Marine Pollution Bulletin 129 (2018) 222–230

Contents lists available at ScienceDirect

Marine Pollution Bulletin

journal homepage: www.elsevier.com/locate/marpolbul

# Response of phytoplankton community and size classes to green *Noctiluca* bloom in the northern Arabian Sea

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ARTICLE INFO

*Keywords:*
*Noctiluca scintillans*
Bloom
Picophytoplankton
Chlorophyll-*a*
MODISA
Arabian Sea

ABSTRACT

A comprehensive analysis on the phytoplankton ecology with special reference to different phytoplankton size classes was carried out at green *Noctiluca scintillans* (hereafter *Noctiluca*) bloom and non-bloom locations in offshore waters of the northern Arabian Sea. At the bloom locations, green *Noctiluca* represented a dense monospecific proliferation with average cell density of $10.16 \pm 5.806 \times 10^4$ cells-$L^{-1}$ and relative abundance share of 98.63%. Active photosynthesis through prasinophytic endosymbiont was depicted from net community production magnitude reaching 85.26 mgC/$m^3$/Day under low prey abundance. Parallel swarming of *Porpita porpita*, a voracious copepod feeder signified the competitive advantage of *Noctiluca* to have the phytoplankton prey. Average concentration of picophytoplankton biomass was eleven times lower in surface waters of non-bloom stations in comparison to bloom. Higher N:P ratio in subsurface waters of non-bloom stations signified non-utilization of nitrogenous nutrients. Green *Noctiluca* bloom onset subsequent to diatom rich conditions was evident from spatio-temporal ocean colour satellite imageries.

## 1. Introduction

Arabian Sea is regarded as the most productive component of the Indian Ocean. Nutrient injection from subsurface to surface due to winter convective mixing is one of the major environmental factors that trigger phytoplankton bloom in the northern Arabian Sea. Physical forcing of winter monsoon plays an important role in this mixing (Madhupratap 1999; Dwivedi et al. 2015). Previous research on phytoplankton dynamics in this region envisaged phytoplankton bloom rank order as diatom, cyanobacteria and dinoflagellates (Sawant and Madhupratap 1996). Annual episodes of green coloured *Noctiluca scintillans* (henceforth *Noctiluca*) bloom has been reported to occur in the open waters of northern Arabian Sea especially during winter (January–March) since early 2000s (Gomes et al. 2014). However, the green *Noctiluca* bloom is believed to be eco-friendly and support fishery in this region. Unlike *Noctiluca* blooms elsewhere, there is no consequent ammonification and oxygen depletion in surface waters of the northern Arabian Sea (Dwivedi et al. 2012). However, green *Noctiluca* bloom was reported to be linked with low dissolved oxygen conditions in the northern Arabian Sea (Gomes et al. 2014). In general, green *Noctiluca* bloom intensifies depending upon the prey availability, especially diatoms. Diatoms often prevail in high density during green *Noctiluca* bloom (Madhu et al. 2012). In context of phytoplankton metabolism, molar ratios of inorganic macronutrients decipher the change in nutrient supply and depict the phytoplankton growth limitations (Redfield et al. 1963; Yin et al. 2001). Variability in ambient concentration of inorganic macronutrients favour metabolism of the endosymbiont of green *Noctiluca* as well as the growth of diatom, the preferred prey of *Noctiluca* (Sriwoon et al. 2008). Although, green *Noctiluca* is slow grower in comparison to coexisting diatoms, the relative abundance of inorganic nutrients provides advantage for green *Noctiluca* growth (Furuya et al. 2006a). In context of different size classes of phytoplankton, smaller sized phytoplankton viz. picophytoplankton and nanophytoplankton plays important role in bloom dynamics apart from microphytoplankton. The heterotrophic green *Noctiluca* also predate upon nanophytoplankton and picophytoplankton (Umani et al. 2004). Phytoplankton size class distribution alters with change in seasons in the northern Arabian Sea (Varunan and Shanmugam 2015; Sahay et al. 2017). In addition, *Noctiluca* presents a complex ecology by feeding upon and being preyed by zooplankton (Prasad 1958; Matondkar et al. 2012). The ecological complexity of the north-eastern Arabian Sea is considered as an ideal expanse to study the

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https://doi.org/10.1016/j.marpolbul.2018.02.031
Received 12 July 2017; Received in revised form 18 February 2018; Accepted 19 February 2018
Available online 25 February 2018

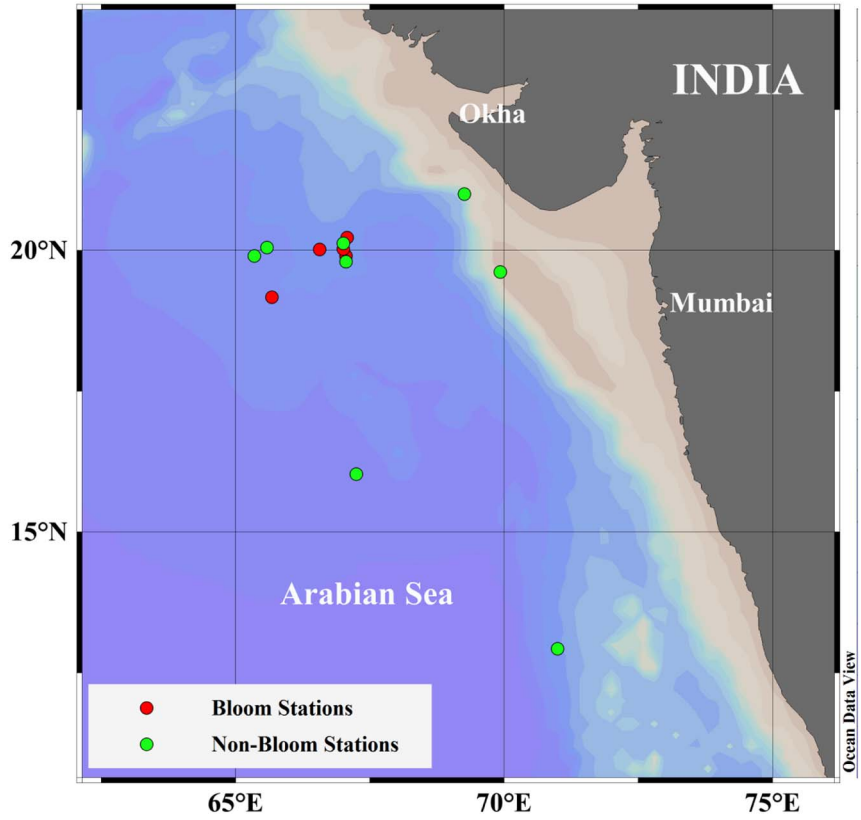


**Fig. 1.** Green *Noctiluca* bloom and non-bloom stations in the northern Arabian Sea.

primary and secondary responses towards mesoscale environment changes (Padmakumar et al. 2016).

