

Shallow convective mixing promotes massive *Noctiluca scintillans* bloom in the northeastern Arabian Sea

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Abstract

The northeastern Arabian Sea (NEAS) experiences convective mixing during winter, but this mixing does not reach up to the silicicline, resulting in the limited supply of silicate (Si) compared to nitrate (N) and phosphate (P) to the mixed layer (ML) and formation of non-diatom blooms. The poleward advection of waters of low surface salinity by the West India Coastal Current (WICC) to the NEAS weakens the vertical mixing and reduces the Si input to the mixed layer, resulting in occurrence of *Noctiluca scintillans* blooms. The saturation of dissolved oxygen in the NEAS varied between 88 and 98%, suggesting *N. scintillans* blooms occur in oxic conditions. Enhanced cell abundance of *N. scintillans* was observed in the bloom region in the upper 10 m. Phytoplankton pigments data revealed higher contribution of Chlorophytes, Prasinophytes, Prymnesiophytes and Prochlorophytes in the bloom than non-bloom region. The isotopic composition of nitrogen and carbon of particulate organic matter indicated that natural and *in situ* processes contributed to both nutrients and organic carbon pool in the NEAS in supporting the massive occurrence of *N. scintillans* blooms than hitherto hypothesized to anthropogenic sources. This study further suggests that the effect of anthropogenic pollutants released into the NEAS from the mega-cities is limited to the neighbourhood of these cities and does not affect the open ocean.

1. Introduction

Cool and dry winds, blowing from the land to the ocean, force convective mixing during winter, leading to nutrient-replete, deep mixed layers in the northern Arabian Sea (e.g., Banse, 1968, 1987; Madhupratap et al., 1996; Morrison et al., 1998). The studies carried out under the Joint Global Ocean Flux Study (JGOFS, 1989–1998) revealed that the mixed-layer (ML) depth during winter was 80-120 m, resulting in input of significant amounts of nitrate (N) and phosphate (P) to the mixed layer (ML), but the input of silicate (Si), however, is limited owing to a deeper silicicline (>100 m; de Sousa et al., 1996; Morrison et al., 1998; Naqvi et al., 2002). This deep silicicline and the limitation of silicate imply that diatoms do not dominate other phytoplankton biomass during winter in the northeastern Arabian Sea (NEAS; Sawant and Madhupratap, 1996; Madhupratap et al., 1996; Naqvi et al., 2002). Instead, the dominance of smaller phytoplankton groups (prymnesiophytes, prasinophytes, and cyanobacteria) were reported in the NEAS during winter with picoplankton (*Prochlorococcus* sp.) contributing up to >50% to the total phytoplankton biomass due to Si limitation (Roy et al., 2015; Roy and Anil, 2015). Recently Prakash et al. (2017) found that intense mixing and deeper ML led to formation of weak *N. Scintillans* blooms and vice versa. The green *N. scintillans* is a heterotrophic dinoflagellate that contains a photosynthetic symbiont - *Protoeuglena noctilucae* (Wang et al., 2016). Generally, *Noctiluca* is heterotrophic whereas the green *Noctiluca* from the Arabian Sea is a mixotrophic (Goes and Gomes, 2016) because it can sustain itself either through carbon fixation by its green autotrophic endosymbiont (*Protoeuglena noctilucae*) or via ingestion of exogenous prey (heterotrophic). *Protoeuglena noctilucae* (family of Marsupiomonadaceae and in the order of Marsupiomonadales) was formerly referred as *Pedinomonas scintillans* under previously assigned order Pedinomonadales (Wang et al., 2016). This species is normally found in the tropical regions with water temperature ranging between 25° and 30°C (Kraberg et al., 2010; Honer, 2002) and occurs mainly in the Red Sea, Bay of Bengal and northern Arabian Sea (Chaghtai and Saifullah, 2006, Harrison et al., 2011). The occurrence of green *Noctiluca* blooms in the Indian waters is common following the enhanced phytoplankton production due to upwelling or winter convective mixing (Sahayak et al., 2005, Padmakumar et al., 2010). Field studies suggested that bloom formation of green *N. scintillans* depends on active phagotrophy (Sriwoon et al., 2008) and that it survives primarily on photoautotrophy under food-limited conditions (Harrison et al., 2011). Once it becomes dominant, its active grazing prevents population growth of co-existing phytoplankton (Hansen et al., 2004). The occurrence of *N. scintillans* was reported as early as 1900 along the east coast of the Arabian Sea (Subrahmanyam, 1954; Devassy et al., 1979; Devassy and Nair, 1987; Devassy, 1989; Gomes et al., 2008; D'Silva et al., 2012), the

coastal and inland waters off Pakistan (Chaghtai and Saifullah, 2006), and the Gulf of Oman (Al-Azri et al., 2007) during both summer and winter. Since last decade, sustained efforts were made to study the occurrence of these blooms in the Arabian Sea (Nayar et al., 2001, Prakash et al., 2008, Madhu et al., 2012; Gomes et al., 2008, 2009; 2014; Lotlikar et al., 2018). Recently, Gomes et al. (2014) reported that phytoplankton group shifted from diatoms to dinoflagellates, specifically *N. scintillans*, in the NEAS and attributed to release of untreated pollutants from the bordering countries. Such shift may disrupt the food chain and may influence regional fisheries and health of ecosystem (Gomes et al., 2014). They hypothesized that the formation of hypoxic conditions at the surface due to decomposition of sewage-borne organic matter facilitated *N. scintillans* to bloom. In this study, we identify possible sources of nutrients and organic matter in the NEAS using stable isotopic composition of carbon and nitrogen in the particulate organic matter in the *N. scintillans* bloom and non-bloom regions. Based on observations we further elucidate different phases of the bloom and expected causes.

