				
West coast of India(red *Noctiluca scintillans*)					
Kerala coast	Sept 2004		0.7	Red discolouration of seawater	Joseph et al. (2008)
Offshore of Kochi, Kerala	19 Aug2008	5 x 10^8		Brick red discolouration of seawater; no fish mortality observed	Padmakumar et al. (2010)
Offshore south of Thiruvananthapuram, Kerala coast	29 Sept 2004	9 x 10^5	0.6	Red discolouration of seawater	Sahayak et al. (2005)
Cochin–Calicut, off Kerala coast	8-10 Aug 1998			Red discolouration of seawater. O_2 depletion resulted in fish mortality	Naqvi et al. (1998)
Cochin, Kerala	Aug 1977	7.7 x 10^2		Red coloration of seawater	Devassy et al. (1979)
Off Quilon, Kerala	Aug 1976	4.1 x 10^2		Red colouration of seawater	Venugopal et al. (1979)
West coast of India(green *Noctiluca scintillans*)					
Arabian Sea	Feb 2009	9.6 x10^3	25	Green *Noctiluca*	Gomes et al. (2014)
Off Gujarat	17 Feb 2009		27.7	Green colouration of seawater	Tholkapiyan et al. (2014)
Off Mangalore	12 May 2011	10.5 x10^5	9.1	Green colouration of seawater	Sulochanan et al. (2014)
Northern Arabian Sea	Mar 2011			Green colouration of seawater	Matondkar et al. (2012)
Northern Arabian sea	Mar 2000	3 x 10^6	2.5	Yellowish-green mat over the surface water	Madhuet al; (2012)
Northern Arabian Sea	9-29 Feb 2009	9600		Green colouration of seawater	Matondkar et al. (2012)
Eastern Arabian sea	20 Feb - 11 Mar 2004		2.7	Green *Noctiluca*	Prakash et al. (2008)
Offshore near Gujarat	Mar 2007	4 x 10^3	21.9	Deep green colouration of	Padmakumar et al. (2008)

				seawater	
Offshore near Goa to Porbandar (Gujarat) coast	26 Feb–15 - Mar 2003	2542		Green colouration to seawater	Matondkar et al. (2004)
Mangalore	Jan 1987	7.6 x 10^6		Intense green coloration of seawater	Katti et al. (1988)
Mandovi & Zuari estuaries; coastal waters of Goa	Feb –Apr 1987	5.1 x 10^4	16.7	Green coloration of seawater; reduced fish yields	Devassy and Nair (1987)
Malbar and Kanara Coast	Oct 1948	0.5 x 10^5		Pink and red discolouration of seawater. No mortality but fish avoided the area; abrupt reduction in fish yield was observed	Bhimachar and George (1950)
West coast of India(no color reported)					
Offshore near Goa	8 Oct 2008	2 x 10^4		No fish kills observed	Sanilkumar et al. (2009)
Offshore near Mangalore	May 1993	1.6 x 10^3		Increased number of *Moraxella*-like bacteria associated with bloom	Nayak et al. (2000)

Table 2 Phytoplankton species abundance (x 10^4cells l^{-1}) and % total abundance (in parenthesis) in April 2014 at stations S1 – S3 (see Figure 1 for locations)

Sampling Date	**April 13**			**April 16**	**April 20**			**April 23**		**April 27**
Stations	**S1**	**S2**	**S3**	**S1**	**S1**	**S2**	**S3**	**S1**	**S2**	**S1**
Diatoms										
Asterionellopsis glacialis				0.35 (2.03)						0.03 (1.13)
Bacteriastrum spp.										
Chaetoceros coarctatus			0.07 (0.27)	0.10 (0.57)						
Chaetoceros decipiens									0.24 (8.8)	
Chaetoceros spp.	0.08 (0.29)				0.04 (0.46)		0.06 (0.7)	0.12 (3.91)		0.01 (0.56)
Corethron spp.								0.03 (1.01)	0.02 (0.81)	
Coscinodiscus ecentricus										
Coscinodiscus radiatus	0.07 (0.25)							0.36 (11.28)		0.02 (1.0)
Coscinodiscus spp.					0.13 (1.6)		0.05 (0.6)	0.01 (0.38)	0.04 (1.28)	0.24 (10.3)
Eucampia zoodiacus										
Hemiaulus sinensis				0.06 (0.33)	0.12 (1.53)	0.12 (1.27)		0.08 (2.52)	0.08 (2.9)	0.04 (1.73)
Lauderia annulata	0.18 (0.69)							0.29 (9.11)	0.24 (8.8)	0.23 (9.9)
Leptocylindrus danicus	0.10 (0.39)	0.14 (0.41)		0.25 (1.45)		0.79 (8.31)		0.05 (1.58)	0.06 (2.24)	0.40 (17.2)
Meuniera membranacea						0.04 (0.43)				

Navicula spp.								0.07 (2.14)	0.06 (2.35)	
Nitzschia closterium	0.02 (0.07)									0.07 (3.16)
Odontella mobiliensis								0.03 (1.01)	0.02 (0.73)	0.04 (1.82)
Planktoneilla sol							0.10 (1.2)	0.04 (1.26)		
Pleurosigma directum				0.07 (0.42)						
Pseudonitzschia pungen			0.09 (0.33							
Rhizosolenia alata	0.30 (1.13)	0.28 (0.81)				0.32 (3.4)		0.33 (10.24)	0.42 (15.4)	0.09 (3.7)
Rhizosolenia castracanei					0.26 (3.4)			0.02 (0.73)		
Rhizosolenia spp.				0.03 (0.2)						0.24 (10.4)
Rhizosolenia stolterfothii							0.22 (2.64)	0.10 (3.1)	0.03 (0.99)	
Rhizosolenia styliformis	0.22 (0.83)	0.22 (0.64)								0.16 (6.93)
Synedra spp.								0.14 (4.32)	0.16 (5.87)	0.04 (1.65)
Thalassiosira spp.	0.66 (2.45)	0.75 (2.19)	0.22 (0.8)	0.85 (4.93)		0.98 (10.4)				
Thalassiothrix frauenfeldii		0.15 (0.44)					1.12 (13.6)	0.39 (12.35)	0.46 (16.7)	
Thalassiothrix longissima				0.06 (0.33)				0.38 (11.91)		0.15 (6.7)
Dinoflagellates										
Noctiluca scintillans	24.64 (94)	32.87 (96)	27.02 (98)	15.46 (90)	7.02 (90)	6.86 (72)	6.26 (76)	0.64 (20)	0.57 (21)	0.15 (6.7)

Alexandrium spp.	0.03 (0.13)						0.01 (0.06)	0.01 (0.16)	0.07 (2.49)	
Ceratium furca			0.08 (0.29							
Ceratium tripos									0.09 (3.15)	
Dinophysis caudata										0.22 (9.35)
Gonyaulax spp.			0.16 (0.58)		0.26 (3.3%)	0.36 (3.8)	0.46 (5.55)	0.09 (2.83)	0.18 (6.6)	0.18 (7.97)
Total Phytoplankton	26.29	34.41	27.65	17.23	7.82	9.47	8.26	3.17	2.73	2.31