



Understanding the microzooplankton mediated food web of the winter–spring *Noctiluca* bloom in the Northeastern Arabian Sea Ecosystem

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ABSTRACT

The dynamics of Northeastern Arabian Sea (NEAS) is governed by convective mixing in winter and stratification during the inter-monsoon spring seasons, wherein blooms of green *Noctiluca scintillans* is a recurrent phenomenon. The study investigated the role of microzooplankton (MZP) in mediating the microbial food web in bloom waters of *Noctiluca scintillans*. The winter monsoon and inter-monsoon spring periods for the years 2009, 2011 and 2012 were considered for the present study as the occurrence and intensity of bloom fluctuates between these seasons. The MZP mediation seems to be through the top-down controls (preferential grazing) on ciliates (CTS) in bloom waters, consequently supporting high mesozooplankton standing stock and inevitably higher stock of copepods. Among the three years of observations, this relation was noticeable for the year 2012, as the intense bloom of *Noctiluca* (3×10^7 cells L⁻¹) coincided with the highest number of copepods. On the contrary, in the non-bloom waters, a simple classical food web seems to be operational as diatoms dominated the phytoplankton community. Furthermore, the functional role of two CTS species viz. *Codonellopsis ecaudata* and *Steenosemella ventricosa* were most influential in structuring the community and microbial food web in the bloom events. The study suggests that during the bloom of *Noctiluca scintillans*, MZP mediated food web seems to be relatively significant in sustaining the high secondary production in the NEAS.

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1. Introduction

The food web structure in the oceanic environments of different regions is variable as they are adapted to regional circulation and climate conditions (Lochte et al., 1993; McCarthy et al., 1996; Longhurst, 1998; Karl, 1999). However, the trophic characteristic of an ecosystem is determined by the physical size of planktonic components, its diverse assemblages and complex feeding relationships. In general, it is assumed that in nutrient-rich systems when large size fraction of phytoplankton predominates, classical food web operates while in oligotrophic/stratified waters when smaller fraction (pico/nano) prevails the microbial food web attains significance (Azam et al., 1983; Cushing, 1989; Sommaruga, 1995; Anjusha et al., 2013). However, different size classes of plankton occupy a discrete ecological niche in the structure and functioning of the plankton food web in marine systems. Amongst

them, the microzooplankton (MZP: 20–200 μm), consisting of the phagotrophic protists, and form the trophic nexus between the classical and the microbial food web (Calbet, 2001). Studies have shown that MZP dominates the grazing processes in the microbial food web, consuming 70% of the primary production on an average, thereby providing steady and supplemental nutrition to mesozooplankton.

In the Northern Indian Ocean occurrence of phytoplankton blooms are observed to be common phenomena and the repeated occurrence of bloom is likely to influence the food web structure and biogeochemical processes. Reports on the *Noctiluca* bloom is documented from the Arabian Sea since the 1950s (Subrahmanyam, 1954; Charernphol, 1958). It is understood that since 2000, the recurrent occurrence of *Noctiluca* bloom is on the rise in the North-Eastern Arabian Sea (NEAS) which seem to influence dynamics of the NEAS (Matondkar et al., 2004; Gomes et al., 2009, 2014; Madhu et al., 2012; Padmakumar et al., 2016); in coastal waters of Pakistan and Oman, South East Asia, Red Sea and Bay of Bengal (Saifullah and Chaghtai, 1990; Harrison et al., 2011). The

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consequences of bloom lead to large organic matter pool resulting from inefficient grazing and this determine the food web structure of the region (Watson and Whitfield, 1985; Longhurst, 1998). Recently, Baliarsingh et al. (2018) has suggested the *Noctiluca* bloom to be eco-friendly and seem to support the fishery.

Generally, *Noctiluca* is an obligate heterotrophic dinoflagellate spanning in size from 300–800 μm with an extensive vacuole occupying most of the cell volume with high growth rate and wide distributional range spanning from temperate to tropical waters (Elbrachter and Qi, 1998; Nakamura, 1998). The occurrence of endosymbiont (prasinophytes/diatoms) within its body gives it either the 'green' or 'red' colour as visually observed during the bloom. However, the formation of *Noctiluca* bloom seems to be consequential of the interaction of biological features and physical concentration mechanisms such as winds, currents, tides etc. The comprehensive information on blooms and erstwhile studies have shown that blooms of green *Noctiluca* are usually observed during winter–spring intermonsoon periods (December–March) in the NEAS, while red *Noctiluca* blooms are mostly reported from the South Eastern Arabian Sea during the late summer monsoon (August–September) (Arunpandi et al., 2017).

From the above understanding it is clear that NEAS experiences repeated occurrence of *Noctiluca* bloom wherein inefficient grazing and eventual sinking develops a large pool of organic carbon in the water column. Concurrently, the trophic structure and functioning of food webs will be strongly influenced by these periodic events due to variations in the trophic interactions (classical/microbial food web). Being key players in the pelagic realm, the planktonic food web exports biogenic carbon, which is strongly influenced by size of the primary producers and also the effect of grazing on production (Cushing, 1989; Legendre, 1990; Legendre and Rassoulzadegan, 1996). However, in the northern Indian Ocean studies about the mediation of MZP is mostly restricted to the South Eastern Arabian Seas (SEAS) for the upwelling and oligotrophic systems (Gauns et al., 1996; Jyothibabu et al., 2008; Asha Devi et al., 2010, 2018) and Cochin Estuary (Jyothibabu et al., 2006; Sooria et al., 2015; Anjusha et al., 2013), whilst its trophic role in the NEAS is least understood. Hence it is proposed that an understanding of the trophic pathways and interactions with special emphasis on the MZP community in such ecologically complex environments would provide insight in defining the structure and functioning of the plankton food web. Because of this the present study attempts to explain the following: (i) variations in MZP and mesozooplankton components in *Noctiluca scintillans* bloom and non-bloom waters (ii) role of MZP in mediating microbial food web in the bloom waters, and (iii) community structure and functional role of CTS.

2. Materials and methods

2.1. Study area

The area for the present study between latitudes 15°N and 22°N and longitude 66°E to 75°E comprises the Northeastern Arabian Sea (NEAS). The cold dry north easterlies combined with high surface salinity drives convective mixing leading to deep mixed layer during winter monsoon (November–February) and subsequently, during the inter-monsoon spring (March–May) the wind weakens leading to stratification and development of oligotrophic conditions. Furthermore, the northern part of Arabian Sea is further demarcated into two zones attributed to poleward flowing West India Coastal Current (WICC). This restricts the deepening of mixed layer to the northern part thereby limiting the high chlorophyll concentration and bloom to this region (Vijith et al., 2016; Shankar et al., 2016). The sampling was carried out onboard FORV Sagar Sampada as part of the Marine Living

Resources Programme, covering the area from 15°N to 22°N during late winter (February) and early intermonsoon spring (March) seasons. The sampling for the years 2009, 2011 and 2012 has been considered for the present study. Although seasonal surveys were conducted in the region, the selection of stations for the present study was restricted to open ocean regions of 22°N and 21°N where bloom events occur recurrently showing spatio-temporal variations (Figs. 1a and b).

2.2. Sampling methods

2.2.1. Hydrographic parameters

A CTD (Sea-Bird Electronics, USA 911 plus) was operated to obtain the hydrographic profiles of water column (temperature: $\pm 0.001^\circ\text{C}$; Conductivity: $\pm 0.0001\text{ S m}^{-1}$ and depth $\pm 0.005\%$ of the full scale) (Fig. 1). Salinity data from the CTD were verified against the water samples collected from different depths and analysed using a high-precision salinometer (Guildline AUTOSAL). The skin layer temperature was measured using a bucket thermometer (accuracy $\pm 0.1^\circ\text{C}$) at each station. In the present study, the mixed layer depth (MLD) was taken as the depth at which the density ($\partial\sigma/\partial z$) increased by 0.2 kg m^{-3} from the surface value (Sprintall and Tomczak, 1993; Shetye et al., 1996). The monthly averaged SST of MODIS Aqua derived from ERDAAP (<http://coastwatch.pfeg.noaa.gov/erdaap>) was used to elucidate interannual variation from 2009 to 2013. The satellite-derived weekly SSH and geostrophic current (AVISO/Niller climatology - <http://oceanwatch.pifsc.noaa.gov/las>) were used to describe the current pattern and presence of eddies in the study region. The monthly averaged chlorophyll-*a* data obtained from Aqua MODIS-4 km (<https://coastwatch.pfeg.noaa.gov/erddap/files/erdMH1chl4/day>) was used to explain the chlorophyll distribution in the study area during February and March months.

2.2.2. Nutrients and dissolved oxygen

The nutrients and dissolved oxygen were analysed using standard protocols. Dissolved Oxygen was estimated following Winkler's titration method. The dissolved nutrients viz. nitrate, phosphate and silicate from the surface, 10, 20, 30, 50, 75, 100 and 120 m depths were collected using Niskin sampler fitted on a CTD carousel unit and estimated by SKALAR Autoanalyser following the standard procedures (Grasshoff et al., 1983).

2.2.3. Phytoplankton studies (Chlorophyll *a* and community composition)

For the estimation of chlorophyll *a* (Chl *a*), one litre of seawater from surface, 10, 20, 30, 50, 75, 100 and 120 m, was filtered through Whatman GF/F filter ($0.7\text{ }\mu\text{m}$, 47 mm). The photosynthetic pigments retained on the filters were extracted in 90% acetone for 24 h in the dark at 4°C and the pigment concentration was estimated (Strickland and Parsons, 1972). For the qualitative analysis of micro phytoplankton, duplicate samples were collected by filtering $\sim 30\text{ L}$ of surface water through $20\text{ }\mu\text{m}$ net and was immediately fixed with Lugol's solution. Quantitative estimation of micro phytoplankton was done by employing a Sedgewick-Rafter counting cell (1 ml in triplicate). Species identification was done under Nikon Eclipse E200 microscope following standard identification keys (Allen and Cupp, 1935; Subrahmanyam, 1959a,b, 1971; Subrahmanyam and Sharma, 1960; Hallegraeff, 1995; Tomas, 1997; Karlson et al., 2010).

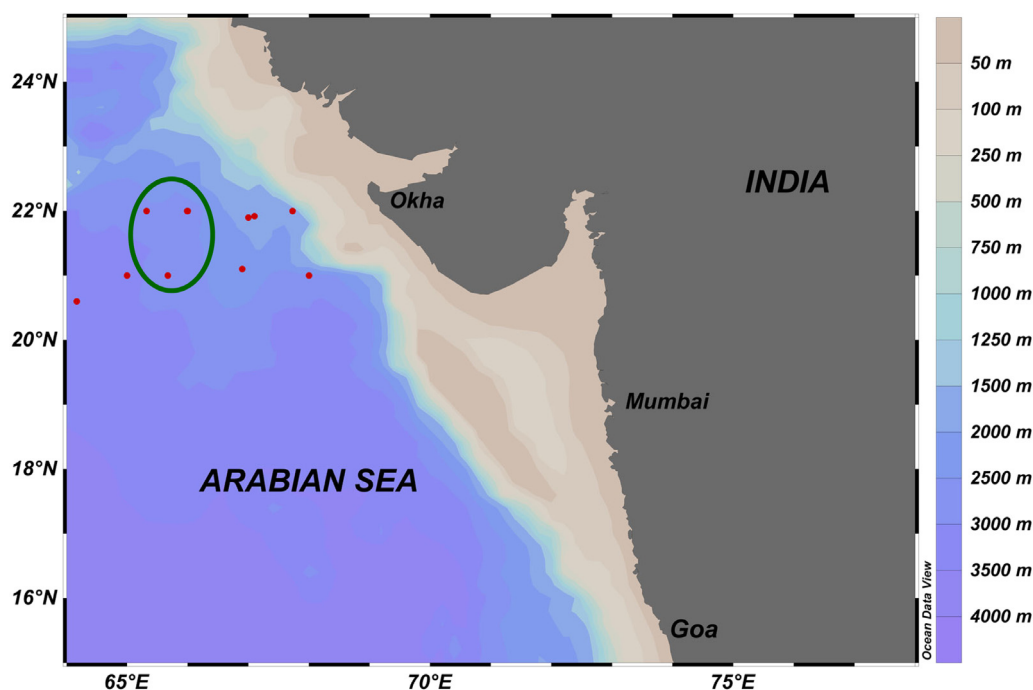


Fig. 1a. Location map and study area. Stations inside the green circle indicates bloom location.