Based on the ecological complexity and wide spatial coverage, the green *Noctiluca* bloom in the northern Arabian Sea need regular monitoring. Against this backdrop, the present study was carried out with aims to (i) discern the distribution of phytoplankton size classes during green *Noctiluca* bloom (ii) understand the variation of inorganic macronutrient molar ratios at bloom and non bloom locations, (iii) decipher bloom conducive factor(s) in the northern Arabian Sea.

## 2. Materials and methods

### 2.1. Study region

The present work was carried out in offshore waters of the northern Arabian Sea (Fig. 1). In situ observations were carried out onboard Indian Ministry of Earth Sciences (MoES) research vessel "Fishery Oceanographic Research Vessel (FORV) *Sagar Sampada*" (cruise no. 348) during winter of 2016 (29th February to 19th March). The aforementioned cruise was planned based on satellite retrieved trend of green *Noctiluca* bloom in the northern Arabian Sea (Dwivedi et al. 2015). Sporadic dense patches of green and yellowish-green discolouration of surface seawater were observed at latitude 19–21°N and longitude 65–68°E during 7 to 12 March 2016 (Fig. 1, Fig. 2a–e).

### 2.2. In situ water sample collection and analysis

During the present survey, seawater samples were collected from 0, 10, 20, 30 m of the water column with aid of a Niskin-Rosette from bloom and non-bloom locations for onboard analysis of chlorophyll-*a* (chl-*a*), phytoplankton taxonomy and inorganic macronutrients.

Different inorganic macronutrients viz. nitrate ($NO_3$), phosphate ($PO_4$) and silicate ($SiO_4$) were estimated by adopting spectrophotometric method using a UV–Visible Double Beam Spectrophotometer (Thermo Scientific, Evolution 201) (Grasshoff et al. 1999). A known volume of seawater (1 to 2 l) was sequentially filtered through different pore size (20 > 2 > 0.2 μ) filter papers in order to estimate biomass of different phytoplankton size classes in terms of chl-*a* concentration (Brewin et al. 2014). Chl-*a* was analyzed flurometrically following 90% acetone extraction method with aid of a Flurometer (make: Turner Designs). The concentration of chl-*a* was expressed as mg-$m^{-3}$. The flurometer was calibrated onboard by using chl-*a* standard (Sigma-Aldrich) with different concentrations. The retention of green *Noctiluca* cells on to the filter is illustrated in Fig. 2c–d. Qualitative and quantitative analysis of phytoplankton was carried out in shore laboratory with aid of a trinocular compound microscope (Labomed LX-400) by referring standard identifications keys (Tomas 1997). Green *Noctiluca* was enumerated onboard soon after collection using an epi-fluorescence microscope (Nikon Eclipse, E600) (Fig. 2 e).

Net Community Production (NCP) and Respiration (R) were measured following the Dissolved Oxygen (DO) method using in situ light (transparent), dark (opaque) and initial bottle (LB, DB and IB, respectively) incubation at the surface, 10, 20, 30 and 50 m depth. Water samples were collected as IB, LB and DB in three BOD (Biological Oxygen Demand) glass bottles (300 ml). Initial concentration of DO was analyzed for each depth (IB). Subsequently each set of bottles (LB and DB) were fixed to a rope and incubated in situ for 24 h at different depths. DO concentration of seawater was analyzed onboard immediately after retrieval of the incubated bottles. The NCP and R were calculated from the differences in DO concentration by following the relation, R = IB–DB and NCP = LB–IB (Gupta et al. 2016). The metabolic rates measured as oxygen were converted to carbon equivalents assuming a photosynthetic quotient of 1.2 and respiratory quotient of 1 (Laws 1991).