2. Material and methods

A cruise was carried out on board R/V Sindhu Sankalp (#SSK-077) during 11-22 February 2015. We observed green *N. scintillans* blooms in the NEAS and carried out observations to delineate the processes leading to the bloom by carrying out observations both within and outside the bloom regime at 23 stations (Fig 1). Samples were also collected from the major sewage channels in the Mumbai city region (that discharge to the coastal Arabian Sea) to measure the isotopic composition of carbon and nitrogen of particulate organic matter. Water-column temperature and salinity were measured using a CTD (conductivity-temperature-depth) profiler (make Sea Bird 911 Plus, USA). The MLD was estimated following Shankar et al. (2015) by estimating density at *in situ* temperature, salinity and pressure and subtracting 0.5°C from temperature profile and estimated again density. The depth of MLD is taken where the difference in density of *in situ* temperature and 0.5°C become zero. The MLD is therefore determined by changes in salinity as well as temperature. Photosynthetic Active Radiation (PAR) was measured at 400-700 nm (Satlantic) and dissolved oxygen (DO) was measured following the Winkler titration method (Carritt and Carpenter, 1966). Dissolved oxygen saturation was estimated based on formulations given by Garcia and Gordon (1992). Nutrients were estimated using Autoanalyzer (Skalar San Plus, The Netherlands) following the colorimetric procedure (Grashoff et al., 1992). The precisions of nitrate+nitrite (NO₃+NO₂), phosphate and silicate were ±0.02, 0.01 and 0.02 µM, respectively. About 10-15 L of water was filtered through GF/F (Whatman) filters and pigments retained on the filter were extracted to 90% acetone and was

measured using High-Performance Liquid Chromatography. The detection limit of a method for all the compounds varied between 0.001 and 0.002 $\mu\text{g l}^{-1}$ and precision in terms of relative standard deviation for multiple injections (5) of standards was well below 3%. Pigment analysis was performed following the method of Van Heukelem (2002) with minor modification of calibration and preinjection procedure as detailed in Roy et al. (2015). Pigments were quantified against the standards procured from DHI (Denmark) and Sigma-Aldrich (USA). The range of pigments found in this study includes chlorophylls (*a*, *b* and *c* family), fucoxanthin, peridinin, 19' hexanoyloxyfucoxanthin (19 HF), 19' butanoyloxyfucoxanthin (19BF), alloxanthin, diadinoxanthin, diatoxanthin, β -carotene, zeaxanthin, lutein, violaxanthin, neoxanthin, prasinoxanthin and pheophytin. Furuya and Lirdwitayaprasit (2000) identified most of the listed pigments in the green flagellated endosymbiont. Further the pigment concentration data were subjected to CHEMTAX chemical taxonomy software (version 1.95) for the calculation of the relative abundance of seven phytoplankton groups (Diatoms, Dinoflagellates, Cyanobacteria, Prochlorophytes, Prasinophytes, Prymnesiophytes and Chlorophytes) (Mackey et al., 1996; Wright et al., 1996; 2009; 2010). About 10 L of water were filtered through pre-combusted GF/F filter to measure content and isotopic composition of particulate organic carbon (POC) and nitrogen (PON) using elemental analyzer coupled to Isotope-Ratio Mass Spectrometer (EA-IRMS; Delta V Plus; M/S Thermo Electron, Germany; Sarma et al., 2012; 2014). The standard gases (CO_2 and N_2) were calibrated with internal reference materials of Glutamic Acid, Alanine, marine sediment, and International Atomic Energy Agency (IAEA) standards. The long-term precision of the instrument is approximately $\pm 0.2\%$ for both C and N.

A known volume of the water samples (1 L) were preserved in 4% Lugol's iodine solution for phytoplankton enumeration. The preserved samples were kept for settling for 48 h, and after that, the volume was concentrated by careful siphoning the top portion using tubing with one end fitted with 10 μm mesh (to avoid particle removal). From the final concentration, 2-3 ml concentrated sample was analyzed using an Olympus inverted microscope (IX-73 Olympus Make) at $\times 100$ to $\times 400$ magnification and their abundance is expressed in terms of cells per liter (L). Empty or broken cells were not counted. Phytoplankton in the seawater is identified based on the standard identification keys (<http://www.algaebase.org>; Taylor 1973, Tomas 1997).

3. Results and discussion

3.1. Hydrographic conditions and nutrients distribution in the NEAS

Cooler (by $<1^{\circ}\text{C}$) and saltier (by 0.2–0.4) water was observed in the upper 100 m north of 20.25°N compared to the south (called non-bloom region), with the ML tending to be relatively shallower in the former (10–40 m) than latter region (60–108 m) (Fig. 2). The West India Coastal Current (WICC) advects slightly fresher water poleward during the winter monsoon (Shetye et al., 1991; Prakash et al., 2014; Shankar et al., 2015). By February, this fresher water is evident in the southern NEAS and the ML shallows as a result (Shankar et al., 2015). The water below this ML is saltier than the water farther south (Fig. 2) owing to the slow equatorward movement of the saltier Arabian Sea High-Salinity Water mass (ASHSW). Hence, the ML tends to be shallower in the north of $\sim 20.25^{\circ}\text{N}$ than farther south. The shallow ML in the north is stable, implying weaker mixing, and the barrier layer below the ML leading to the weak vertical gradient of temperature. This result in changes in temperature is minimal despite shallowing of ML significantly (Shankar et al., 2015) (Fig. 2). One consequence of this dependence of density and the depth of the ML on salinity in addition to temperature is seen in the relatively flat MLD curve in the region influenced by ASHSW. The stronger stratification weakens the impact of the diurnal cycle of temperature, and the ML does not respond to the day-time heating and night-time cooling, unlike in the non-bloom region to the south, where the day-time ML tends to be shallower than the ML at night (Fig. 2). Dissolved oxygen saturation was relatively higher north of 20.25°N (89–98%; mean 95%) compared to the non-bloom region (85–91%; mean 88%) due to deep mixing in the latter region injecting oxygen-minimum-zone waters into the ML (Fig. 2).

The upper 50 m of water column suggests relatively higher concentrations of nutrients in the non-bloom region compared to north of 20.25°N . ML mean nitrate concentrations were above $2\ \mu\text{M}$ in the non-bloom region whereas it was undetectable to $>2\ \mu\text{M}$ in the north (Fig. 2). Similarly, phosphate was $<0.3\ \mu\text{M}$ north of 20.25°N , and it increased to $>0.5\ \mu\text{M}$ in the non-bloom region. More importantly, the concentration of Si in the mixed layer was 0.2 to $1.5\ \mu\text{M}$ north of 20.25°N , and it was $>2\ \mu\text{M}$ in the non-bloom region (Table 1). The spatial and vertical distribution patterns of nutrients are consistent with temperature and salinity and vertical mixing of the upper ocean (Fig. 2). The prevalence of low Si could be due to (i) limited supply of Si from subsurface water due to stratification in the north of 20.25°N that limits the deeper ML resulting in less Si but significant supply of nitrate and phosphate (Fig. 2) as the silicicline is deeper than nitracline and phosphocline in the NEAS (Madhupratap et al., 1996; Naqvi et al., 2002), and (ii) active utilization by diatoms: under natural conditions diatoms rapidly take up Si when other macronutrients are available

(Mousing et al. 2018). Under such conditions, outburst of heterotrophic *N. scintillans* due to availability of food (particularly diatoms) and suitable conditions for its endosymbiont proliferation can be expected.