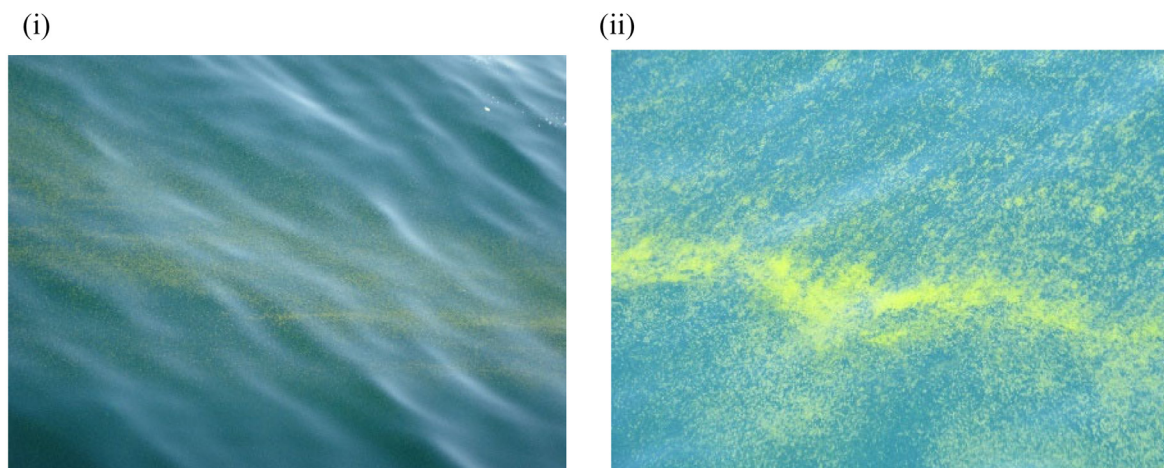


Fig. 1b. Photographs of bloom of *Noctiluca scintillans* observed in the NEAS during the study period.

2.2.4. Microzooplankton studies

The estimates of MZP were obtained from water samples collected at discrete depths (surface, 10, 20, 30, 50, 75, 100 and 120 m). About five to eight litres of water were pre-filtered through a 200 μ M bolting silk (Hydro-Bios) to eliminate the larger fraction and filtrate was then carefully collected and fixed in 3%–8% of acid Lugol's iodine. Before the microscopic analysis, samples were concentrated by allowing it to settle for two days. Three to five subsamples were analysed in Sedgwick rafter counting chamber under a Leica DMI Led Inverted microscope with phase contrast optics (100–400) $\times$ magnifications. The organisms present in the samples were identified and categorized in to groups viz., ciliates (CTS), heterotrophic dinoflagellates (HDS), radiolarians (RAD), foraminiferans (FORM) and crustacean nauplii (NAUP) (Kofoid and Campbell, 1939; Jorgensen, 1924; Marshall, 1969; Corliss, 1979; Maeda and Carey, 1985; Maeda, 1986; Lynn et al., 1988). The column integrated abundance was calculated by integrating values at the sampled depths and represented as individuals per metre square (ind. m^{-2}).

2.2.5. Mesozooplankton studies

Mesozooplankton was collected by Multiple Plankton Net Sampler (Hydro-Bios - 0.25 m^2 in mouth area and 200 μ M in mesh size). The mesozooplankton samples were collected from mixed layer and the biovolume was estimated by the displacement volume method to represent the secondary standing stock (Postel et al., 2000). As the mixed layer is uniform, the mesozooplankton collection from this layer was considered to express the secondary standing stock. The aliquot or whole sample, based on displacement volume was sorted into various taxonomic groups using standard manuals and protocols and expressed as ind. m^{-3} (ICES, 1947; Newell and Newell, 1973; Todd and Laverack, 1991).

2.2.6. Statistical tools

The diversity measures are an expression of community structure and represent characteristics unique to the organization of the community. The species diversity can be measured by ecological phenomena viz. species richness, abundance and evenness. (i) Species richness (d), is a measure of a total number of

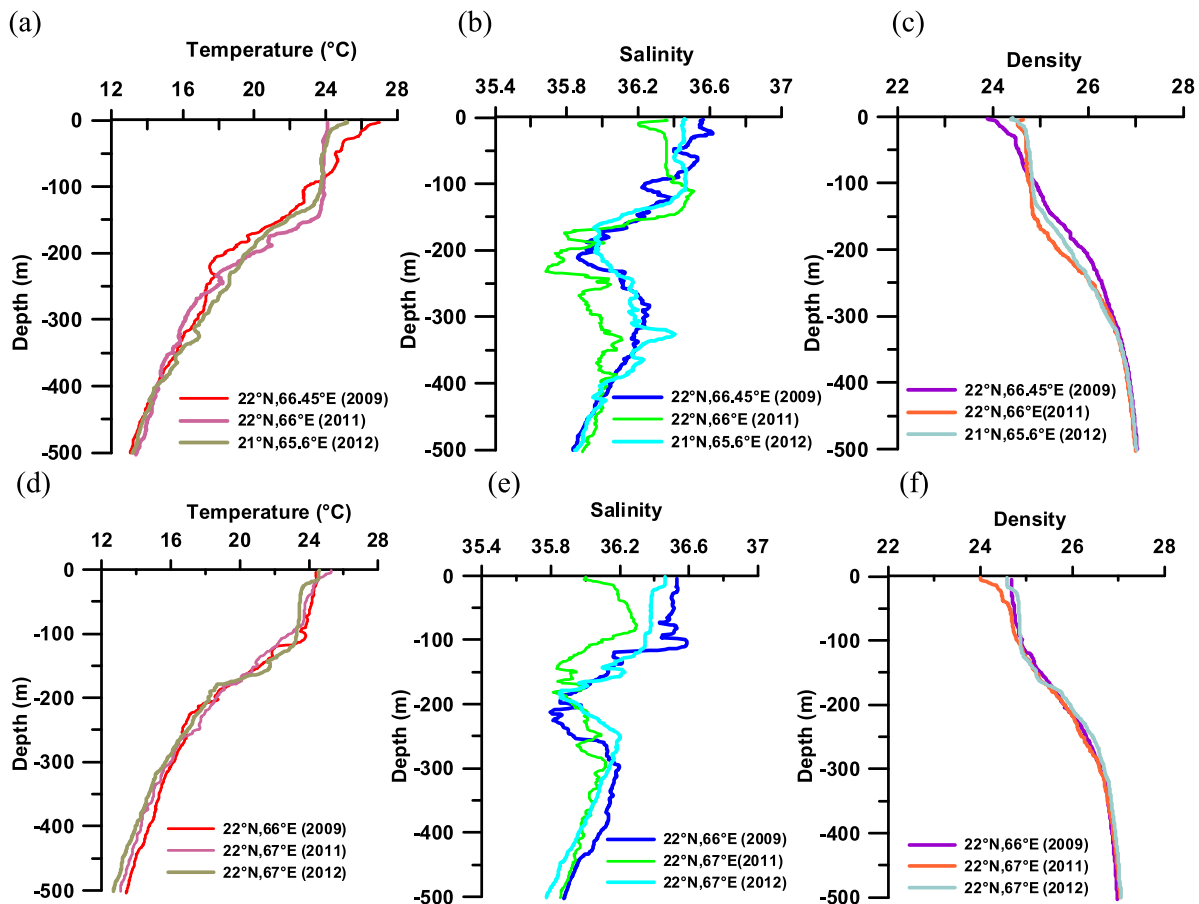


Fig. 2. Vertical section of Sea Surface Temperature (SST °C), Salinity (SSS) and Density (σ_t) during bloom (a, b and c) and non-bloom locations (d, e and f) during the years 2009, 2011 and 2012 in the NEAS.

different species in a community in a particular area (Margalef, 1968) (ii) Species evenness (J' Pielou's evenness) – the relative abundance with which each species is represented in an area (Pielou's, 1977) and (iii) Species diversity (H') – this index takes into account the number and the evenness of the species. The index is increased either by having more unique species or by having greater species evenness (Shannon and Weaver, 1963). The abundances of all species were analysed as a multivariate data set using Plymouth Routines in Multivariate Ecological Research (PRIMER 6 version 6.1.6) (Clarke and Gorley, 2001). Similarity Percentage Analysis (SIMPER) was performed to check the similarity/dissimilarity between bloom and non-bloom stations. SIMPER identifies the species that are most responsible for the observed patterns (e.g. the species that typify each level of a factor and those that contribute the most to the dissimilarity between levels). The more abundant a species is within a group, the more it contributes to the intra-group similarity, while species with a consistently high contribution to the dissimilarity between groups is a good discriminating species (Clarke and Warwick, 1994).

3. Results

3.1. Hydrographic features

The differences in the physicochemical and biological observations for bloom and non-bloom were considered based on the aggregation of *Noctiluca* cells (hereafter bloom/non-bloom). Interestingly in most instances, the bloom was observed in the oceanic regions of 22°N and 21°N quadrates between 66°E and

68°E during late winter/early spring periods with varying intensities. It was observed that during the years 2009 and 2012 the bloom event happened during March (Intermonsoon spring), whereas during 2011 the bloom occurred during late February. Nonetheless, the inter-seasonal/inter-annual variations in hydrographic characteristics did not show any discrete trend between the bloom and non-bloom locations. Moderately high SST (27 °C) coincided with weak bloom event during 2009, while during the intense bloom of 2012 the SST was low (25 °C). Nonetheless, when a moderate bloom was observed during February 2011 (Late winter) the SST was 24 °C, due to the prevalence of convective mixing (Fig. 2a). Hence it is suggested that the ambient temperature favouring bloom formation was observed to be between 24–25 °C. However, in the present study, the low SST (25 °C) during 2012 March indicated extended winter monsoon characteristics even in the early phase of intermonsoon spring. However, the salinity distribution indicated the presence of high saline water (Sal >36.2, σ_t >24) in the upper 100 m of the water column in the bloom locations during all three years of observation (Fig. 2b and c). The mixed layer was observed to be shallow (12 m & 13 m respectively) during 2009 and 2012, whereas it was deep (108 m) during 2011, due to the co-existence of an anticyclonic eddy along with convective mixing (Fig. 3). On the contrary, in the non-bloom locations, the low SST (24.3 °C) was due to the low temperature usually observed during the February months. The SST was slightly high and varied between 25.2 °C during 2011 and 24.5 °C during 2012, characterizing intermonsoon spring features (Fig. 2d). Furthermore, the upper 100 m of the water column was occupied with high saline water (~36.3) the study period (Fig. 2e and f). The mixed layer showed

