

Characterization of oceanic *Noctiluca* blooms not associated with hypoxia in the Northeastern Arabian Sea



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ABSTRACT

Intense blooms of the heterotrophic dinoflagellate, green *Noctiluca scintillans*, have been reported annually in the Northern Arabian Sea since the early 2000s. Although not known to produce organic toxins, these blooms are still categorized as a harmful due to their association with massive fish mortalities. Recent work has attributed these blooms to the vertical expansion of the oxygen minimum zone, driven by cultural eutrophication from major coastal cities in western India. As diatoms are preferred prey of green *Noctiluca scintillans*, more frequent blooms of this mixotroph will likely impact the productivity of important fisheries in the region. The present study uses a satellite algorithm to determine the distribution of both diatom and green *Noctiluca* blooms in the Northeastern Arabian Sea from 2009 to 2016. The results from shipboard microscopy of phytoplankton community composition were used to validate the satellite estimates. The satellite algorithm showed 76% accuracy for detection of green *Noctiluca* and 92% for diatoms. Shipboard measurements and data from biogeochemical-Argo floats were used to assess the relationship between oxygen concentrations and green *Noctiluca* blooms in the Northeastern Arabian Sea. Regardless of the presence of a *Noctiluca* bloom, the dissolved oxygen in the photic zone was always >70% saturated, with an average oxygen saturation >90%. The variability in the relative abundance of diatoms and green *Noctiluca* is not correlated with changes in oxygen concentration. These findings provide no evidence that cultural eutrophication has contributed to the decadal scale shifts in plankton composition in the Northeastern Arabian Sea oceanic waters. Conversely, the climatic warming of surface waters would have intensified stratification, thereby reducing net nutrient flux to the photic zone and decreasing silicate to nitrate ratios (Si:N); both factors that could increase the competitive advantage of the mixotroph, green *Noctiluca*, over diatoms. If so, the decadal-scale trajectory of phytoplankton community composition in the Northeastern Arabian Sea may be a harbinger of future climate-driven change in other productive oceanic systems.

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1. Introduction

The Arabian Sea experiences a tropical monsoonal climate, with seasonal reversal of winds. The southwest monsoon extends from June through September, when the surface currents move northward along the western boundary and southward along

the eastern boundary of the Arabian Sea. Upwelling occurs along Somalia and the southern tip of eastern Arabian Sea (Kochi) during this season, leading to highly productive coastal waters. The wind reversal during the northeast monsoon (December to March) brings cold and dry continental air over the Northern Arabian Sea, and the resultant cooling of surface waters generates convective mixing. Surface currents also reverse direction, leading to onshore transport and downwelling along the western and eastern boundary of the Arabian Sea (Shankar et al., 2002; Kumar and Prasad, 1996; Rao et al., 2008).

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Winter blooms of the heterotrophic dinoflagellate, green *Noctiluca scintillans* (henceforth green *Noctiluca*) have been reported annually during the winter monsoon since the early 2000s in the Northern Arabian Sea. Oceanic blooms of green *Noctiluca* have been observed between 17 and 21°N and 66 to 70°E with an explosive growth (averaging 3 million cells/L) over an extensive area of the Northeastern Arabian Sea (Madhu et al., 2012). Matondkar et al. (2012) also indicated that blooms of green *Noctiluca* appear in this same region during February – March. Unlike the red form of *Noctiluca*, the green variant contains the

prasinophytic endosymbiont *Pedinomonas noctilucae*. While red *Noctiluca* are obligate heterotrophs, the green form exhibits both heterotrophic and autotrophic behavior depending on the availability of prey and light (Saito et al., 2006).