3.2. Distribution of phytoplankton abundance and pigments in the NEAS

Phytoplankton cell abundance was 4–6 times higher north of 20.25°N (>3000 cells/L) than in the non-bloom region (<1000 cells/L; Fig. 3). Enhanced cell abundance of diatoms (3000–7000 cells/L) was observed in association with shallowing of ML between 20.25°–21.25°N compared to the non-bloom region (Figs. 2 and 3), but the diatom abundance decreased north of 21.25°N (henceforth called bloom region) in association with increase in dinoflagellates (300–1500 cells/L) cell abundance. Though the green coloration to surface water was observed visually, the abundance of *N. scintillans* in samples collected using Niskin bottles in the bloom region ranged between 600 and 1200 cells/L only (Fig. 3). Green *N. scintillans* are buoyant and remain afloat at the sea surface. However, it gets easily dispersed with physical disturbances, such as surface winds, vessel movements and even during CTD rosette operation. Further, the surface water collected using Niskin bottles attached to rosette represents the subsurface water, i.e. ~ 1 m below the surface due to technical limitation. Since Niskin bottle sampling did not collect sample 1 m below surface *N. scintillans* abundance was underestimated as they float at the surface (Fig 3). In order to get the realistic abundance, surface water was collected using a bucket, in which the *N. scintillans* abundance was found up to 15000 cells/L. The abundance of *N. scintillans* found in this study were higher than in Gomes et al. (2014; 9600 cells/L), but lower than in Prakash et al. (2017; >40000 cells/L) and Madhu et al. (2012; 300000 cells/L). Prakash et al. (2017) suggested that the *N. scintillans* bloom is tightly coupled with the strength of winter mixing as deep mixing supports diatom bloom. This is because the strong winter mixing deepens the ML and supplies Si-rich water to ML and vice versa conducive for *N. scintillans* blooms. Miller and Wheeler (2012) suggested that shallow ML, then the euphotic zone, triggers diatom bloom. The higher diatom abundance (2000–8000 cells/L) between 20.25° and 21.25°N (Fig. 3) coincided with low Si concentration (~0.5 μM; Fig. 2) suggesting removal of Si from the water column and weak Si supply due to shallow ML further decreases Si availability. This condition presumably triggers *N. scintillans* bloom in the NEAS. Generally, *Noctiluca* grows faster via heterotrophic mode when food (prey) is available (Furuya et al., 2006) and switches over to autotrophic mode through its endosymbiont when nutrients are available, and the food is scarce. The low diatom abundance (800–3000 cells/L) in the bloom region could be attributed to active grazing by *N. scintillans*. Green *Noctiluca* bloom onset

subsequent to diatom-rich conditions was evidenced from ocean color satellite imageries (Baliarsingh et al. 2018). Even the laboratory experiments confirmed that the diatoms, in particular, centrics, are the preferred feed for *Noctiluca* (Suzuki et al., 2013). It is to be noted, however, that the dietary choice of *N. scintillans* may be a trade-off between maximizing food and nutrient intake and minimizing the energy cost of handling different prey (Zhang et al. 2016). Though *N. scintillans* blooms were observed north of 21.25°N, they may spread southward owing to the availability of prey (i.e., diatoms). Once *N. scintillans* become dominant, their active grazing can prevent population growth of co-existing phytoplankton (Hansen et al., 2004; Harrison et al., 2011). We opine that this grazing and low Si availability led to the observed decrease in diatoms abundance in the *N. scintillans* bloom region (Fig. 3). The maximum *N. scintillans* abundance was confined to the upper 10 m of water column and decreased with depth (Fig. 3). Similarly, enhanced phytoplankton biomass (as Chl-*a*) was observed in the upper 35 m in the bloom region compared to the non-bloom region, with the maximum occurring in the upper 10 m. The enhanced phytoplankton abundance and biomass (Chl-*a* of 0.4-0.8 mg m⁻³) resulted in a shallower euphotic zone in the bloom (34±4 m) compared to the non-bloom region (52±6 m; Fig. 2). The green appearance of *N. scintillans* is due to the presence of a large number of free swimming cells of endosymbiont, *Protoeuglena noctilucae*. As evidenced from pigment data, relatively higher concentrations of Chlorophytes, Prasinophytes, Prymesiohytes and Prochlorophytes were also observed in the bloom than the non-bloom region (Fig. 4). Since green *N. scintillans* is a mixotrophic (Goes and Gomes, 2016), it feeds on several phytoplankton (in particular larger forms) (Fig. 4). In addition to Dinophyceae, several other organisms may be found within *N. scintillans* owing to ingestion of zooplankton and their eggs (Hansen et al., 2004). Despite high concentrations of nutrient, lower phytoplankton abundance and biomass was observed in the non-bloom region (Fig. 3 and 4). This discrepancy is possibly due to the ML being deeper than the euphotic zone, resulting in mixing of phytoplankton below the euphotic zone (dark region) and within it (light region) at short time scales, which may affect phytoplankton growth, leading to decrease in phytoplankton biomass (Naqvi et al., 2002). Our study suggests that green *Noctiluca* bloom formation can be categorized into three phases (Fig. 5). In phase I, active utilization of Si by diatoms resulting in high diatom population. Advection of low saline water from the south by the WICC (Shankar et al., 2015) shallows ML and inhibits the supply of only Si but not N and P from sub-surface waters. This condition triggers the proliferation of heterotrophic *Noctiluca* by feeding actively on diatoms resulting in a decline in diatoms and Si but not N and P (Phase II). In phase III, mixotrophic green *Noctiluca* (i.e., autotrophic endosymbiont and heterotrophic *Noctiluca*) proliferate due to the availability of adequate N and P, along with low

Si concentration and a shallow ML Fig. 5). Such conditions facilitate non-diatom blooms (including *Noctiluca*) in the NEAS. The dominance of non-diatoms was reported earlier during winter in the NEAS (Sawant and Madhupratap, 1996; Roy et al., 2015; Roy and Anil, 2015). In addition, the low mean N:P (4.5 ± 0.6) and Si:N (0.8 ± 0.4) ratios does not favor autotrophs to grow due to the limitation of nutrients while it favors growth of mixotrophs/heterotrophs in the NEAS (figure not shown). The wide spread and sustenance of green *Noctiluca* bloom for several days is supported by mixotrophic mode as well as the highly buoyant nature of cells.