### 2.3. Satellite data processing

In the present study, phytoplankton group/species images were

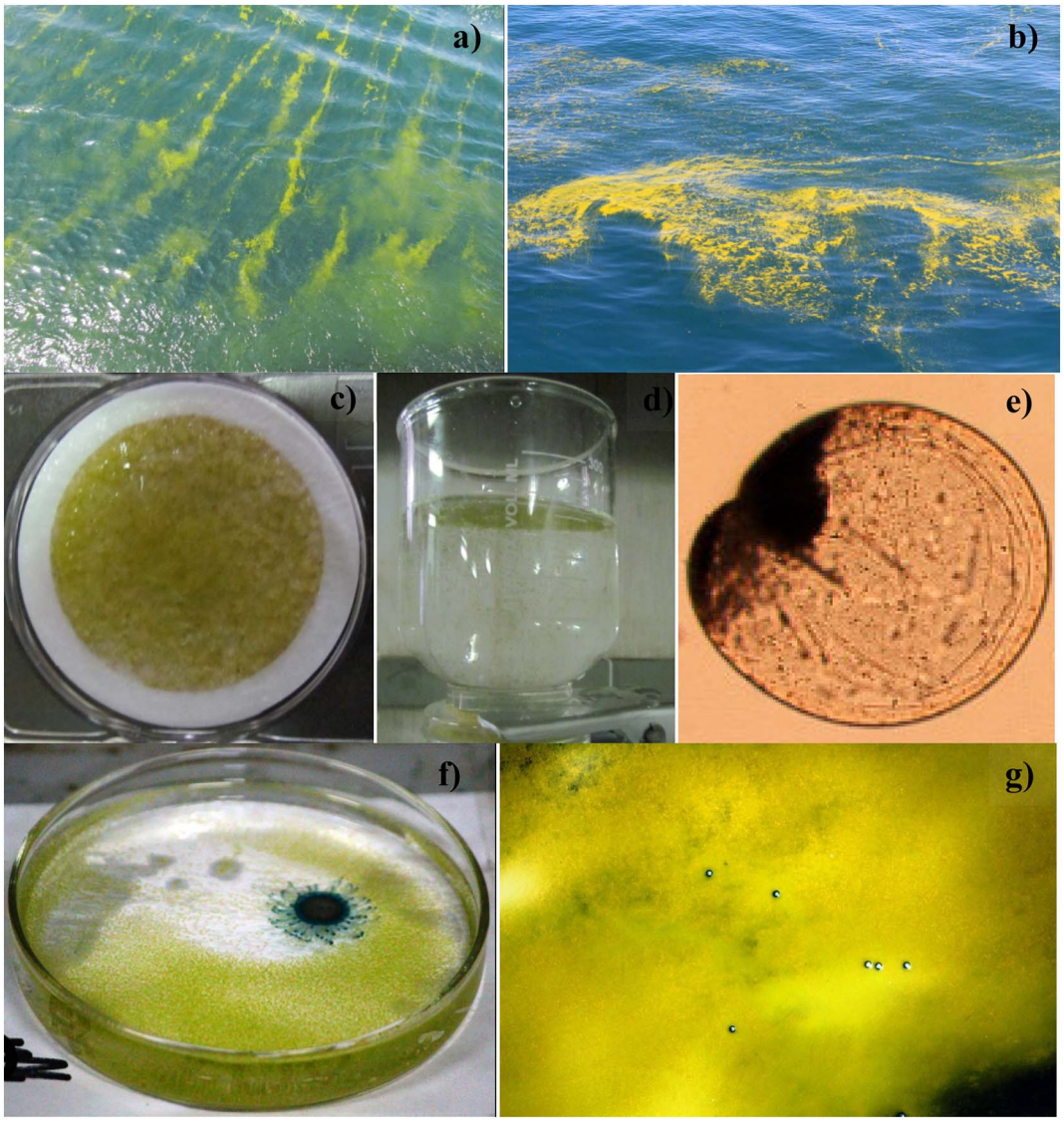


**Fig. 2.** a) Thick green and b) yellowish patch of green *Noctiluca* in the northern Arabian Sea, c) green *Noctiluca* cells concentration on a GF/F filter, d) green *Noctiluca* cells in filtering flask, e) green *Noctiluca* cell under microscope f–g) *Porpita porpita* (blue button) within thick patch of green *Noctiluca*. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

generated using satellite retrieved remote sensing reflectance ($R_{rs}$) at 443, 488 and 531 nm of Moderate Imaging Spectroradiometer onboard Aqua satellite (MODISA). The $R_{rs}$ data were downloaded from OceanColor Web (http://oceancolor.gsfc.nasa.gov/) for cloud free dates during winter period of 2016 and processed following Dwivedi et al. (2015) using SeaDAS (version 7.4) software. The algorithm of Dwivedi et al. (2015) discriminates blooms of green *Noctiluca*, diatom and other non-bloom areas using spectral slope difference of $R_{rs}$ within 448–531 nm and 488–443 nm. The phytoplankton type discriminating coefficients used by Dwivedi et al. (2015) for genesis of the algorithm was determined from several in situ radiometric observations in bloom and non-bloom regions of the northern Arabian Sea. The picophytoplankton images from MODISA were also generated using the regionally tuned size class algorithm developed by Sahay et al. (2017). This algorithm is an abundance based model that considers total chl-*a* magnitude as the sum of this pigment contribution by picophytoplankton, nanophytoplankton and microphytoplankton.

## 3. Results

A total number of 37 phytoplankton species comprising of 21 diatoms, 12 dinoflagellates, two cyanobacteria and two chrysophyta were observed in surface waters during the present study (Table 1). The phytoplankton community was dominated (98.63%) by dinoflagellate green *Noctiluca* (average abundance 10.16 ± 5.806 × $10^4$ cells-$L^{-1}$) discerning mono-specific bloom. The distribution range of phytoplankton abundance at different depths is provided in Table 2. The total phytoplankton abundance was between 0.077 and 19.013 × $10^4$ cell-$L^{-1}$ in the water column of bloom stations (Fig. 3). However, total phytoplankton abundance varied between 0.008 and 0.554 × $10^4$ cell-$L^{-1}$ in the water column of non-bloom stations (Fig. 3). In comparison to the bloom stations, total phytoplankton abundance was observed homogenous in the water column of non-bloom stations. The individual phytoplankton species abundance other than green *Noctiluca* was lower in the water column of bloom stations. In surface waters of the bloom locations, total phytoplankton abundance ranged within 4.610–19.013 × $10^4$ cell-$L^{-1}$ with predominance of green *Noctiluca* and subsequently decreased in the water column towards bottom (Fig. 3). The well pronounced preponderance of green *Noctiluca* deciphered bloom in the northern Arabian Sea.

At surface waters of bloom stations, range of average diatom abundance was observed lower (0.002–0.01 × $10^4$ cells-$L^{-1}$) in

**Table 1**
List of phytoplankton species observed in surface waters of bloom and non-bloom stations in the northern Arabian Sea. The average abundance with standard deviation of each species is presented as $10^4$ cells-$L^{-1}$.