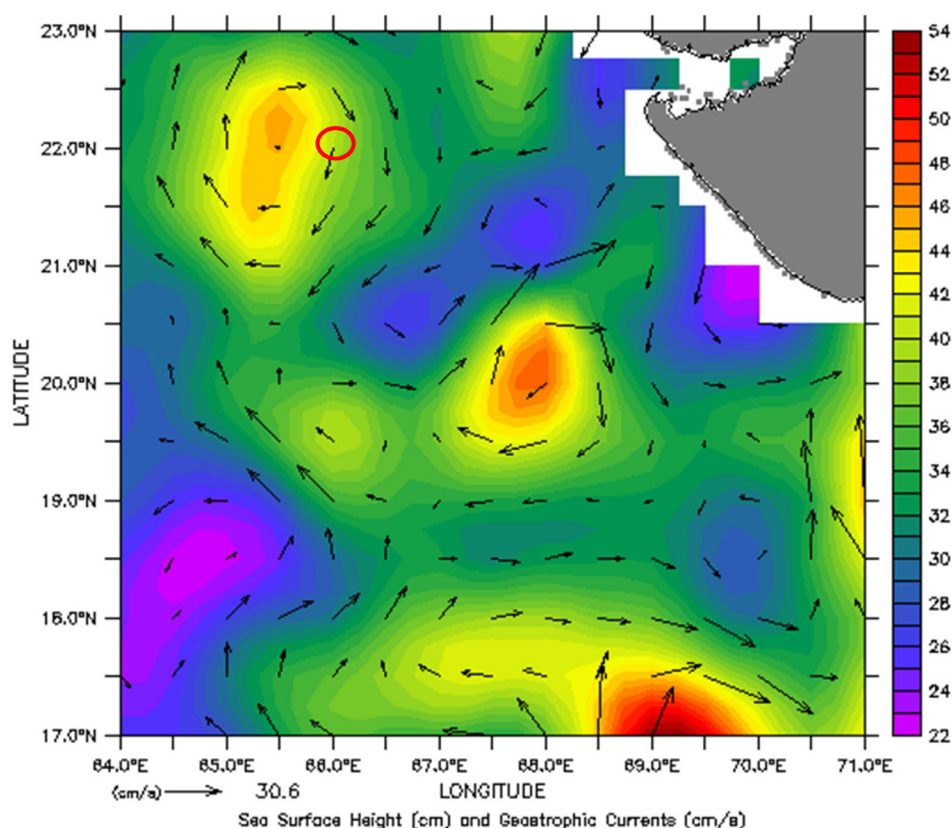


Fig. 3. Weekly SSH and geostrophic current (from merged AVISO & Niller climatology-<http://oceanwatch.pifsc.noaa.gov/las>) during end of Feb 2011 showing warm core eddy along the sampling location (Red circle).

variations between the years, it was deep (76 m-late winters) during 2009 while it was shallow (23 m and 25 m –early March) during 2011 and 2012.

3.2. Nutrients and dissolved oxygen

Even though the distribution of nutrients did not show any discrete pattern, it varied between bloom and non-bloom locations. The surface nitrate concentration was comparatively low ($0.18 \mu\text{M}$) during the less intense bloom of 2009, whereas it was considerably high ($1.13 \mu\text{M}$ and $1.18 \mu\text{M}$) during 2011 and 2012. However, phosphate was comparably higher during 2012 ($0.82 \mu\text{M}$ compared to 2009 and 2011 ($0.26 \mu\text{M}$ and $0.02 \mu\text{M}$ respectively)). The vertical profile of NO_3 in bloom stations showed consistent concentration up to 75 m depth ($0.3 \mu\text{M}$ and $\sim 1 \mu\text{M}$) during 2009 and 2011. During 2012, when the intense bloom was observed, NO_3 concentration was $> 1 \mu\text{M}$ in the surface as well as in the water column. The column phosphate concentration showed consistent values with the surface in the upper 50 m beyond which an increase was observed.

However, in non-bloom locations, the NO_3 was $0.77 \mu\text{M}$ during 2009, and the concentration was $0.32 \mu\text{M}$ during 2011 and 2012. Moreover, the subsurface layers in the non-bloom locations recorded comparatively high NO_3 ($> 1 \mu\text{M}$) during 2009 and 2012, while it was $0.3 \mu\text{M}$ during 2011 (Fig. 4a and b). Nevertheless, in the non-bloom locations, the PO_4 concentration did not vary significantly between 2009 and 2011 ($0.29 \mu\text{M}$ and $0.38 \mu\text{M}$) while it was high during 2012 ($0.64 \mu\text{M}$). The dissolved oxygen concentration was $> 5 \text{ mL}$ in the bloom locations during all the three years of observation. In the non-bloom locations, the dissolved oxygen concentration did not exhibit significant variations from that of bloom locations.

3.3. Chlorophyll *a*

Concurrently, the Chl *a* concentration varied between bloom and non-bloom waters as well as among the years. However, among the three years of observation, it was observed that high Chl *a* concentration (52.5 mg m^{-3}) was associated with intense bloom during the year 2012, followed by 2011 (2.24 mg m^{-3}) and minimum during 2009 (1.96 mg m^{-3}). The Chl *a* concentration in non-bloom waters was comparable to bloom waters in most of the instances. In the non-bloom waters Chl *a* was 2 mg m^{-3} and 1.69 mg m^{-3} during 2011 and 2009 and was the least during 2012 (0.9 mg m^{-3}). High Chl *a* concentration was observed at the surface, which was persistent up to 50 m during 2009 and 2011, while during 2012 high Chl *a* was observed up to 100 m depth. However, in the non-bloom waters Chl *a* was $> 1 \text{ mg m}^{-3}$ at the surface (Fig. 5 a and b).

3.4. *Noctiluca* abundance and phytoplankton composition

The abundance of *Noctiluca* cells showed variation and seasonality in bloom locations among the years of observation. During year 2009, when the bloom was less intense, only a few hundred *Noctiluca* cells were recorded ($1465 \text{ cells L}^{-1}$) during intermonsoon spring. During year 2011, the abundance was adequately high ($14400 \text{ cells L}^{-1}$) during the winter monsoon, and it was remarkably high ($3 \times 10^6 \text{ cells L}^{-1}$) during the intense bloom year 2012 during intermonsoon spring (Table 2). However, in non-bloom waters, the phytoplankton community was chiefly comprised of diatoms ($12141 \text{ cells L}^{-1}$ –91%) with the predominance of *Rhizosolenia hebetata* ($6334 \text{ cells L}^{-1}$), followed by *Proboscia alata* ($4321 \text{ cells L}^{-1}$) and *Chaetoceros lorenzianus* ($1123 \text{ cells L}^{-1}$) during year 2009. During 2011, the contribution of diatom

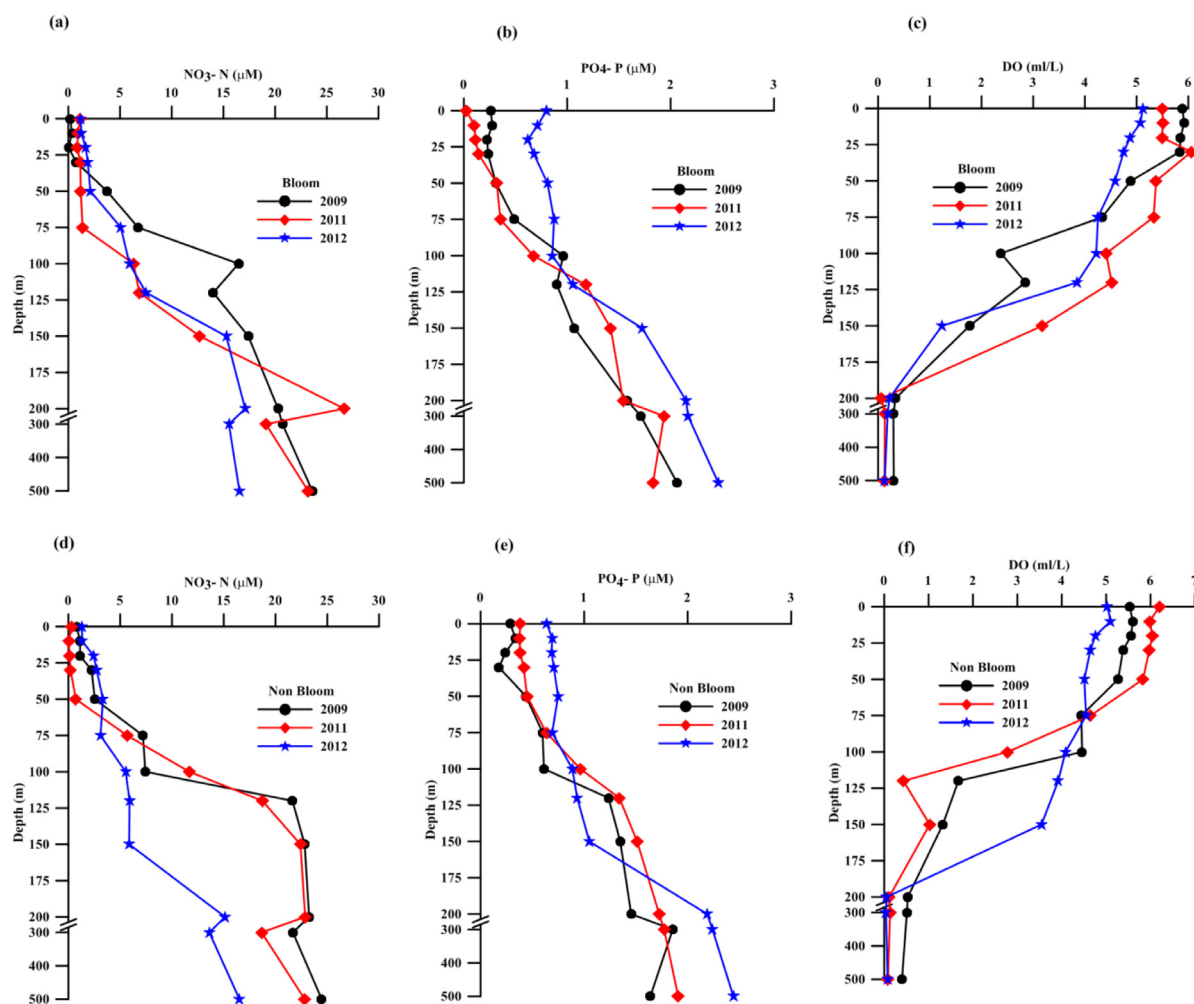


Fig. 4. Vertical distribution of Nitrate (NO_3), Phosphate (PO_4) and Dissolved Oxygen in bloom (a, b & c) and non-bloom locations (d, e & f) during the years 2009, 2011 and 2012 in the NEAS.

to phytoplankton community was $\sim 99\%$ with a cell density of $310\,168\text{ cells L}^{-1}$, represented mainly by *Haslea* spp ($300\,015\text{ cells L}^{-1}$). Other dominant species were *Rhizosolenia hebetata*, *Chaetoceros lorenzianus* etc but with low abundance. During the year 2012, diatoms contributed 60% to the phytoplankton community (190 cells L^{-1}). The diatom community during the year consisted mainly of *Chaetoceros* spp., *Thalassiosira* spp., *Rhizosolenia* spp etc. (see Table 1).

3.5. Microzooplankton (MZP)

3.5.1. Abundance

The column integrated MZP abundance and community structure was studied to understand the relative response exhibited by the heterotrophic community in *Noctiluca scintillans* bloom and non-bloom waters. The observations showed that MZP abundance exhibited variation between bloom and non-bloom locations as well as between years. During 2009, the abundance in bloom location was $90 \times 10^3\text{ ind. m}^{-2}$, while it was higher ($347 \times 10^3\text{ ind. m}^{-2}$) during 2012 and the maximum during the study period was observed during 2011 ($1200 \times 10^3\text{ ind. m}^{-2}$). However, the MZP abundance in the non-bloom location was $156 \times 10^3\text{ ind. m}^{-2}$ and $821 \times 10^3\text{ ind. m}^{-2}$ during 2009 and 2011. During intense bloom of 2012, the MZP abundance in non-bloom location was comparable to that of bloom ($380 \times 10^3\text{ ind. m}^{-2}$) (Fig. 6).