3.3. Source of nutrients in the NEAS

Gomes et al. (2014) attributed the occurrence of *N. scintillans* blooms in the NEAS to nutrients sourced from untreated pollutants released by the bordering countries. In order to decipher the possible sources of nutrients, we measured the isotopic composition of particulate nitrogen ($\delta^{15}\text{N}_{\text{PON}}$), which reflects the source of nitrogen utilized by the plankton (Saino and Hattori, 1980, 1985, 1987; Mino et al., 2002). The isotopic composition of regenerated nitrogen from the deep water is quite uniform ($5\text{--}6\pm 1\text{‰}$; Sigman et al., 1997; Bristow et al., 2017) in the world oceans, whereas depleted isotopic composition is observed due to atmospheric deposition (close to $0\text{--}1\text{‰}$; Agnihotri et al., 2015) and enriched isotopic composition is observed in sewage ($12\text{--}25\text{‰}$; Connolly et al., 2013; Rozic et al., 2014; Corbett et al., 2015; Savage, 2005). We collected isotopic composition PON of sewage in the Mumbai city region and the mean $\delta^{15}\text{N}_{\text{PON}}$ of sewage was $15.8\pm 1.6\text{‰}$ ($n=3$).

The $\delta^{15}\text{N}_{\text{PON}}$ in the NEAS varied from 3 to 14.5‰ , and the higher values were associated with the deep ML in the non-bloom region (Fig. 6). Since the sub-surface water of the northern Arabian Sea is denitrified (Banse et al., 2014, and references therein), $\delta^{15}\text{N}_{\text{NO}_3}$ is enriched ($15\pm 2\text{‰}$) owing to reduction of isotopically lighter NO_3 , resulting in enrichment of $\delta^{15}\text{N}_{\text{NO}_3}$, and utilization of such nitrate yields heavier isotopic composition of PON (Brandes et al., 1998). On the other hand, $\delta^{15}\text{N}_{\text{PON}}$ varied from 3 to 8‰ (mean $5.4\pm 1\text{‰}$), a typical marine nitrogen signal ($5\text{--}6\text{‰}$; Sigman et al., 1997; Bristow et al., 2017), in the bloom region, whereas enriched values of $6\text{--}14.8\text{‰}$ were found in the non-bloom region, suggesting entrainment of nutrients from above and within the denitrifying layer, respectively. The shallow mixing in the bloom than non-bloom region further supports that nutrients from the upper boundary of the denitrifying layer entered to the bloom region. The observations presented in this study suggest that the *N. scintillans* blooms are supported by nutrients entrained from the sub-surface waters through vertical mixing. The isotopic composition of nitrogen in the NEAS is significantly lighter ($3\text{--}8\text{‰}$) than that of nitrogen in the Mumbai sewage ($15.8\pm 1.6\text{‰}$),

ruling out the contribution of sewage-borne nutrients to the study region. Connolly et al. (2013) observed incorporation of sewage signals in the ecosystem (phytoplankton, sea grass, and crabs) using $\delta^{15}\text{N}$ of tissues of organisms dwelling at different distances from the coast. Stable isotopic signals of sewage were observed in the marine organisms dwelling close to the coast, and these signal decreased with increasing distance from the coast up to 10–15 km offshore, suggesting that sewage impact is expected to be minimal in the far offshore. The identified *N. scintillans* blooms in the study region are more than 250 km from the coast. Therefore, the present study suggests that *in situ* shallow mixing supported *N. scintillans* blooms in the NEAS rather than sewage-borne nutrients.

3.4. Source of organic carbon in the NEAS

Gomes et al. (2014) attributed the *N. scintillans* bloom in the NEAS to the decomposition of sewage-borne organic matter, which leads to the development of suboxic or hypoxic conditions at the surface. We measured the content and isotopic composition of particulate organic carbon (POM) to test this hypothesis. The mean C:N ratio of POM in the ML was 3.4 ± 1.6 ($n=42$), below the Redfield ratio of 6.6, indicating possible alteration of organic matter. The mean C:N ratio indicates a marine rather than a terrestrial source for the organic matter because terrestrial sources have relatively high ratios (>10 ; Hamilton and Lewis, 1992; Middelburg and Nieuwenhuize, 2001; Barth et al., 1998). The POC/Chl-*a* ratio is an indicator of the contribution of *in situ* phytoplankton biomass to the POC pool. The POC/Chl-*a* ratio of fresh organic matter produced by marine phytoplankton varies from ~ 40 (Montagnes et al., 1994), <70 (Geider, 1998), <100 (Head et al., 1996), and even higher ratios (140-200; Thompson et al., 1992; Cifuentes et al., 1988; Bentaleb et al., 1998) owing to regional differences in temperature, irradiance, growth rate and species composition (Heath et al., 1990; Montagnes et al., 1994; Geider et al., 1998). The mean POC/Chl-*a* ratio was $\sim 42 \pm 4$ ($n=42$) over the ML, strongly suggesting that *in situ* biological production is the dominant source of organic matter in the region.

The isotopic composition of $\delta^{13}\text{C}_{\text{POC}}$ is another potential indicator of the source of organic matter in the aquatic environment. For instance, the isotopic composition of marine plankton varies narrowly between -23.3 and -21.6‰ (Laws et al., 1995). The isotopic composition of phytoplankton in the NEAS varied between -23.1 and -22.5‰ during the study period, consistent with the inference of an *in situ* source for the organic matter. The $\delta^{13}\text{C}_{\text{POC}}$ in the NEAS varied narrowly between -24 and -22‰ in the entire study region (Fig. 6), strongly suggesting that POM was mainly of marine origin. The isotopic composition of sewage was lighter ($\delta^{13}\text{C}_{\text{POC}}$ of $-31.5 \pm 1\text{‰}$) than marine sources in the Mumbai region. Therefore, the ratios of C:N and POC/Chl-*a* and isotopic composition of $\delta^{13}\text{C}_{\text{POC}}$

clearly suggest that *in situ* biological production contributed to the POM pool. The significantly lighter values of $\delta^{15}\text{N}_{\text{PON}}$ than sewage clearly indicate that the contribution of sewage is minimal in the *N. scintillans* bloom region.