| Group/species | Non-Bloom | Bloom |
|---|---|---|
| Diatoms | | |
| *Actinoptychus senarius* | 0.023 ± 0.004 | – |
| *Asteromphalus flabellatus* | 0.007 ± 0.001 | 0.004 ± 0.001 |
| *Coscinodiscus centralis* | 0.008 | – |
| *Coscinodiscus granii* | 0.004 ± 0.002 | 0.005 ± 0.004 |
| *Coscinodiscus marginatus* | 0.029 ± 0.032 | – |
| *Dactyliosolen fragilissimus* | 0.008 ± 0.001 | 0.003 |
| *Eucampia cornuta* | 0.004 | 0.004 ± 0.002 |
| *Gyrosigma balticum* | 0.033 ± 0.031 | – |
| *Leptocylindrus danicus* | 0.063 | 0.008 |
| *Meuniera membranacea* | 0.01 ± 0.01 | – |
| *Navicula transitrans* | 0.004 | – |
| *Nitzschia sigma* | 0.017 ± 0.002 | – |
| *Pleurosigma directum* | 0.074 | – |
| *Rhizosolenia alata* | 0.028 ± | 0.004 ± 0.002 |
| *Rhizosolenia crassispina* | 0.019 ± 0.023 | 0.004 |
| *Rhizosolenia imbricata* | 0.005 | – |
| *Stephanopyxis turris* | 0.078 ± 0.005 | – |
| *Thalassiosira punctigera* | 0.012 | 0.002 |
| *Thalassiosira subtilis* | 0.004 ± 0.001 | – |
| *Thalassionema frauenfeldii* | 0.074 ± 0.041 | – |
| *Thalassiothrix longissima* | 0.051 ± 0.066 | 0.01 |
| Dinoflagellates | | |
| *Alexandrium monilatum* | 0.2 | – |
| *Ceratim fusus* | 0.025 ± 0.035 | – |
| *Ceratim declinatum* | 0.063 | – |
| *Gymnodinium breve* | 0.03 ± 0.044 | – |
| *Noctiluca scintillans* | 0.011 | 10.16 ± 5.806 |
| *Oxytoxum scolopax* | 0.004 ± 0.003 | – |
| *Peridinium quinquecorne* | 0.01 | – |
| *Prorocentrum mexicanum* | 0.004 | – |
| *Podolampas palmipes* | 0.001 | – |
| *Pyrocystis noctiluca* | 0.002 | 0.093 ± 0.099 |
| *Pyrophacus horologium* | 0.046 ± 0.058 | – |
| *Scroppsiella trochoidea* | 0.014 ± 0.01 | 0.004 |
| Cyanobacteria | | |
| *Trichodesmium erythraeum* | 0.005 ± 0.002 | – |
| *Trichodesmium thiebautii* | 0.008 | – |
| Chrysophyta | | |
| *Octactis octonaria* | 0.005 ± 0.001 | – |
| *Dictyocha fibula* | 0.007 ± 0.005 | – |

**Table 2**
Distribution of different phytoplankton size class biomass as observed in terms of chlorophyll-*a* concentration and total phytoplankton abundance in the water column of bloom (B) and non-bloom (NB) stations in the study area.

| Depth | | 0 m | 10 m | 20 m | 30 m |
|---|---|---|---|---|---|
| Microphytoplankton | NB | 0.02–0.91 | 0.11–0.43 | 0.13–0.34 | 0.07–0.33 |
| Biomass ($mg\text{-}m^{-3}$) | B | 1.86–8.02 | 0.20–0.49 | 0.08–0.15 | 0.03–0.12 |
| Nanophytoplankton | NB | 0.02–0.10 | 0.03–0.10 | 0.05–0.13 | 0.03–0.14 |
| Biomass ($mg\text{-}m^{-3}$) | B | 0.16–1.18 | 0.07–0.13 | 0.05–0.08 | 0.04–0.09 |
| Picophytoplankton | NB | 0.02–0.63 | 0.01–0.56 | 0.12–0.43 | 0.03–0.44 |
| Biomass ($mg\text{-}m^{-3}$) | B | 1.39–6.36 | 0.48–1.06 | 0.12–0.34 | 0.06–0.32 |
| Total Phytoplankton | NB | 0.04–0.55 | 0.08–0.33 | 0.01–0.25 | 0.10–0.27 |
| Abundance ($10^4$cells-$L^{-1}$) | B | 4.61–19.01 | 0.15–3.11 | 0.08–0.81 | 0.09–2.42 |

comparison to the non-bloom stations (0.004–0.078 × $10^4$ cells-$L^{-1}$) (Table 1). Diatom species diversity was also observed higher in non-bloom stations (21 species) in comparison to the green *Noctiluca* predominated stations (9 species). Similarly, dinoflagellate species diversity other than green *Noctiluca* was observed higher in non-bloom locations. Two species of cyanobacteria, *Trichodesmium erythraeum* and *Trichodesmium thiebautii* were observed in non-bloom waters. Interestingly, swarming of jellyfish like hydrozoa *Porpita porpita* (commonly known as blue button) was observed in the thick bloom waters (Fig. 2 f & g).

In the present study, different size classes of phytoplankton such as pico, nano and micro was quantified in the water column of the bloom and non-bloom regions. The distribution range of different phytoplankton size class biomass at different depths is provided in Table 2. Microphytoplankton biomass was observed within 1.86–8.02 $mg\text{-}m^{-3}$ in surface waters of the bloom stations and 0.02–0.91 $mg\text{-}m^{-3}$ in non-bloom stations. Total phytoplankton abundance and microphytoplankton biomass co-varied in the surface waters of bloom stations. A similar pattern of variability was also observed between these two parameters in non-bloom stations with marginal offset (Fig. 3). In surface waters of bloom stations, micro, nano and picophytoplankton contributed 60.5%, 7.1% and 32.4% respectively to the total phytoplankton biomass (Fig. 4a). Picophytoplankton biomass was ranged from 0.02 to 0.63 $mg\text{-}m^{-3}$ in surface waters of non-bloom stations, whereas from 1.39 to 6.36 $mg\text{-}m^{-3}$ in the bloom stations. The rank order of contribution of different phytoplankton size classes to total phytoplankton biomass was picophytoplankton (47.2%) > microphytoplankton (44.4%) > nanophytoplankton (8.3%) in surface waters of non-bloom stations. In order to depict synoptic temporal distribution of picophytoplankton in conjunction with green *Noctiluca* bloom, satellite images were generated for similar dates based on data availability (Fig. 5). Higher magnitude of picophytoplankton biomass in terms of chl-*a* concentration was discerned at green *Noctiluca* bloom regions.

In contrast to surface, pico and nanophytoplankton contributed relatively more at 10 m depth in non-bloom and bloom stations despite lower concentration (Fig. 4a, b). Total phytoplankton biomass was observed with 45.6% contribution from picophytoplankton and 13.2% from nanophytoplankton at 10 m depth of bloom stations. Picophytoplankton concentration was ranged from 0.01 to 0.56 $mg\text{-}m^{-3}$ and 0.16 to 0.48 $mg\text{-}m^{-3}$ at 10 m depth in non-bloom and bloom stations, respectively. Subsequently, percentage contribution of picophytoplankton to total phytoplankton biomass remained high at 20 m and 30 m depth in bloom stations (Fig. 4c, d). Nanophytoplankton contribution to total phytoplankton biomass increased with depth at both bloom and non-bloom stations. In contrast, concentration of microphytoplankton biomass decreased with depth at bloom stations. At non-bloom stations, microphytoplankton biomass followed bottom-ward decreasing trend except a marginal increase in rate of contribution at 20 m depth. At 20 m depth, microphytoplankton biomass was ranged from 0.13 to 0.34 $mg\text{-}m^{-3}$ at non-bloom stations and 0.08 to 0.15 $mg\text{-}m^{-3}$ at bloom stations (Fig. 4c). Picophytoplankton biomass was observed with comparative higher concentration than other phytoplankton size classes at non-bloom stations (0.12–0.43 $mg\text{-}m^{-3}$) and bloom stations (0.12–0.34 $mg\text{-}m^{-3}$) at 20 m depth (Fig. 4c). Maximum restriction of green *Noctiluca* assemblage to surface waters was observed from the distribution of total phytoplankton abundance in the water column.