The relative contribution of column integrated CTS to the MZP community was high during all three years of observation. During

2009 the contribution of CTS was low ($48 \times 10^3\text{ ind. m}^{-2}$), while it was noticeable during 2012 ($150 \times 10^3\text{ ind. m}^{-2}$) in bloom waters. Moreover, during 2011 the contribution of CTS was comparably higher ($812 \times 10^3\text{ ind. m}^{-2}$) than 2009 and 2012. In non-bloom locations, the relative contribution of CTS showed a similar trend to that of bloom locations. During 2009 and 2012 the abundance of CTS was $56 \times 10^3\text{ ind. m}^{-2}$ and $91 \times 10^3\text{ ind. m}^{-2}$ respectively. However, coinciding with the high MZP abundance during 2011, the abundance of CTS was comparably high in non-bloom locations ($585 \times 10^3\text{ ind. m}^{-2}$). The HDS was the second abundant group and did not show any distinct trend between bloom and non-bloom locations. Although inter-annual variations were observed, in most instances the abundance did not vary significantly between bloom and non-bloom locations. During 2009 and 2012, the contribution of HDS in bloom location was almost comparable ($40 \times 10^3\text{ ind. m}^{-2}$ and $81 \times 10^3\text{ ind. m}^{-2}$ respectively). Furthermore, the abundance was noticeably higher ($293 \times 10^3\text{ ind. m}^{-2}$) in bloom location during the year 2011. Nevertheless, the abundance of HDS in non-bloom locations did vary significantly from that of bloom locations, it was low during 2009 ($42 \times 10^3\text{ ind. m}^{-2}$) compared to 2012 and 2011 ($148 \times 10^3\text{ ind. m}^{-2}$ and $150 \times 10^3\text{ ind. m}^{-2}$).

The contribution of metazoan component NAUP to the MZP community was substantial in bloom location only during the year 2012 ($111 \times 10^3\text{ ind. m}^{-2}$) compared to 2011 ($32 \times 10^3\text{ ind. m}^{-2}$) and 2009 ($21 \times 10^3\text{ ind. m}^{-2}$). Among the sarcodines, RAD was reported to be present in considerable numbers (63

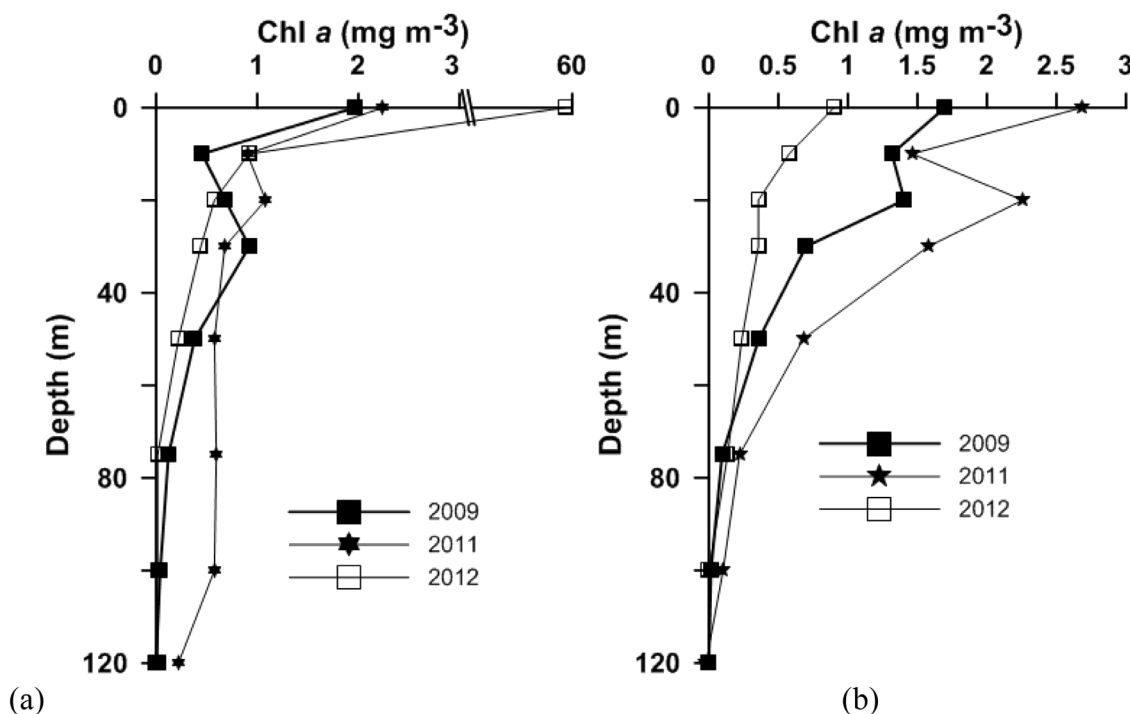


Fig. 5. Vertical distribution of Chlorophyll a (mg m^{-3}) in (a) bloom and (b) non-bloom locations during the years 2009, 2011 and 2012 in the NEAS.

Table 1

Distribution of Chl-a (mg m^{-3}), Phytoplankton cell density (Cells L^{-3}), Abundance of *Noctiluca* (Ind L^{-3}) in bloom and non-bloom locations during the years 2009, 2011 and 2012.

Year	Bloom/Non bloom	Latitude ($^{\circ}\text{N}$)	Longitude($^{\circ}\text{E}$)	Chlorophyll (mg m^{-3})	Total phytoplankton abundance (Cells L^{-1})	Diatoms (Ind L^{-1})	Dinoflagellates (Ind L^{-1})	<i>Noctiluca</i> cell density (Ind L^{-1})
2009	Bloom	22 $^{\circ}\text{N}$	66 $^{\circ}30'\text{E}$	1.96	3595	1978 (55%)	1617 (45%)	1465
	Non-Bloom	22 $^{\circ}\text{N}$	66 $^{\circ}\text{E}$	1.69	11 695	11 385 (91.8%)	310 (2.5%)	173
2011	Bloom	22 $^{\circ}\text{N}$	66 $^{\circ}\text{E}$	2.24	20 977	6170 (4%)	14 807 (96%)	14 400
	Non-Bloom	22 $^{\circ}\text{N}$	67 $^{\circ}\text{E}$	2.68	311 866	309 995 (99.4%)	1559 (0.5%)	1460
2012	Bloom	21 $^{\circ}\text{N}$	65 $^{\circ}30'\text{E}$	59.2	6 618 400	2 912 096 (44%)	3 706 304 (56%)	3.7×10^6
	Non-Bloom	22 $^{\circ}\text{N}$	67 $^{\circ}\text{E}$	0.9	311	190 (61%)	121 (39%)	108

Table 2

Variation in the diversity indices of CTS in *Noctiluca* bloom and non-bloom locations in NEAS during 2009, 2011 and 2012.

Year	Seasons	Latitude ($^{\circ}\text{N}$)	Longitude ($^{\circ}\text{E}$)	Richness (d)	Evenness (J)	Diversity (H')
2009	Bloom (March)	22 $^{\circ}\text{N}$	66 $^{\circ}30'\text{E}$	0.65	0.95	1.53
	Non bloom (February)	22 ($^{\circ}\text{N}$)	66 $^{\circ}\text{E}$	0.57	0.98	1.08
2011	Bloom (February)	22 ($^{\circ}\text{N}$)	66 $^{\circ}\text{E}$	2.04	0.95	2.28
	Non bloom (March)	22 ($^{\circ}\text{N}$)	67 $^{\circ}\text{E}$	2.28	0.90	2.66
2012	Bloom (March)	21 ($^{\circ}\text{N}$)	65 $^{\circ}30'\text{E}$	1.80	0.96	2.54
	Non bloom (February)	22 ($^{\circ}\text{N}$)	67 $^{\circ}\text{E}$	1.04	0.96	2.00

$\times 10^3 \text{ ind. m}^{-2}$) in bloom location during the year 2011, while contribution was negligible during both 2009 and 2012. The otherwise less abundant group like FORM were recorded from

bloom location only during the year 2009. In non-bloom locations the contribution of NAUP was comparable ($140 \times 10^3 \text{ ind. m}^{-2}$) to bloom location during the year 2012 (Fig. 7a and b).

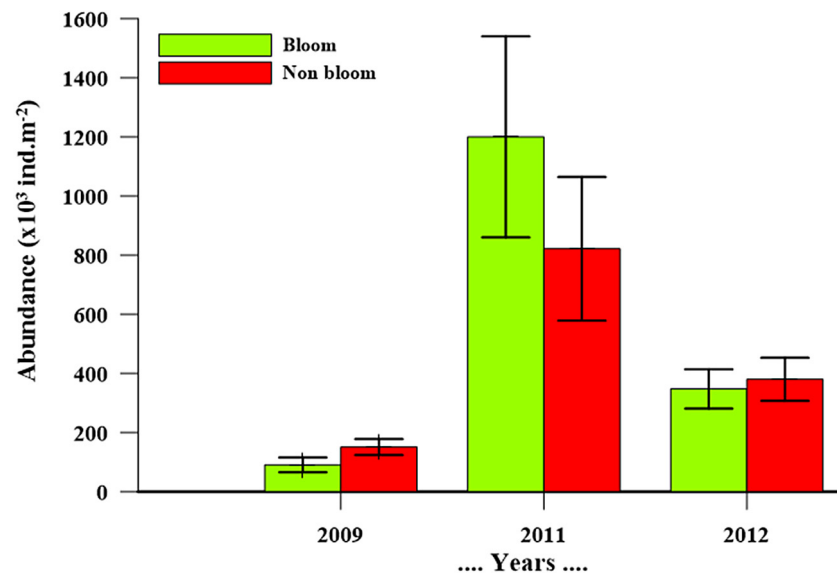


Fig. 6. Relative Abundance of total MZP ($\times 10^3$) ind. m^{-2} in bloom and non-bloom locations during the years 2009, 2011 and 2012 in the NEAS.