3.5. Possible occurrence of *Noctiluca* blooms in the oxic environment

Gomes et al. (2014) attributed the intensification of *N. scintillans* bloom in the NEAS to decomposition of untreated pollutants, which, they claimed, led to the formation of suboxic or hypoxic conditions at the surface. The occurrence of suboxic or hypoxic conditions are reported in the bottom waters along the west coast of India because of intense upwelling and supply of nutrients to the surface ML (Naqvi et al., 2000; Zhang et al., 2013; Sudheesh et al., 2016). No reports have been made on the occurrence of such conditions at the surface because the surface of the ocean constantly exchanges oxygen with the atmosphere (Zhang et al., 2010). Nevertheless, the mean DO saturation levels in the ML in the present study varied between 90 and 98%, with relatively lower values in the non-bloom region ($88\pm 2\%$) compared to the bloom region ($95\pm 2\%$) owing to the deeper ML in the former. This association of lower DO with deeper ML suggests that injection of suboxic waters to the surface decreased DO saturation (Fig. 2). In spite of much higher DO levels than reported by Gomes et al. (2014) ($\sim 70\%$), we observed blooms of *N. scintillans*, suggesting that the green *N. scintillans* blooms in the NEAS occur in oxic conditions (Figs. 2 and 3). The difference in DO saturation between the present and Gomes et al. (2014) study is not due to variable intensity of blooms as the abundance of *N. scintillans* were observed to be higher in the present study (15000 cells/L) than in Gomes et al. (2014; 9600 cells/L). In addition, Prakash et al. (2017) observed that the abundance of *N. scintillans* exceeded 40000 cells/L in the NEAS where DO saturation was $\sim 98\%$. Therefore, it is unlikely that suboxic or hypoxic conditions are required to trigger blooms of *N. scintillans*; it is equally unlikely that these blooms lead to suboxic or hypoxic conditions in the surface ML owing to its constant exchange of oxygen with the atmosphere. Further more, oxic conditions were reported at the surface water in the coastal waters of the Arabian Sea, where seasonal occurrence of hypoxia was noticed (Naqvi et al., 2000; Sudheesh et al., 2016).

It has been reported that *N. scintillans* blooms occur in the northern Arabian Sea over a period of 3–14 days and the typical period of occurrence of these blooms is during mid-February (Chaghtai and Saifullah, 2006; Al-Azri et al., 2007), as was true of our study period as well. Hence, the time of sampling in the NEAS is critical for the interpretation of data. Neither the Indian nor US JGOFS programs sampled the NEAS during this period. It is therefore not surprising that no blooms were reported in these studies (Sawant and Madhupratap, 1996; Shalapyonok et al., 2001). Note, however,

that the occurrence of these blooms has been reported earlier in the NEAS by several investigators (e.g., Devassy and Nair, 1987; Gomes et al., 2008).

Though inter-annual variability in the occurrence of *N. scintillans* blooms is unknown owing to unavailability of data, but this study suggests that occurrence of *N. scintillans* blooms in the NEAS may be a regular phenomenon driven by natural processes: shallow vertical mixing caused by the advection of lower-salinity waters by the WICC, which leads to a severe limitation of Si. These blooms occur over a period of a few days to weeks, and there is no evidence for a shift in the community of phytoplankton in the recent years. The implication of untreated sewage from neighboring countries is also similarly unfounded.

3.6. *The coastal and open-ocean regimes*

We note that the absence of a sewage signature in the open-ocean regime of the NEAS does not rule out a role for sewage in the near-coastal waters: for example, the occurrence of green *N. scintillans* blooms close to the coast and in inland waters of Pakistan were attributed to coastal pollution (Chaghtai and Saifullah, 2006), and it is likely that a similar situation may prevail in the coastal waters off Mumbai and other major coastal cities. Dispersion, however, limits the impact of sewage to a distance of 10–20 km from the coast, as observed at several places (Connolly et al., 2013; Rozic et al., 2014; Corbett et al., 2015). Hence, if the sewage off Mumbai or Karachi is responsible for the blooms of *N. scintillans* in the NEAS, these blooms should be far more widespread and should be observed over practically the entire NEAS. Neither did Gomes et al. (2014) report such a widespread bloom, nor is such a bloom reported in the literature, again suggesting a cause other than sewage for the *N. scintillans* blooms.

4. Summary and conclusions

In order to understand the causes behind *N. scintillans* blooms in the NEAS, a cruise was undertaken in the region during February 2015. The NEAS experienced convective mixing during the study period, but this mixing was weak and did not reach the silicicline, resulting in the supply of significant amounts of N and P, but not Si, to the ML. Our study suggests that diatoms actively removed Si when deep ML associated with high Si supplied through mixing. Availability of high diatoms triggered faster growth of heterotrophic *Noctiluca*. Further poleward advection of low saline water by the WICC inhibited vertical mixing, and thus Si inputs, leading to decrease in diatoms abundance in addition to active grazing by *Noctiluca*. Upon decrease in diatoms abundance and nutrients, mixotrophic green *Noctiluca* proliferated and sustained through active phagotrophy

and photoautotrophy respectively (Fig. 5). A massive occurrence of green *N. scintillans* was observed, but the isotopic composition of carbon and nitrogen of particulate organic matter (POM) clearly indicated that *in situ* production contributed to the organic carbon pool, while the biological processes are supported by vertical mixing of nutrients from sub-surface waters. No signatures of sewage were observed, suggesting that the massive occurrence of *N. scintillans* bloom in the NEAS were due to natural, *in situ* processes, not anthropogenic sources as hypothesized earlier by Gomes et al. (2014).

The endosymbiont (*Protoeuglena noctilucae*) required both N and P to grow and the feeding experiments indicate that when food is available, *Noctiluca* is capable of meeting its metabolic requirements via heterotrophic mode and switching to an autotrophic mode, via carbon fixation by its autotrophic endosymbiont, when food is scarce but nutrients are available (Gomes et al., 2014). It is not known, however, whether these two modes can operate simultaneously. Hence, in order to understand the need of nutrients and feeding habits of *N. scintillans*, specific experiments are needed to unravel whether the autotrophic and phagotrophic modes can operate simultaneously or there exist resource-dependent (in particular, nutrient or food) switching mechanisms. Our study suggests that when diatoms cells are abundant, *N. scintillans* graze upon them and turns to autotrophic once their abundance decreases (Fig. 5). Therefore measurements of photosynthetic or grazing rates in this region will further improve our understanding on their feeding habits.

One point of interest from the viewpoint of climate change and associated warming of the oceans concerns the basic process identified in this study, i.e., the stabilization of the mixed layer by the advection of low-salinity surface waters by the WICC. The salinity difference noted by Shankar et al. (2015) was just 0.2 , which is equivalent to 0.8–1°C if the same stratification were to be caused by a change in temperature (Shankar, 1998). Whether a 1°C rise in the near-surface temperature and the resulting increase in stratification can lead to a similar situation over a larger region is probably a more serious question for the open-ocean Arabian Sea than is the possible effect of untreated sewage being released into the coastal ocean.