In order to quantify the primary production, a mooring experiment was carried out at a bloom location. NCP estimates depicted higher values in surface (85.26 $mgC/m^3$/Day), whereas the NCP at discrete depths up to 50 m was observed with negative values (Fig. 6). The magnitude of respiration was 34.56 $mgC/m^3$/Day at surface whereas 100.81 $mgC/m^3$/Day at 50 m depth.

Inorganic macronutrient concentrations were compared between the surface and subsurface (10 m) in both bloom and non-bloom conditions (Fig. 7a and b). The average concentration of nitrate was higher (0.97 μM) in surface waters of bloom stations in comparison to non-bloom stations (0.20 μM). Similar to nitrate, average concentration of phosphate was higher (0.34 μM) in surface waters of bloom stations in comparison to non-bloom stations (0.22 μM). However, average silicate concentration was similar (2.33 μM) in surface waters of both bloom as

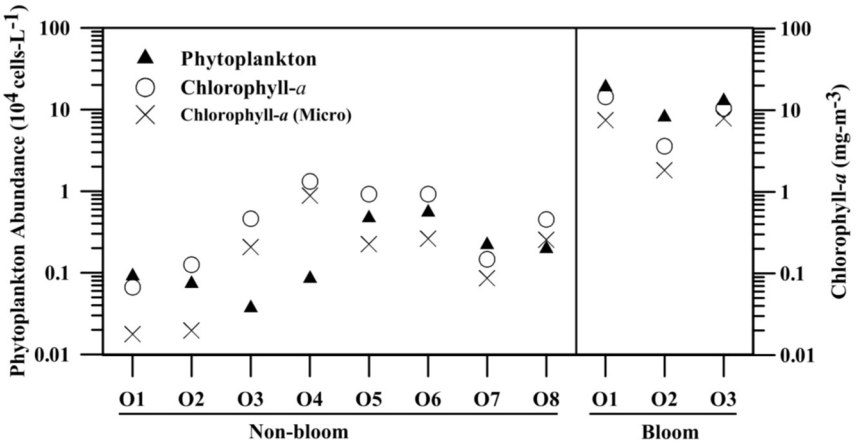


**Fig. 3.** Distribution of phytoplankton abundance and chlorophyll-*a* (chl-*a*) concentration at green *Noctiluca* bloom and non-bloom stations in the northern Arabian Sea.

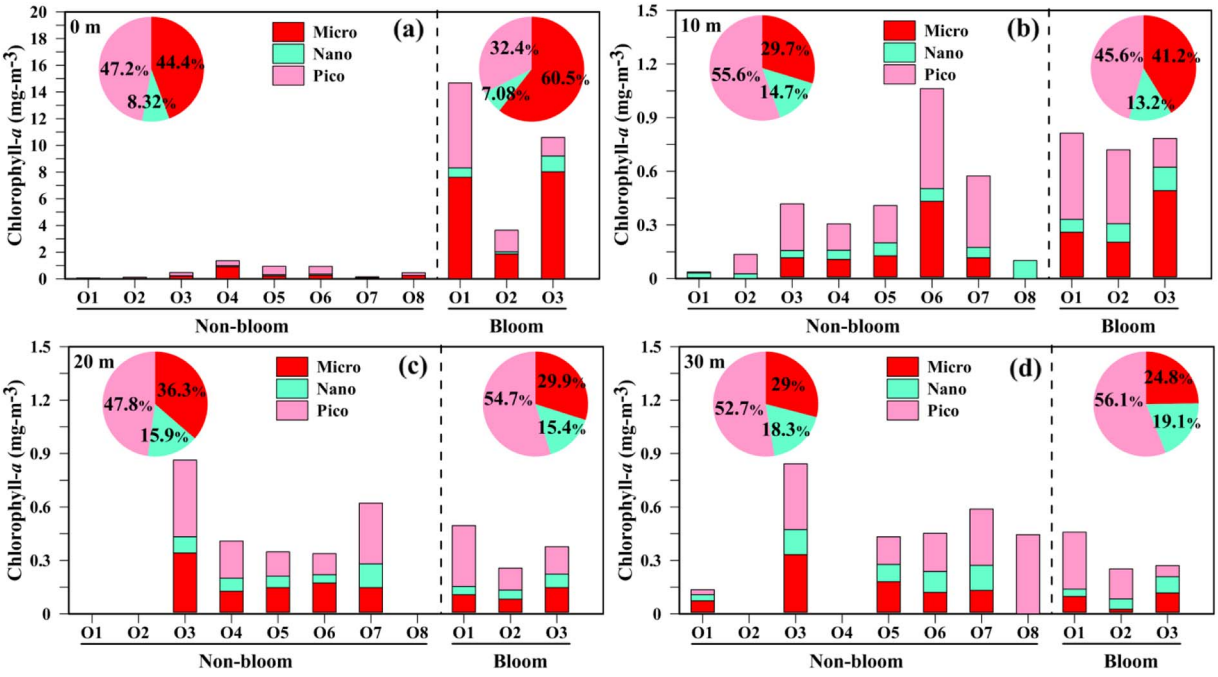


**Fig. 4.** Chlorophyll-*a* (chl-*a*) concentration (in mg $m^{-3}$) of pico, nano and microphytoplankton at (a) surface, (b) 10 m, (c) 20 m and (d) 30 m depths of green *Noctiluca* bloom and non-bloom stations in the northern Arabian Sea. The inset pie charts show average percentage contribution of micro, nano and picophytoplankton. Micro: Microphytoplankton, Nano: Nanophytoplankton, Pico: Picophytoplankton.