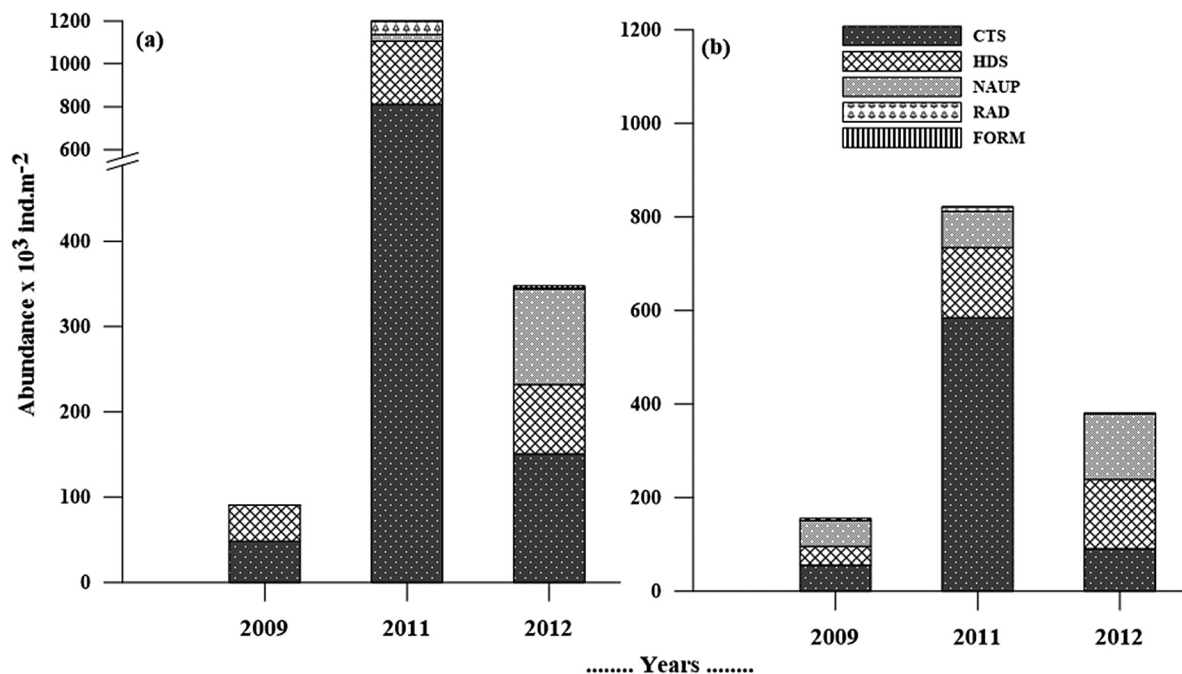


Fig. 7. Distribution pattern of relative contribution of Ciliates (CTS), Heterotrophic Dinoflagellates (HDS), Nauplii (NAUP), Radiolarians (RAD) and Foraminifera (FORM) ($\times 10^3$) ind. m^{-2} in (a) bloom location and (b) non bloom locations during the years 2009, 2011 and 2012 in the NEAS.

3.5.2. Vertical distribution

The column distribution of MZP showed low abundance at the surface during all the years, except during the intense bloom year of 2012 wherein high abundance was observed at the surface. During 2009, abundance at the surface was 1000 ind. m^{-3} and showed an increase towards the subsurface depths (20 m–2250 ind. m^{-3}). A similar pattern was observed during the year 2011 as well. The surface abundance was 3500 ind. m^{-3} and showed a fourfold increase towards deeper depths, with the maximum at 20 m (~ 12000 ind. m^{-3}). On the contrary during 2012, MZP abundance was high at the surface and 10 m depths (6250 ind. m^{-3} and 6000 ind. m^{-3} respectively) and then showed a decreasing trend, with a substantial-high at 75 m (8500 ind. m^{-3}). On

the contrary, in non-bloom waters, the MZP abundance was comparatively higher at the surface. The abundance was comparably high (13500 ind. m^{-3} and 11000 ind. m^{-3} respectively) during 2011 and 2012, compared to 2009 (2500 ind. m^{-3}). Similarly, the column distribution pattern of MZP also exhibited a reverse trend to that of bloom locations (Fig. 8a and b). Consistent with total MZP abundance, the abundance of CTS was low at the surface in bloom locations and showing an increase towards the subsurface depths. The maximum column abundance was observed at 100 m and 75 m during 2011 (9750 ind. m^{-3}) and 2012 (2250 ind. m^{-3}) respectively. On the contrary in the non-bloom locations comparably high abundance of CTS was observed in the surface during 2011 (8500 ind. m^{-3}) than 2009 (1500 ind. m^{-3}) (Fig. 8 c and d).

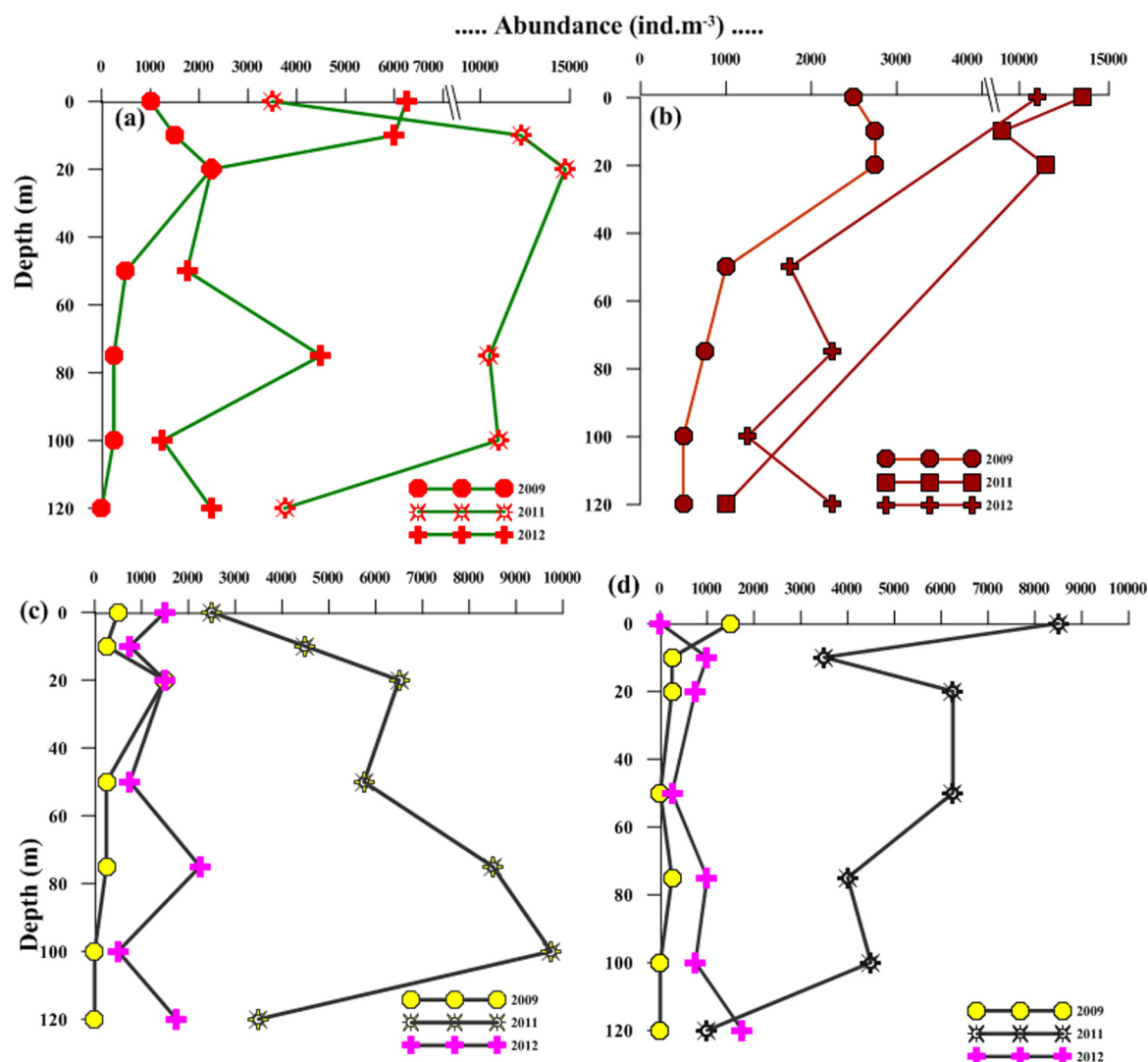


Fig. 8. Vertical distribution of MZP abundance (ind. m⁻³) (a and b) and CTS (ind. m⁻³) (c and d) in bloom (Left Panel) and non-bloom (Right Panel) locations during the years 2009, 2011 and 2012 in the NEAS.

3.5.3. Community structure and species composition

The diversity indices were studied based on the column integrated values on the occurrence of species, and it was observed that the occurrence of species did not exhibit any discrete pattern in the column. It was observed that the contribution of the CTS to MZP community was high during all the three years of study, but the species composition differed between years. The species numbers varied from 5 Sp. during 2009 to 11 Sp. and 14 Sp. during 2011 and 2012 respectively. However, in non-bloom locations, the number of species ranged from 3 to 19 sp. Nonetheless, the species diversity of column integrated CTS seemed to co-vary with the intensity of bloom, with the maximum diversity observed during intense bloom year of 2012 (H' -2.5), followed by 2011 (H' -1.88) and the least during 2009 (H' -1.53). Moreover, in non-bloom locations, the diversity did not show any discrete pattern and was considerably high during the year 2011 (H' -2.66), followed by 2012 (H' -2.0) and least during 2009 (H' -1.03). Although species diversity varied between bloom/non-bloom locations, the evenness (0.97) was more or less similar. The dominant genera in bloom locations were *Codonellopsis* during years 2009 and 2011, while it was *Parundella* during intense bloom year of 2012. During 2009 *Codonellopsis nipponica* was the dominant species followed by *Codonellopsis tessellata* and

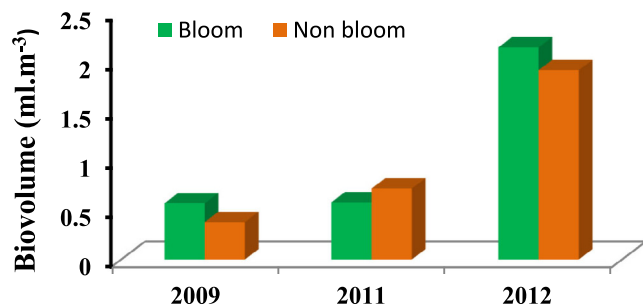
Dictyocysta magna. During 2011 *Codonellopsis ecaudata* was predominant followed by *Steenosemella ventricosa* and *Petalotricha ampulla*. However, during 2012 the dominant genera was *Parundella*, with *Parundella caudata* as dominant species followed by *Parundella lohmani*. The list of species and abundance in bloom and non-bloom locations during the study period is shown in Table 3.

3.6. Mesozooplankton standing stock

Consistent with abiotic and other biotic factors, the mesozooplankton standing stock also showed variation between bloom and non-bloom locations. It was apparent that bloom location seems to sustain high secondary standing stock when it happened during intermonsoon spring rather than the winter monsoon period. The intense bloom during 2012 recorded comparably high mesozooplankton biovolume (2.32 ml m⁻³) and numerical abundance (3191 ind. m⁻³) compared to 2011 (0.58 ml m⁻³ and 1830 ind. m⁻³) and 2009 (0.57 ml m⁻³; 434 ind. m⁻³) respectively (Fig. 9). However, in non-bloom locations, the biovolume and numerical abundance was low (0.58 ml m⁻³; 1242 ind. m⁻³) during 2012. Even though, during 2011 the biovolume was noticeable (0.72 ml m⁻³); numerical abundance was significantly low (365

Table 3Abundance of CTS (ind m^{-3}) recorded from bloom and non-bloom locations during the years 2009, 2011 and 2012.