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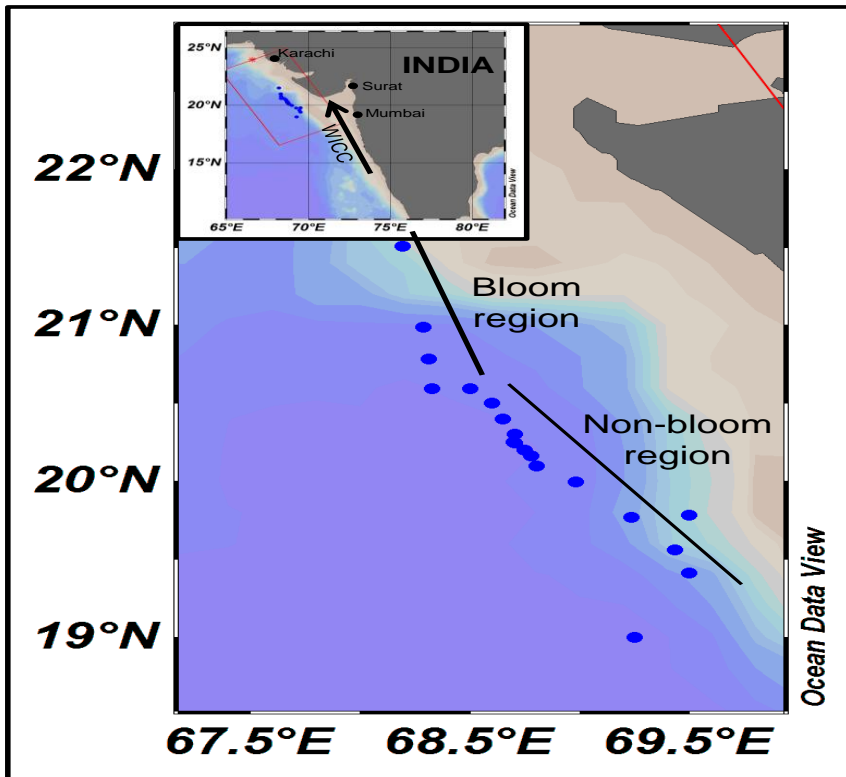
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Figure 1: a) Map of station locations in the NEAS where sampling was carried out. The stations fallen within bloom and non-bloom regions were shown. The major cities in the northeastern coast of Arabian Sea, which has coastal population > 1 million are shown, (b) Green *Noctiluca* bloom in NEAS

a.



b.



Figure 2: Meridional (latitudinal) variation of temperature ($^{\circ}\text{C}$), salinity, dissolved oxygen saturation (%), nitrate, phosphate and silicate in the upper 100 m of the water column in the study region. The black curves are isolines; the light red and light green curves denote the depth of the mixed layer and euphotic zone (1% of the surface photosynthetic available radiation), respectively. The mixed-layer depths at stations 2 and 3 are given in black numbers because they exceed the maximum depth marked on the ordinate. The time of sampling is given at the top of the panel for temperature. The bloom and non-bloom regions are also marked at the top of the temperature panel.

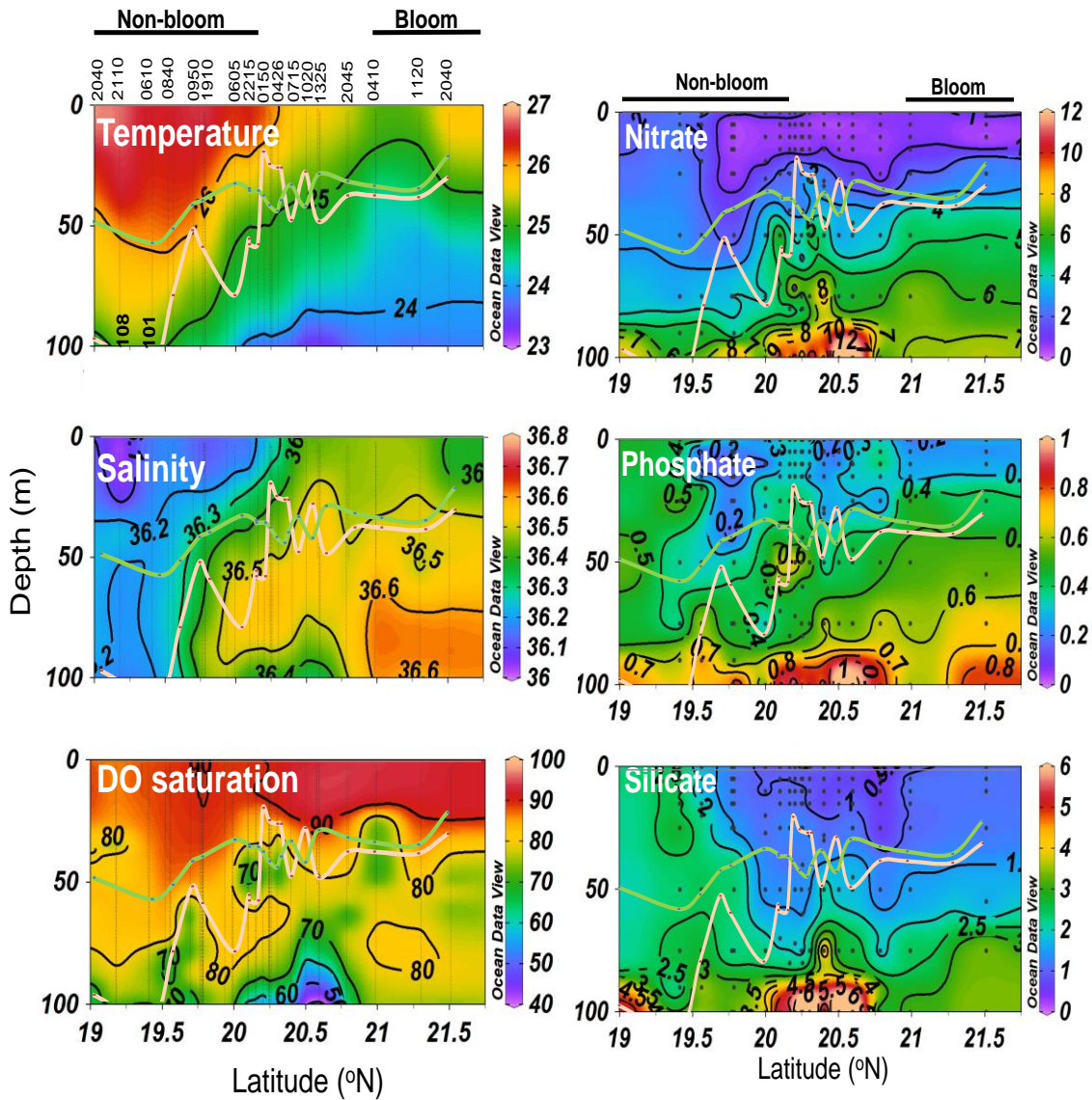


Figure 3: Meridional variation in the abundance of total phytoplankton, diatoms, dinoflagellates (including *N. scintillans*), and *Noctiluca scintillans* (all in cells/L) over the upper 50 m in the study region. The black curves are isolines. The bloom and non-bloom regions are marked at the top of the panels in the top row. Note that the cell counts of *N. scintillans* are underestimated since they float and are undersampled by Niskin bottles (cf. text for further details).