well as non-bloom locations. In the subsurface (10 m), the average concentration of nitrate was comparatively higher (1.01 μM) at non-bloom stations than bloom stations (0.34 μM). Average concentration of silicate was observed higher (2.81 μM) in subsurface of bloom locations in comparison to non-bloom stations (2.33 μM). Similar to nitrate, phosphate concentration was higher at subsurface in bloom location (0.31) in comparison to non-bloom stations (0.22 μM). In general, the phytoplankton growth is controlled by the proportions of nitrate, phosphate and silicate in marine aquatic ecosystems. Hence, molar ratios of inorganic macronutrients were compared between bloom and non-bloom stations. Different molar ratios followed similar pattern as like total chl-*a* in surface waters at bloom stations. N:P (nitrate:phosphate), N:Si (nitrate:silicate) and Si:P (silicate:phosphate) ratios varied from 1.02 to 7.24, 0.18 to 0.71 and 5.43 to 10.18 respectively in surface waters of bloom stations. The molar ratios were observed with comparative lower values in surface waters of non-bloom stations with N:P ranged from 0.23 to 2.50, N:Si from 0.02 to 0.28 and Si:P from 2.51 to 15.39. A condition of $N:P < 10$ and $N:Si < 1$ signified potential nitrogen limitation conditions in both bloom and non bloom stations. In the subsurface, the molar nutrient ratios were observed with different pattern. Peak values of N:P, N:Si and Si:P were observed as 19.56, 6.58 and 32.0 respectively at non-bloom stations whereas 1.80, 0.15 and 15.51 at bloom waters. In contrast to surface, potential nitrogen limitation condition was observed only in subsurface waters of bloom stations.

## 4. Discussion

Phytoplankton community structure responds quickly to different phases of *Noctiluca* bloom. The contribution rate of individual phytoplankton groups to total phytoplankton abundance often oscillates due to grazing pressure as well as environmental consequences of *Noctiluca* bloom. Total phytoplankton abundance with predominance of green *Noctiluca* gradually decreased towards sub-surface in the water column. The previous study in the same geographical region also reports green *Noctiluca* cell abundance of $3 \times 10^6$ cells-$L^{-1}$ in 2000 in the northern Arabian Sea (Madhu et al. 2012). In 2012, *Noctiluca* abundance was between $6.4 \times 10^4$ and $3.7 \times 10^6$ cells-$L^{-1}$ in this region (Padmakumar

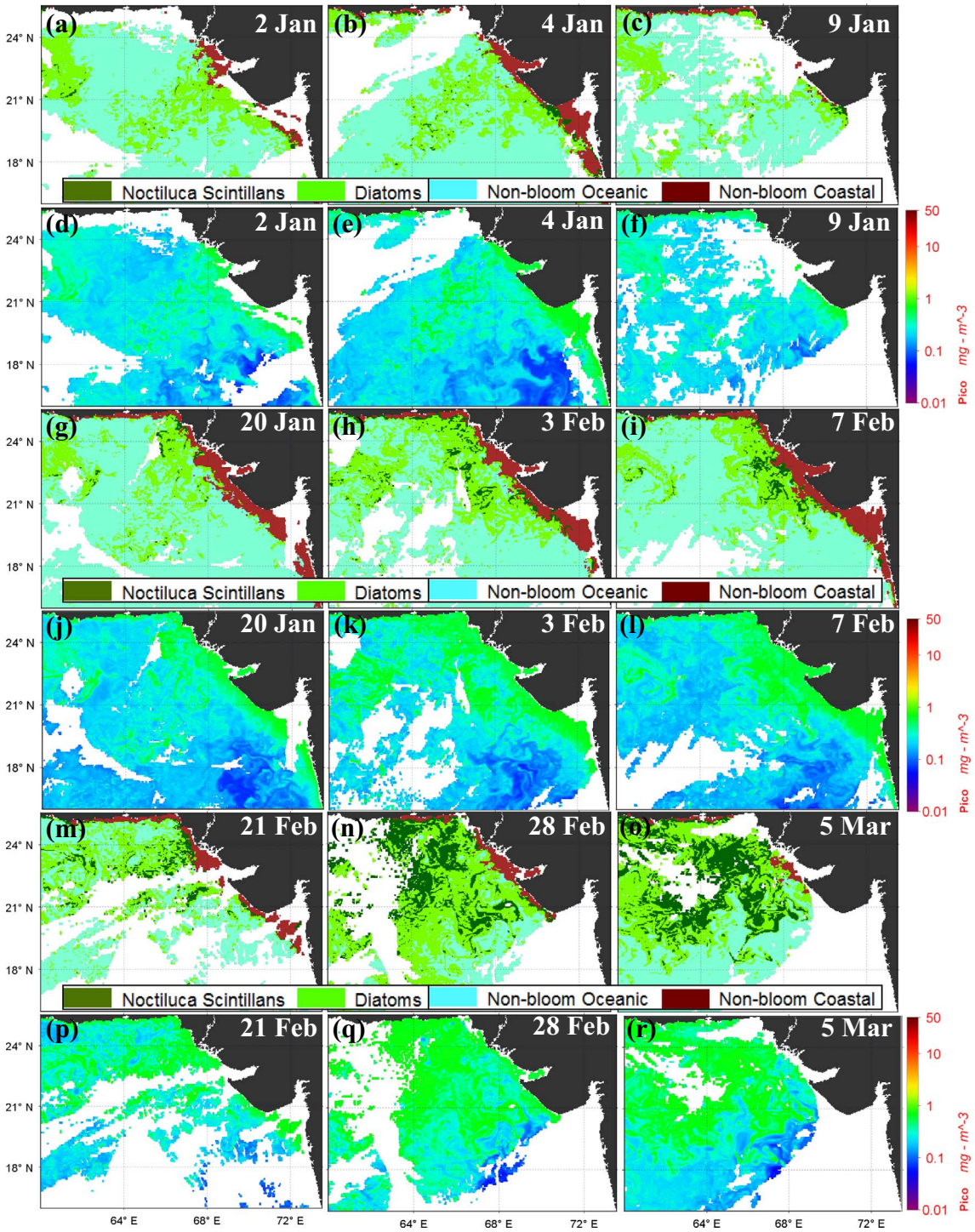


**Fig. 5.** Satellite (MODISA) retrieved temporal distribution of diatom-green *Noctiluca* (a–c, g–i, m–o) and picophytoplankton (d–f, j–l, p–r) during winter of 2016 in the northern Arabian Sea.