S. No	Name of species	2009		2011		2012	
		Bloom	Non bloom	Bloom	Non bloom	Bloom	Non bloom
1	<i>Amphorella tetragona</i>	–	–	–	1 250	–	–
2	<i>Amphorellopsis acuta</i>	–	–	–	2 500	–	–
3	<i>Codonella amphorella</i>	–	–	17 500	–	–	–
4	<i>Codonella nationalis</i>	20 000	–	–	–	–	–
5	<i>Codonellopsis ecaudata</i>	–	–	800 625	108 750	–	–
6	<i>Codonellopsis orthoceros</i>	–	33 750	–	–	–	–
7	<i>Codonellopsis ostenfeldii</i>	10 000	–	3 750	–	1 250	11 250
8	<i>Codonellopsis tessellata</i>	10 000	–	–	5 000	–	10 000
9	<i>Coxiella annulata</i>	–	–	–	–	2 500	–
10	<i>Dadayiella bulbosa</i>	–	–	–	46 875	–	–
11	<i>Dadayiella ganymedes</i>	–	–	5 000	25 000	6 875	–
12	<i>Dictyocysta magna</i>	–	–	–	5 000	6 250	–
13	<i>Dictyocysta lepidia</i>	–	–	5 000	–	6 250	5 000
14	<i>Epiplocylis reticulata</i>	–	6 875	–	–	–	–
15	<i>Eutintinnus lusus undae</i>	–	–	–	1 250	5 000	–
16	<i>Eutintinnus elongatus</i>	–	–	–	2 500	–	–
17	<i>Eutintinnus frakonii</i>	–	–	–	38 750	–	–
18	<i>Favella brevis</i>	–	–	–	–	20 625	–
19	<i>Lohmaniella oviformes</i>	–	–	–	–	–	–
20	<i>Lohmaniella spiralis</i>	6 875	–	–	6 875	–	–
21	<i>Metacylis jorgensenii</i>	–	–	–	0	21 250	7 500
22	<i>Parundella caudata</i>	–	–	–	63 125	26 875	6 875
23	<i>Parundella lohmanii</i>	–	–	–	6 250	25 000	–
24	<i>Petalotricha ampulla</i>	–	–	30 000	–	–	–
25	<i>Proplectell clapedei</i>	1 250	–	–	–	–	–
26	<i>Proplectella globosa</i>	–	–	6 250	–	–	–
27	<i>Protorhabdonella simplex</i>	–	–	5 000	–	10 000	11 250
28	<i>Protorhabdonella caudata</i>	–	–	–	–	–	36 875
29	<i>Rhabdonella spiralis</i>	–	–	5 000	19 375	–	–
30	<i>Salpingacantha ampla</i>	–	–	–	6 875	–	2 500
31	<i>Salpingella acuminata</i>	–	–	–	25 625	5 625	–
32	<i>Steenosemella ventricosa</i>	–	–	137 500	–	–	–
33	<i>Streenstrupiella steenstrupii</i>	–	–	–	2 500	–	–
34	<i>Tintinnopsis incertum</i>	–	–	–	5 625	–	–
35	<i>Undella globosa</i>	–	10 000	–	–	11 250	–
36	<i>Undella hyalina</i>	–	–	11 875	222 500	–	–

**Fig. 9.** Distribution of mesozooplankton biovolume (ml m^{-3}) in the bloom and non bloom locations during the years 2009, 2011 and 2012 in the NEAS.

ind. m^{-3}), while during 2009 both the biovolume and abundance was considerably low (0.38 ml m^{-3} and 709 ind. m^{-3}).

Concurrent variation was also observed in the mesozooplankton community between bloom and non-bloom locations. As usual, the Copepoda was dominant taxa in both bloom and non-bloom locations. Consistent with high biovolume and abundance, bloom also seems to support the sustenance of copepods as high abundance (3000 ind. m^{-3}) coincided with intense bloom during the year 2012. Likewise, comparably high abundance of copepods (1755 ind. m^{-3}) was also observed from bloom during the year 2011. However, the copepod abundance was low (195 ind. m^{-3}) during the weak bloom of 2009. The non-copepod taxa did not show any discrete pattern between bloom and non-bloom locations. It was observed that the abundance of non-copepod taxa was more when bloom occurred during intermonsoon spring viz.

years 2009 and 2012 (239 ind. m^{-3} ; 191 ind. m^{-3} respectively). Furthermore, the contribution of non-copepod taxa varied significantly between bloom and non-bloom locations during 2009 (231 ind. m^{-3} and 82 ind. m^{-3}), while it was only marginal during 2011 (75 ind. m^{-3} and 88 ind. m^{-3}) and 2012 (190 ind. m^{-3} and 103 ind. m^{-3}).

Among the non-copepods, the contribution of various taxa differed between bloom and non-bloom locations. It was apparent that the number of non-copepod taxa was more in bloom locations when it occurred during the winter monsoon period, compared to the intermonsoon spring period. However, during the years 2011 and 2012, Chaetognatha was the most abundant non-copepod taxa (30% and 60% respectively) in bloom locations. The other predominant groups during 2011 were Siphonophores (20%) followed by Polychaeta, Medusa and Pteropoda while it was Amphipoda (20%) followed by Decapoda and Appendicularians contributing 10% and Siphonophores was 5%. The predominant groups during the less intense bloom of 2009 were Ostracoda (50%) followed by Appendicularians (30%) and Chaetognatha (20%). In non-bloom location, Ostracoda and Appendicularians were predominant taxa with a contribution of 30% followed by Chaetognatha (20%). In non-bloom location during 2011, the occurrence of only a few non-copepod taxa was observed and among them, Chaetognatha and Salpa were predominant (34% & 32% respectively) (Fig. 10).

4. Discussion

The study attempts to explain the trophic mediatory role of MZP in structuring the planktonic food web in bloom waters of *Noctiluca scintillans* and compared it with non-bloom waters in

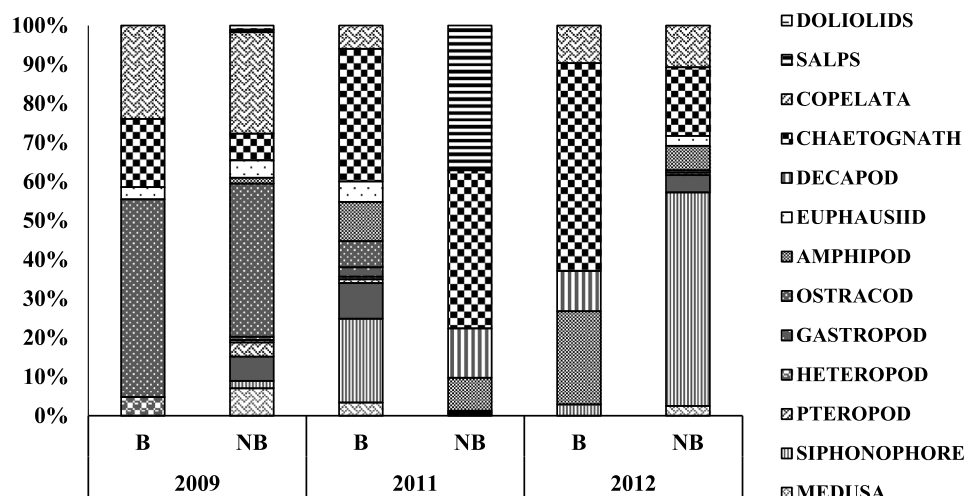


Fig. 10. Relative contribution of non-copepod mesozooplankton taxa in the bloom and non-bloom locations in the NEAS during the years 2009, 2011 and 2012 in the NEAS.

the NEAS. It is a well-known fact that the bloom of green *Noctiluca scintillans* is a recurring phenomenon in the oceanic waters of NEAS which exhibits variability in intensity inter-annually. Therefore it is presumed that the variations in atmospheric, physical and chemical properties influence dynamics of bloom in the region. In such instances, the plankton components would be an interesting entity to be looked upon to understand the trophic level interactions and food web structure of such a dynamic system.

The hydrographic characteristics of the study area showed the existence of comparably low SST (24–25 °C) and high saline waters due to convective mixing, fuelling high production in the region, at times leading to the bloom of green *Noctiluca scintillans*. The occurrence and intensity of bloom in the NEAS seem to fluctuate between late winter and inter monsoon spring seasons. The dry and strong northeasterly winds and presence of Arabian Sea High Saline Water (>35.3, sigma-t-24) in the upper 100 m water column supported convective mixing, transporting nutrients triggering phytoplankton blooms which are agreeing with historical studies of Banse (1987) and Madhupratap et al. (1996a,b). From the observations made in the offshore waters (22°N to 18°N) during the three years (2009, 2011 and 2012), it was apparent that winter monsoon characteristics were weak during 2009 as evident from the relatively high SST (25 °C–27 °C), compared to 2011 (24.5 °C–26.5 °C) and 2012 (23.5 °C–25.5 °C). These in-situ observations could be confirmed with monthly averaged satellite-derived SST for February and March which showed a steady decrease (~1 to 1.5 °C) from 2009 to 2012 (Fig. 11a and b). However, the intense bloom observed during 2012 was in conjunction with low SST suggesting that temperature (~24 °C) is considered as one of the factors supporting *Noctiluca* bloom formation. Umani et al. (2004), have reported that the maximum growth rate for *Noctiluca* was observed at 24 °C and is in agreement with the present observation. In most instances, the bloom was observed along the latitudinal grid of 22°N (2009 and 2011) to 21°N (2012) and intensified during the late February–early March. Also, satellite imageries of the monthly averaged chlorophyll-a data derived from Aqua MODIS-4 km (<https://coastwatch.pfeg.noaa.gov/erddap/files/erdMH1chla/day>) for five years including the observation period (2009, 2011, 2012, 2013 and 2015) provided a synoptic picture on the persistence and expanse of high chlorophyll concentration ($Chl > 1 \text{ mg m}^{-3}$) in the NEAS (Fig. 14). The sustenance of high chlorophyll in the region is due to the joint effect of convective mixing and bloom in the region. The high

chlorophyll is chiefly supported by high nutrient concentration (NO_3 and PO_4) in the region as observed in the present study and is in agreement with earlier reports from NEAS as well (Madhupratap et al., 2001; Jyothibabu et al., 2010; Padmakumar et al., 2016). Furthermore, the high NO_3 observed during 2012 is attributed to the extended winter monsoon characteristics, persisting till early spring and resulting in intense bloom. The reports on the occurrence of *Noctiluca* bloom during the past decade reveal the fact that the bloom signatures appear towards the fag end of February and intensify during March due to entrainment (McCreary et al., 2009).

Studies have shown that in the pelagic ecosystem, the size of the primary producers ultimately determines the pathway of interaction and structure of the food web. It is known that classical food web operates in the nutrient-enriched system when larger phytoplankton predominates and microbial food web in the oligotrophic system when smaller fraction dominate (Malone, 1980; Legendre, 1990; Harris et al., 1987; Cushing, 1989; Froneman, 2006). However, in a dynamic system like bloom, the relative contribution of planktonic components at all trophic level is an important aspect to be considered to understand the structure and functioning of the planktonic food web. In the event of the bloom of *Noctiluca scintillans* when the abundance of other phytoplankton is negligible, it is presumed that the mesozooplankton is mainly sustained through alternate prey *ie.* MZP. Therefore, in the present study, an attempt has been made to understand the relative role of MZP in mediating the microbial food web in bloom waters and compare it with non-bloom waters. The differential response exhibited by the MZP and mesozooplankton in the *Noctiluca* bloom and non-bloom waters were looked into and hypothesis put forward are as follows: (i) In bloom waters: the MZP mediation was significant through the **Top-Down controls** by the mesozooplankton. The preferential grazing on MZP could be substantiated by the fact that it falls in the suitable prey size, whilst *Noctiluca* (300–800 μM) seems to be larger than the optimal feeding size of the mesozooplankton. The grazing on MZP by mesozooplankton eventually resulted in an increase in the secondary standing stock with the subsequent reduction in MZP. Besides in such instances, inefficient grazing in bloom waters, resulted in high organic matter flux due to sinking, seem to sustain the microbial loop and thereby MZP (Fig. 15) (ii) In non-bloom waters, on the other hand, the predominance of diatoms indicates the prevalence of Classical food web, which seemed to be only partially supported by MZP (Fig. 15).