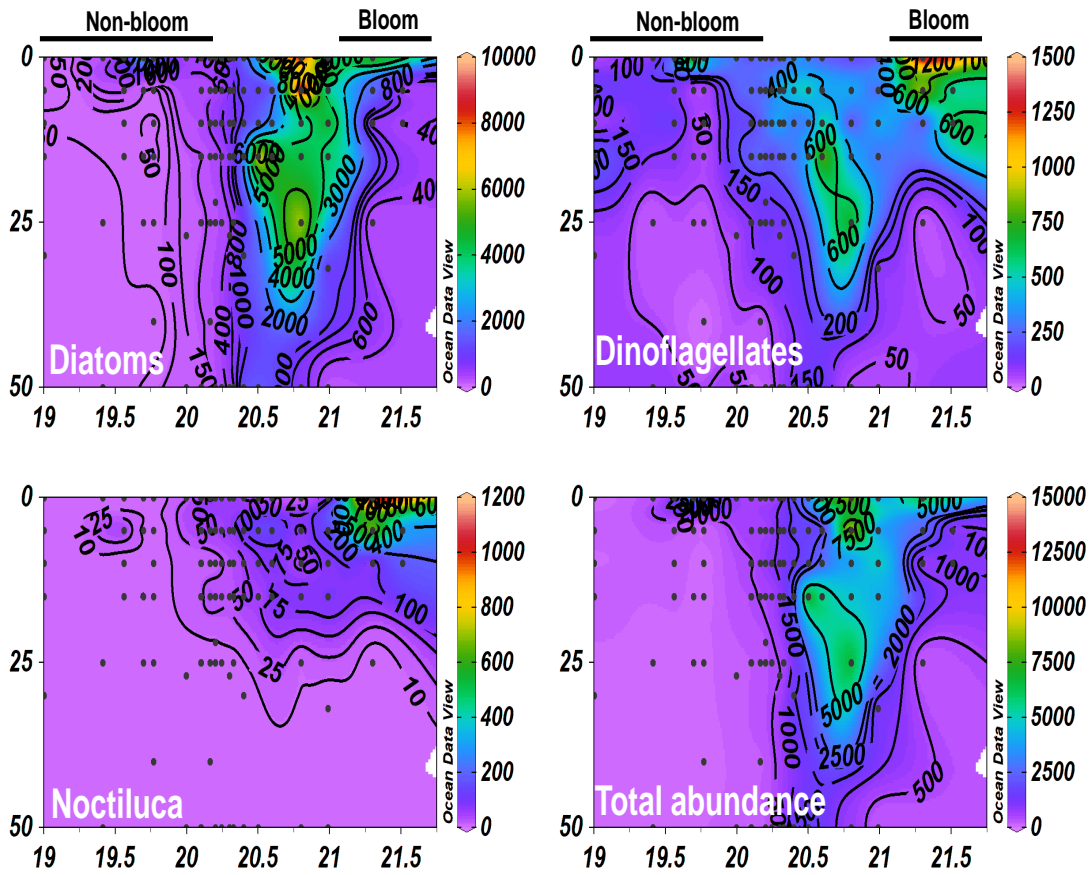


Figure 4: Meridional variation of different groups of phytoplankton groups, derived from marker pigments (mg/m⁻³) (given in the bracket), in the upper 50 m of water column in the study region. The black curves are isolines. The bloom and non-bloom regions are marked at the top of the panels in the top row.

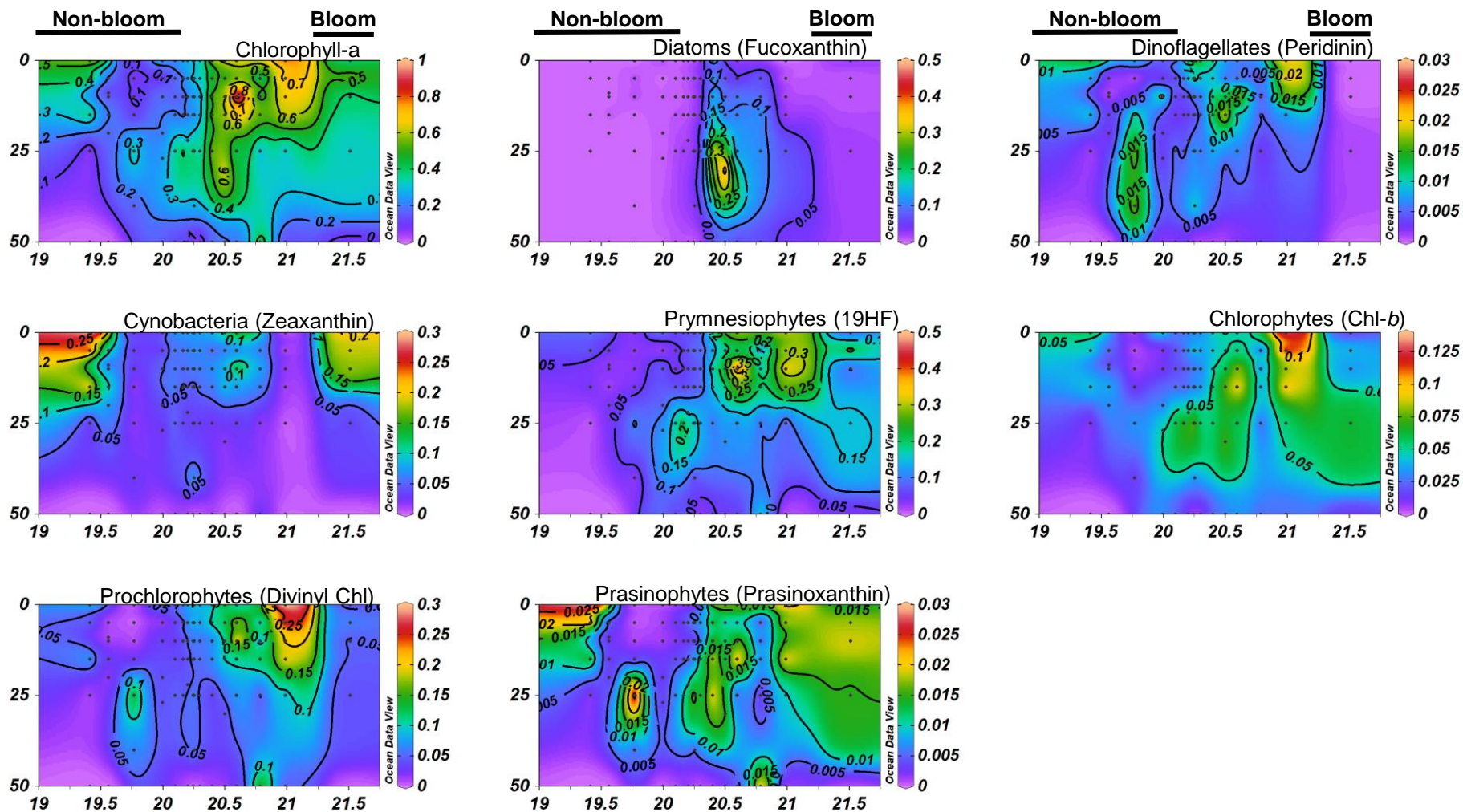
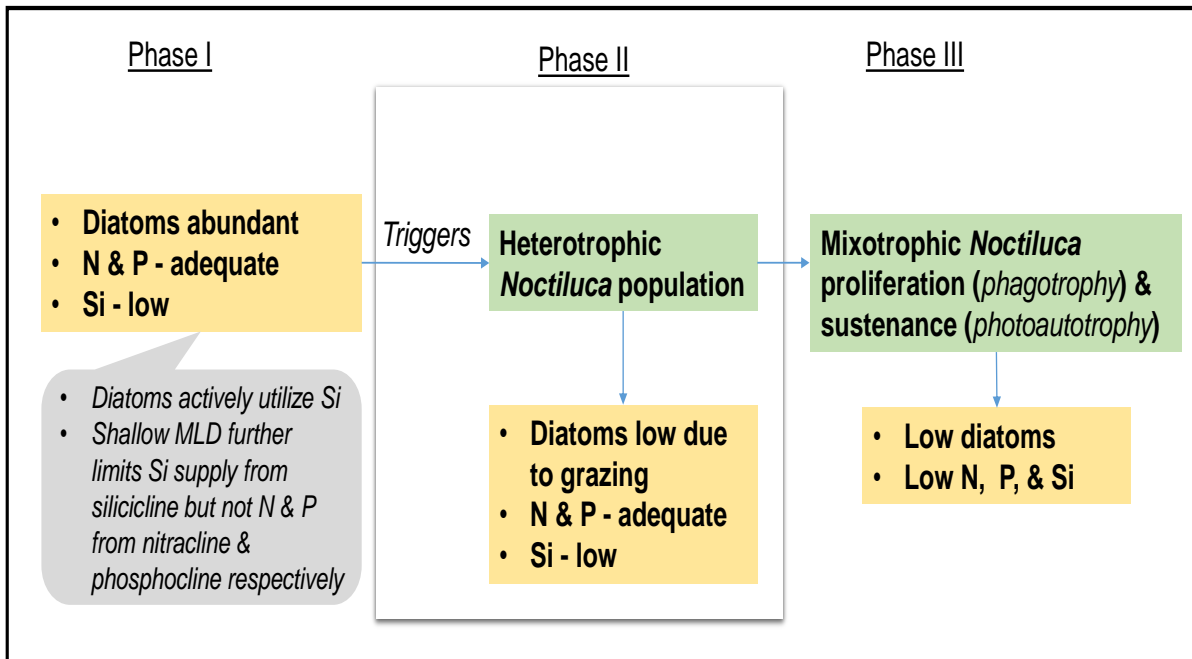