et al. 2016). The present observed average abundance of green *Noctiluca* ($10.16 \times 10^4$ cell-$L^{-1}$) is within the previous reported range. The difference in green *Noctiluca* abundance in the north-eastern Arabian Sea during bloom period could be attributed to the quantum of prey availability and stage of bloom. In general, spread and intensity of *Noctiluca* bloom depends on the abundance of prey, especially diatoms (Kiørboe and Titelman 1998; Dwivedi et al. 2015). In general, the active phase of the bloom contains higher number of cells in comparison to the onset and waning phase. The lower species diversity and abundance of other phytoplankton species at bloom stations could be attributed to the predation pressure by green *Noctiluca* (Mohamed and Messaad 2007). Further, the sustenance of bloom despite low prey availability signified active photosynthesis by the endosymbiont subsequent to grazing induced depletion of prey abundance. The active photosynthesis by the prasinophyte endosymbiont was evidenced through high NCP values at surface. Earlier studies have also reported higher primary production values at *Noctliluca* bloom locations in the northern Arabian Sea during 2000 ($> 50$ mgC/$m^3$/Day) and 2009 (more than 2 gC/$m^3$/Day) (Madhu et al. 2012; Gomes et al. 2014). Hence, it is evident that the magnitude of primary production at surface

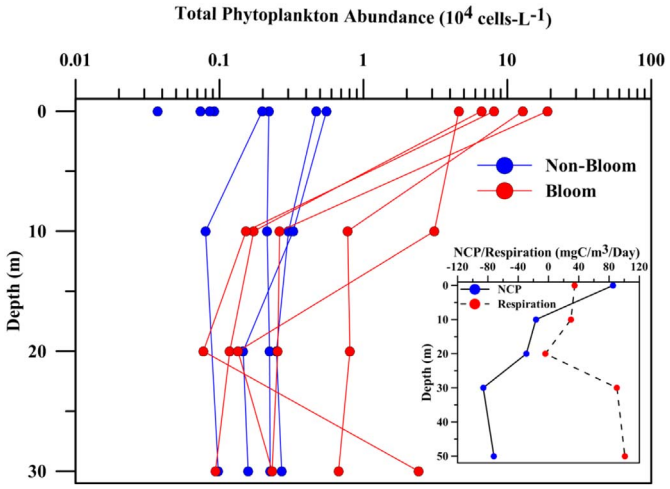


**Fig. 6.** Vertical distribution of total phytoplankton abundance at bloom and non-bloom locations in the northern Arabian Sea. Inset: Net Community Production (NCP) and respiration at bloom station.

during green *Noctiluca* bloom in the northern Arabian Sea could be attributed to the ecology of this species which switches over to autotrophy via prasinophytic endosymbiont *Pedinomans noctilucae* upon reduction in prey abundance. In general, the symbiotic metabolism of green *Noctiluca* keeps it photosynthetically active which sustains up to two weeks and the laboratory strains can live up to more than two year (Hansen et al. 2004; Furuya et al. 2006b). Hence, the present observed active primary production during low prey abundance signified the efficient carbon fixation by *Pedinomaonas noctilucae*.

Green *Noctiluca* dominated the phytoplankton community sharing about 98.63% of the total abundance. However, the green *Noctiluca* assemblage found to be restricted to the surface layers attributed to the large cell size and buoyant nature. Further, light limitation in the subsurface due to congregation of large size green *Noctiluca* could be a cause of low phytoplankton density. Homogenous distribution of phytoplankton with very low density at non-bloom stations indicated oligotrophic conditions. One of the preferred diatomic diet of *Noctiluca*, *Thallassiosira* was observed in the bloom stations (Saito and Furuya 2006), however, the species abundance was low might be due to predation by *Noctiluca*. As evidenced from the reports of last decade, green *Noctiluca* bloom onset occurs in early February and crashes in late March (Dwivedi et al. 2006, 2015). The bloom intensifies by utilizing the entrained nutrients through winter convective mixing (Dwivedi et al. 2008). In addition, availability of preferred diatomic prey in good abundance is required for the bloom onset and growth (Kiørboe and Titelman 1998; Zakaria and Ibrahim 2007). In order to detect the prevalence of diatoms during pre and onset phase of green *Noctiluca* bloom during winter season of 2016, satellite (MODISA) retrieved phytoplankton information was studied (Fig. 5). Spatio-temporal imageries of phytoplankton depicted prevalence of diatom during January. Subsequently, signatures of green *Noctiluca* proliferation were observed over the diatom patches in mid of February which increased and sustained till March. The initial proliferation and sustenance of green *Noctiluca* in the diatom abundant regions leading to bloom signified high density of diatom as a suitable preconditioning factor for the onset and growth of green *Noctiluca* bloom (Dwivedi et al. 2015).

Further, the co-occurrence of *Porpita porpita*, a voracious copepod feeder (Bieri 1970) signified the competitive advantage of *Noctiluca* to have the phytoplankton prey. Copepod is the major zooplankton group prevails in the north-eastern Arabian Sea that grazes on the phytoplankton assemblage. Chl-*a* concentration, the suitable proxy of