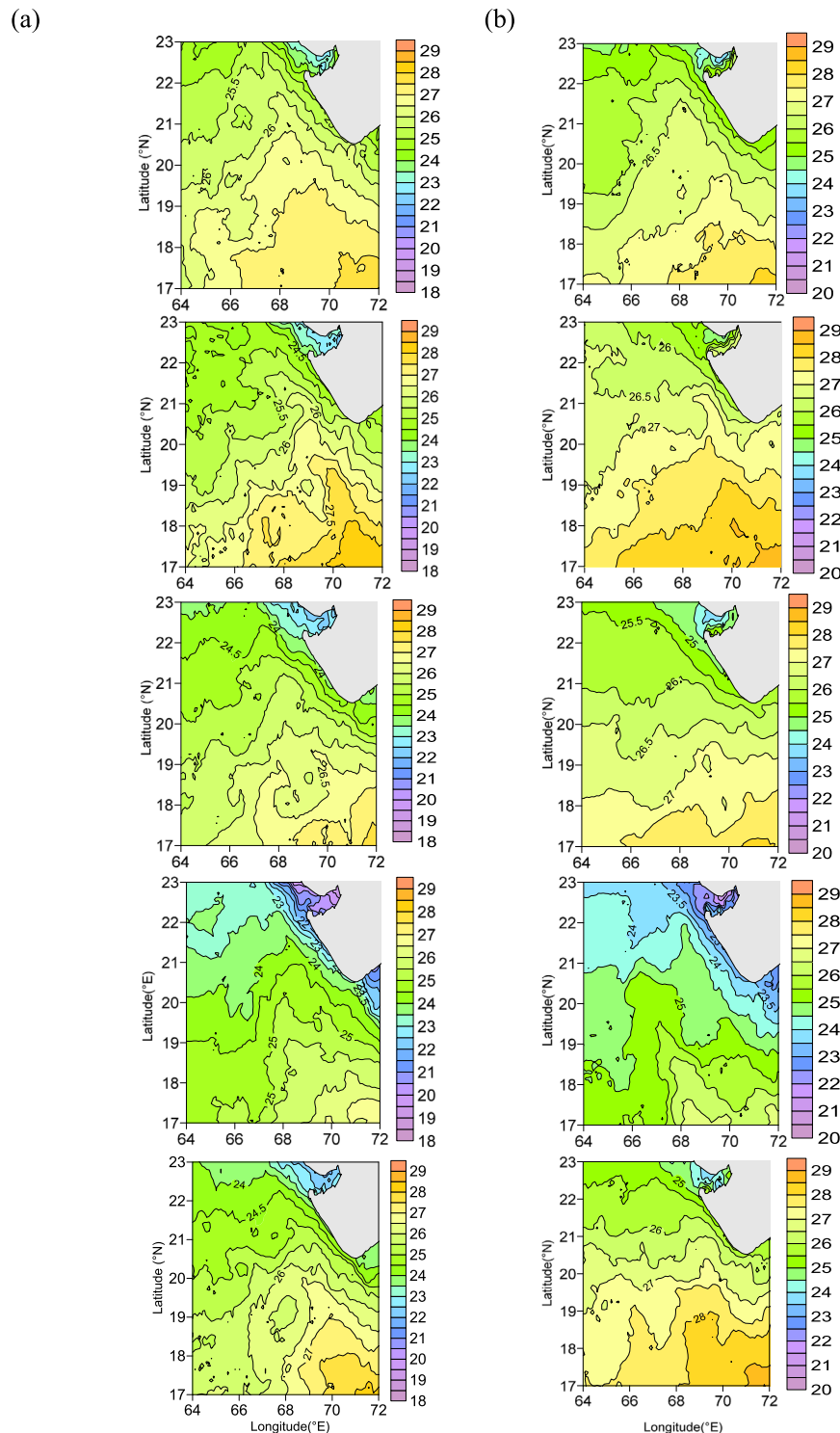


Fig. 11. Interannual variation of SST in the study region during (a) February – Left Panel and (b) March – Right Panel from 2009–2013.

However, the low abundance of MZP consequential to grazing results in an eventual increase in the mesozooplankton standing stock in bloom locations and vice versa in non-bloom conditions indicates the trophic importance of MZP in these systems. Although there are no direct data from the present observation, study by [Baliarsingh et al. \(2018\)](#) has reported higher concentration of pico/nanoplankton in the subsurface layers from the same region, which would support the sustenance of MZP in the bloom locations. Hence it is suggested that the availability of resources

at lower levels and grazers at higher trophic levels and their interactions are decisive in structuring the community and ultimately the plankton food web. Such distinct environmental setting in the NEAS, where the recurrent bloom of *Noctiluca* are observed will undoubtedly influence the organisms at different trophic levels, the structure of the planktonic food web and ultimately biological pump of the region. Besides, the significance of the study lies in the fact that unlike South Eastern Arabian Sea, the NEAS remains productive throughout the year through different physical processes and hence can be considered as a discrete ecosystem.

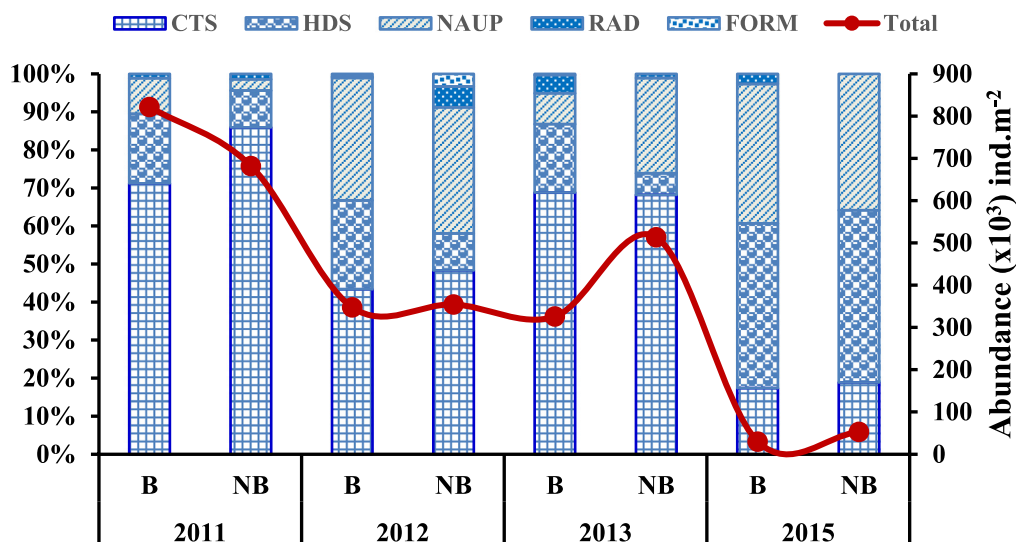


Fig. 12. Relative contribution of Ciliates (CTS), Heterotrophic Dinoflagellates (HDS), Nauplii (NAUP), Radiolarians (RAD) and Foraminifera (FORM) overlaid with the total MZP abundance ($\times 10^3$ ind. m^{-2}) in (a) bloom and (b) non-bloom locations during the years 2011, 2012, 2013 and 2015 in the NEAS.

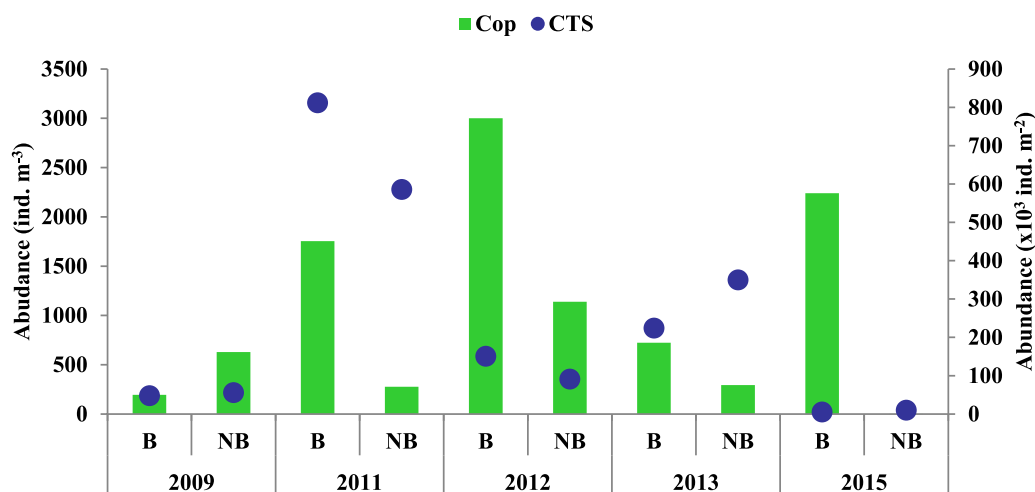


Fig. 13. Variation in abundance of Copepods (ind. m^{-3}) overlaid with abundance of CTS ($\times 10^3$ ind. m^{-2}) showing the inter-relationship in bloom and non-bloom locations during the years 2009, 2011, 2012, 2013 and 2015 in the NEAS (Bar chart represents abundance of Copepods and Dots represents the abundance of CTS).

Besides, the annual occurrence of extensive and recurrent blooms of *Noctiluca* during late winter–early spring seasons, makes the region highly dynamic (recycling and high microbial food web activity) and therefore a discrete food web structure exist in the region. However, to fully establish a concrete understanding of the plankton food web structure, the entire spectrum of plankton fraction must be considered and suggest that NEAS would be an ideal system for such studies.

It is well-known fact that the CTS form the major component of the MZP community (Fig. 12) and play important ecological roles in structuring marine microbial food web which is agreeing with our observation (Calbet, 2001; Calbet and Saiz, 2005). In the present study, the grazing effect on CTS by mesozooplankton increased the secondary standing stock. The preferential feeding of copepods on CTS could be corroborated in the present study as shown in Fig. 13. This was perceptible in the year 2012, wherein the exceptionally high abundance of copepods (3000 ind. m^{-3}) coincided with intense bloom location and consequently fewer numbers of CTS (150×10^3 ind. m^{-2}) indicating grazing effects. The above relationship was also observed for the years 2009 and 2011 and further substantiated by analysing MZP Community and trend of Copepod vs. CTS for subsequent

years 2013 and 2015. The opposite trend between CTS and Copepod was observed during all these years, thereby confirming the grazing effects (Fig. 13). Also, the low abundance of CTS at the surface in bloom waters indicated grazing preferences of Copepods, as mixed layer harbours high mesozooplankton stock which agrees with the behaviourally driven feeding preference on CTS. Nonetheless, studies have shown the relative importance of ciliate consumption depends on the trophic state of the system which depends on factors such as meagre availability of other prey and also due to size constraints of the available prey (Calbet and Saiz, 2005). Therefore, from the present study, the preferential feeding on CTS by Copepods supports the hypothesis of *Top-Down controls* on MZP (CTS) in bloom locations.