Figure 5: Schematic diagram representing different phases of *N. Scintilans* bloom occurrence in the NEAS. MLD, N, P and Si corresponds to mixed layer depth, nitrate, phosphate and silicates respectively. The Bold text are observations and the text in italics are expected causes.



Note: Bold text are observations and the text in italics are expected causes.

Figure 6: Meridional variation in isotopic composition of POC ($\delta^{13}\text{C}_{\text{POC}}$) and PON ($\delta^{15}\text{N}_{\text{PON}}$) (in per mil or ‰) in the upper 100 m of water column in the study region. The black curves are isolines; the light red and light green curves denote the depth of the mixed layer and euphotic zone (1% of the surface photosynthetic available radiation), respectively. The bloom and non-bloom regions are marked at the top of the panels in the top row.

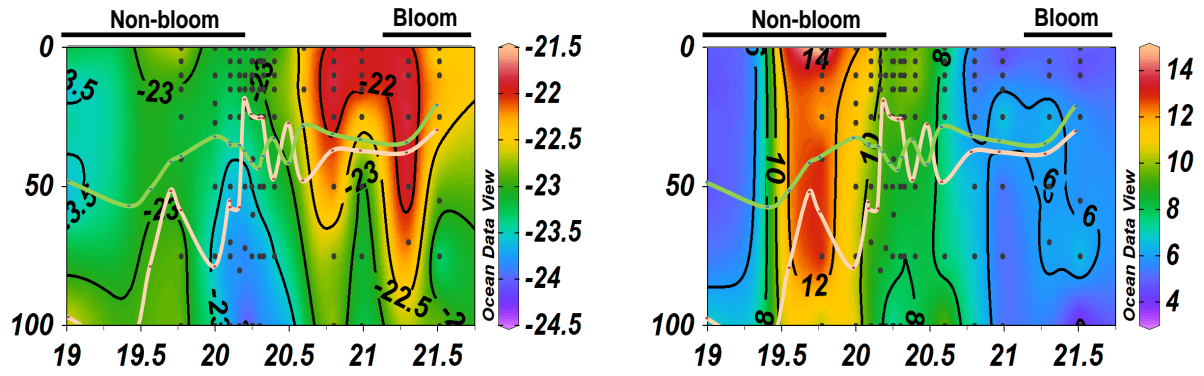


Table 1: Comparison of mixed layer mean physical, chemical and biological properties in the bloom and non-bloom regions.

| Parameter | Non-Bloom region | Bloom region | T _{stat} and p-values |
|--------------------------------------|------------------|--------------|--------------------------------|
| Temperature (°C) | 26.6±0.5 | 25.3±0.3 | 7.0; p<0.001 |
| Salinity | 36.2±0.1 | 36.4±0.2 | -8.1; p<0.001 |
| Mixed layer (m) | 35±10 | 68±10 | -6.1; p<0.001 |
| Chl- <i>a</i> (mg/m ³) | 0.2±0.0 | 0.6±0.2 | -6.2; p<0.001 |
| DO saturation (%) | 88±3 | 93±2 | -4.2; p<0.001 |
| Nitrate (μM) | 1.7±0.6 | 1.3±0.8 | 3.2; p<0.05 |
| Phosphate (μM) | 0.5±0.2 | 0.3±0.1 | 4.6; p<0.05 |
| Silicate (μM) | 2.4±0.8 | 1.1±0.5 | 1.67; p<0.05 |
| δ ¹³ C _{POC} (‰) | -23.4±0.1 | -22.1±0.2 | -9.8; p<0.001 |
| δ ¹⁵ N _{PN} (‰) | 9.8±2 | 6.6±1 | 5.5; p<0.001 |