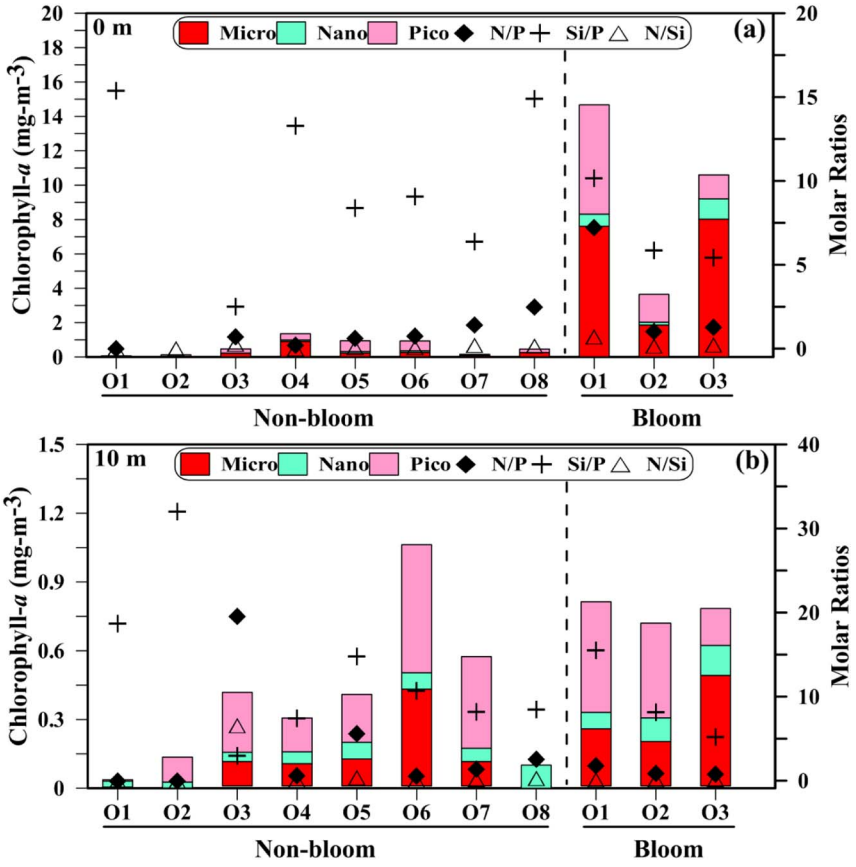


**Fig. 7.** Nutrient molar ratios and size fractionated chlorophyll-*a* concentration at (a) surface (0 m) and (b) subsurface (10 m) of bloom and non-bloom stations in the northern Arabian Sea. Micro: Microphytoplankton, Nano: Nanophytoplankton, Pico: Picophytoplankton, N: Nitrate, P: Phosphate, Si: Silicate.

phytoplankton biomass was observed with similar pattern with total phytoplankton abundance in green *Noctiluca* bloom waters. It's important to mention here that the magnitude of chl-*a* quantified in the present study was the mixture of all the three phytoplankton size classes i.e. pico, nano and micro wherein picophytoplankton contributed largely next to microphytoplankton. The total phytoplankton abundance was mostly enumerated for large size class, microphytoplankton and accordingly microphytoplankton biomass followed similar pattern with phytoplankton abundance. The higher percentage contribution of micro fraction of phytoplankton to total chl-*a* in surface waters at bloom stations could be attributed to the active photosynthesis by endosymbiont of green *Noctiluca* as the other phytoplankton abundance was comparatively low. Despite bloom conditions, picophytoplankton contributed > 30% to the total phytoplankton biomass which could be due to non-predation of green *Noctiluca* on picophytoplankton flora. In general, picophytoplankton prevails in open ocean due to its high surface to volume ratio enabling to utilize available nutrients. Further, it's important to mention here that *Noctiluca* can graze upon picophytoplankton. However, the green *Noctiluca* sustained through endosymbiotic photosynthesis under low abundance of preferred prey rather than predating upon the small sized phytoplankton in the northeastern Arabian Sea. Although, average concentration of picophytoplankton biomass was eleven times lower in surface waters of non-bloom stations in comparison to bloom, this small sized phytoplankton assemblage contributed > 30% to the total phytoplankton biomass both in bloom and non-bloom waters. This indicated the ecological adaptability of picophytoplankton to survive in low nutrient oligotropic non-bloom conditions as well as in convective mixing induced nutrient-rich green *Noctiluca* bloom regions. In depth profile, bottomward increasing trend of nanophytoplankton could be attributed to the reduced grazing by microzooplankton. In general, nanophytoplankton is preferentially grazed by microzooplankton. The present study depicted maximum restriction of green *Noctiluca* assemblage to the surface layers attributed to larger cell size and higher positive buoyancy.

The molar ratios of inorganic macronutrients in surface waters presented nitrogen limiting conditions both in bloom and non-bloom waters. In general, variability in nutrient supply and biological demand are key determinants of oceanic nutrient limitation. In the Arabian Sea, surface waters are generally nitrogen limited (Woodward et al. 1999). Lower N:P ratio in surface waters at both bloom and non-bloom waters indicated biological removal of nitrogen. Comparative higher N:P ratio in subsurface waters of non-bloom stations signified low utilization of nitrogenous nutrients which might be due to low population of microphytoplankton. In general, the microphytoplantkton utilizes available nutrient rapidly due to high growth rate. The northern Arabian Sea becomes nutrient-rich during winter attributed to convective mixing and this can be traced through the ambient concentration of nitrate due to its quick response to primary production (Sambrotto 2001; Bange et al. 2005; Padmakumar et al. 2016). Green *Noctiluca* bloom significantly enhances total productivity as well as new production attributed to high total nitrogen uptake in the Arabian Sea (Prakash et al. 2008).

## 5. Conclusion

The present study infers the following important outcomes, (i) Possible non predation of green *Noctiluca* on picophytoplankton assemblage or non preference of green *Noctiluca* to graze upon picophytoplankton. This is evident from > 30% contribution of picophytoplankton to the total phytoplankton biomass during mono-specific bloom of green *Noctiluca* (ii) Maximum restriction of green *Noctiluca* assemblage to upper few meters of water column attributed to larger cell size with positive buoyancy (iii) Prey availability for green *Noctiluca* boosted through removal of other phytoplankton grazers by zooplankton predator. This is evident from swarming of *Porpita porpita*, a voracious copepod feeder at green *Noctiluca* bloom locations which signified the competitive advantage of green *Noctiluca* to have the phytoplankton prey (iv) Active autotrophy of green *Noctiluca* in the northern Arabian Sea under low prey density through the prasinophytic endosymbiont *Pedinomonas noctilucae*. (v) Availability of prey i.e. diatom is evident as an important preconditioning factor for green *Noctiluca* proliferation in the northern Arabian Sea. This is evident from the ocean colour satellite retrieved phytoplankton group/species images during winter period in the northern Arabian Sea.

## Acknowledgements

Authors are thankful to Director, INCOIS and Director, CMLRE for their encouragement and support. Special thanks to all participants of FORV *Sagar Sampada* (cruise no. 348) for assisting in sample collection. The authors wish to acknowledge NASA-GSFC for making available satellite data products of MODIS-Aqua. This is INCOIS contribution no. 316.

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