From the understanding on the significance of MZP mediation in bloom locations which was perceptible at the group level, it is presumed that information on species assemblage will provide insight into whether any particular species or one or more species is influential in structuring the microbial food web of NEAS. Because of this the species composition of CTS, the predominant MZP community from the column was considered for explaining the trophic role of MZP. This information could also help in assessing the functional role of CTS in governing the trophic

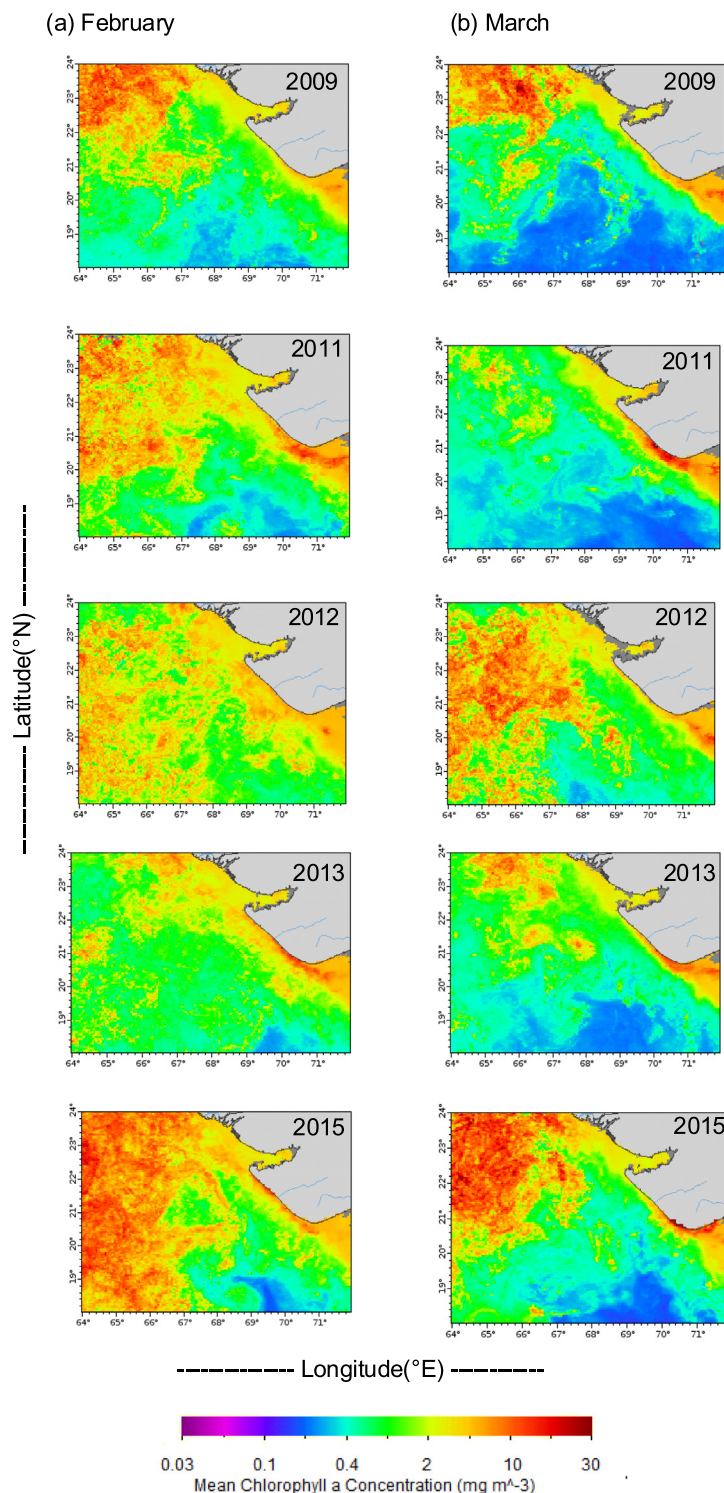


Fig. 14. Satellite imageries of monthly averaged Chl *a* (mg m^{-3}) for the months of (a) February — Left Panel and (b) March — Right Panel showing patches of high chlorophyll concentration in the study region where blooms of *Noctiluca scintillans* occur repetitively.

structure, as the functional groups seem to exhibit a direct link with the environmental variables. The species response to bloom and non-bloom conditions were done through SIMPER analysis. It was observed that the dissimilarity in the species assemblage was noticeably high (83%) indicating significant variability between bloom and non-bloom locations. The list of discriminating species and their percentage contribution is given in Table 4. It was observed that the percentage of dissimilarity was due to the high abundance of *Codonellopsis ecaudata* in the bloom location whereas *Undella hyalina* was most abundant species in

non-bloom location. Study on the species assemblage from the Arabian Sea has observed the presence of *Codonellopsis ecaudata* in high chlorophyll waters agreeing with our study (Gauns et al., 1996). The other major species contributing to the dissimilarity in bloom location was *Steenosemella ventricosa*, *Parundella caudata* and *Codonella nationalis*. Hence it can be inferred that CTS viz. *Codonellopsis* and *Steenosemella* play a functional role in structuring the microbial food web of *Noctiluca* bloom waters in the NEAS.

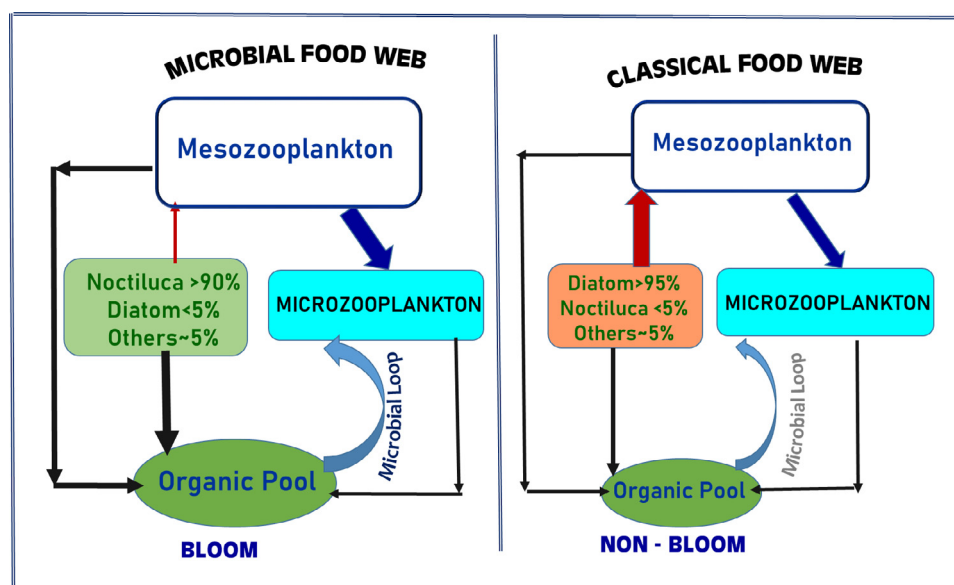


Fig. 15. Schematic representation of the pathway of interaction showing the microzooplankton mediation and interaction between the components at different trophic levels (Note the size of the shapes and arrows indicates the relative strength of the components and their trophic interaction).

Table 4

Species of CTS contributing to the percentage of dissimilarity and their respective contribution in bloom and non-bloom locations during the years 2009, 2011 and 2012.

Species	Non bloom 83%	Bloom
<i>Codonellopsis ecaudata</i>	109.92	298.26
<i>Steenosemella ventricosa</i>	0	123.6
<i>Codonellopsis ostensfeldii</i>	35.36	65.53
<i>Undella hyalina</i>	157.23	36.32
<i>Parundella caudata</i>	111.39	54.65
<i>Codonellopsis orthoceros</i>	61.24	0
<i>Codonella nationalis</i>	0	47.14
<i>Petalotricha ampulla</i>	0	57.74
<i>Protorhabdonella caudata</i>	64.01	0
<i>Metacyclis jorgensenii</i>	28.87	48.59
<i>Codonellopsis tessellata</i>	56.9	33.33
<i>Undella globosa</i>	33.33	35.36
<i>Dadayiella ganymedes</i>	52.7	51.21
<i>Parundella lohmanii</i>	26.35	52.7
<i>Protorhabdonella simplex</i>	35.36	56.9
<i>Lohmaniella spiralis</i>	27.64	27.64
<i>Favella brevis</i>	0	47.87
<i>Salpingella acuminata</i>	53.36	25
<i>Epiplocylis reticulata</i>	27.64	0
<i>Dadayiella bulbosa</i>	72.17	0
<i>Dictyocysta lepida</i>	23.57	49.92
<i>Eutimninus frakonii</i>	65.62	0
<i>Rhbadonella spiralis</i>	46.4	23.57
<i>Salpingacantha ampla</i>	44.31	0
<i>Codonella amphorella</i>	0	44.1

Besides the fact that bloom supports the secondary production in NEAS, no discrete pattern was observed among the non-copepod taxa, attributed to the fact that minor environmental changes influenced their occurrence pattern. However, during the study period preponderance of active grazers like Chaetognatha during the years 2011 and 2012 could be linked to the higher number of Copepoda in the bloom location, agreeing with earlier observations from the Arabian Sea (Anjusha et al., 2013; Asha Devi et al., 2018) (Figs. 9 and 10). Conventionally Copepoda comprise the major part of the mesozooplankton at the second trophic level and are also considered as the major grazers of phytoplankton (Madhupratap et al., 1996a,b, 2001; Calbet, 2001; Saiz, 2011; Arunpandi et al., 2017). However, it is also apparent that

in addition to the environmental conditions other factors such as size and composition of prey/predators are also accountable for structuring the community of an ecosystem and such variability is discernible at all trophic levels. Nonetheless, experimental studies have also shown that grazing and ingestion rate by Copepoda depends on many factors such as food type, quality, quantity and size structure of phytoplankton (Jagadeesan et al., 2017). Furthermore, grazing experiments solely with *Noctiluca* have suggested that it does not form the preferred food for mesozooplankton (Gomes et al., 2014). The above-mentioned facts are in agreement with the present study as the high secondary standing stock observed in the bloom locations was sustained through Top-Down controls on MZP, which provided ample evidence for size selection feeding preferences of copepods.

From the above understanding, the trophic role of MZP was ascertained by the differential response exhibited at both group and species level of CTS. The fact that functional species differed with the environmental variability and this could be established from the study made in the stratified system in the SEAS developed due to the intrusion of low saline BoB water. In the SEAS the functional species were *Dictyocysta lepida* and *Tintinnopsis tocaninensis*, which differed from that of the NEAS (Asha Devi et al., 2018). Based on the above understanding, it is therefore obvious that functional roles of CTS depend upon multiple factors like physical processes governing the region and also the size of producers at primary level and grazers at the secondary level. It is also suggested that in both systems it is presumed that the size of phytoplankton may play a detrimental role in structuring and pathways of the plankton food web. Hence it is recommended that in the Eastern Arabian Sea Ecosystem, the functional species are found to be discrete between the NEAS and SEAS and attributed to different physical forcings and the resultant environmental settings. Therefore, it is proposed to consider the functional role of CTS species, to fully understand the functioning of plankton food web rather than generalizing on basin-scale approach.

From the above, all factors put together the study explains that trophic mediation of MZP was noteworthy, and through Top-down effects (grazer controlled) in *Noctiluca* bloom locations while in non-bloom locations Classical Food Web operates through diatom to mesozooplankton. Since the NEAS oceanic regime is

very dynamic and distinct due to the complexities involved, the food web dynamics happen to be an intricate phenomenon as short-lived processes are active upon in space and time. The study signifies the trophic role of MZP in productive systems through *Top-Down controls* and suggests the food web to be defined by short-term interactions between trophic levels. Hence it can be inferred that in productive pelagic systems the microbial food web is linked at both ends to metazoans explaining an efficient transfer between the trophic levels to sustain the generally high production in NEAS.

5. Conclusion

The present study discusses the role of MZP in mediating microbial food web in *Noctiluca* bloom and non-bloom locations. In bloom locations, *Top-down* controls on MZP seem to support high secondary stock indicating the significance of MZP and prevalence of microbial food web in supporting the mesozooplankton. On the other hand in non-bloom locations, the predominance of diatoms points towards a Classical Food Web as shown in the schematics (Fig. 15). Furthermore, the relationship between Copepoda and CTS indicates preferential grazing on CTS in bloom locations which support the hypothesis of *Top-Down controls* on MZP (CTS) in bloom locations. The functional role of CTS was assessed based on SIMPER analysis and species of CTS viz. *Codonellospsis ecaudata* and *Steenosemella ventricosa* were most influential in structuring the community and microbial food web of NEAS ecosystem during the winter–spring season when *Noctiluca* blooms are frequent. The effect of such short-lived dynamic events on all the trophic levels and the biological attributes of the open ocean region of the NEAS are also explained.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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