Green *Noctiluca* blooms exert a significant impact on prevailing biogeochemical processes in the ocean. The accelerated rates of primary production associated with these blooms leads to an upsurge in carbon sequestration (Prakash et al., 2008). Green *Noctiluca* blooms control the phytoplankton community dynamics through phagotrophy and endosymbiosis resulting in top down

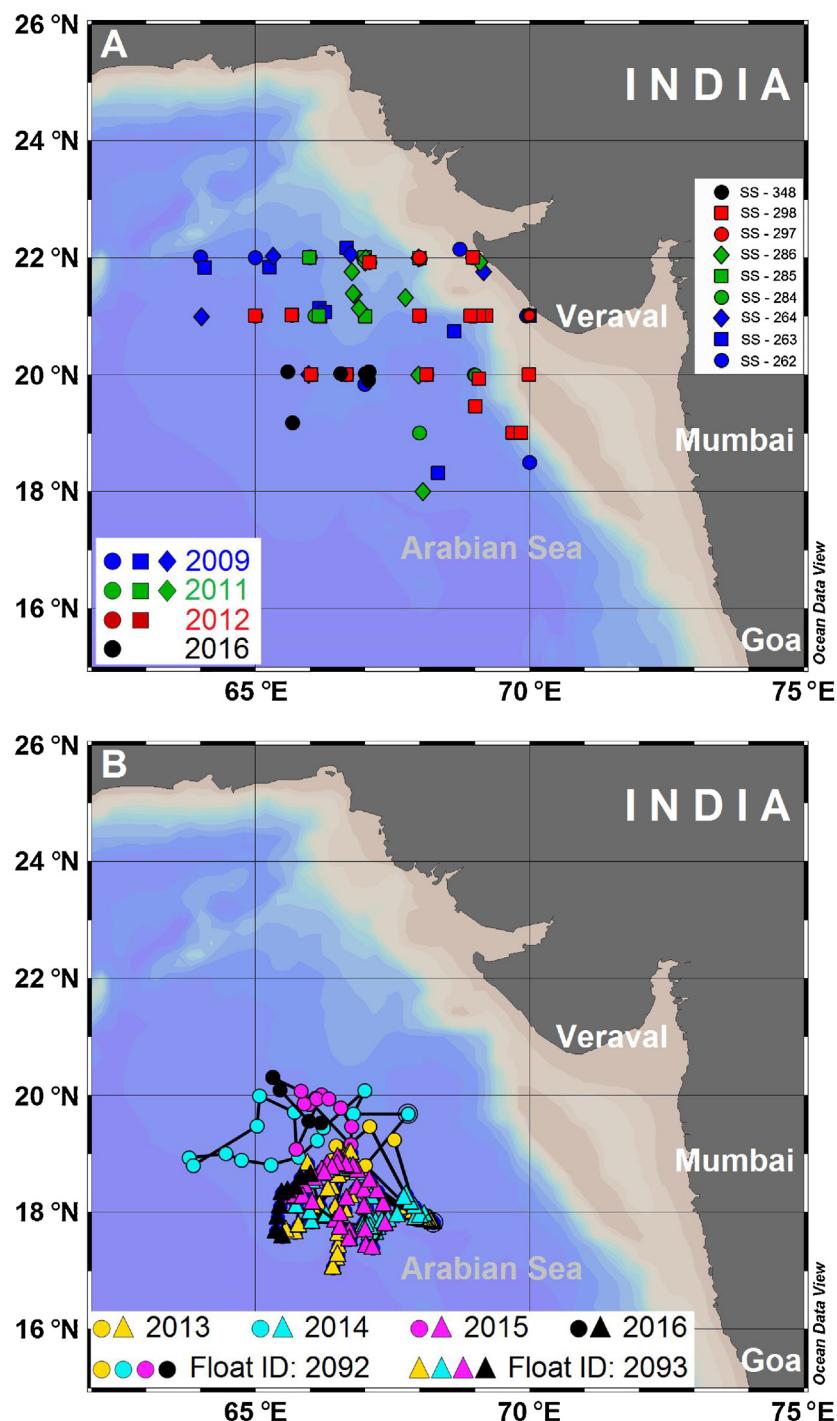


Fig. 1. Map of study area. (A) Sampling stations during FORV Sagar Sampada cruises and (B) Bio-Argo float locations (closed circles: float 2092 and closed triangles: float 2093). The sampling sites for individual years are shown in separate colours. The symbols represent different cruises as detailed in Table 1.

control of the ecology in these systems (Sriwoon et al., 2008). Although green *Noctiluca* are not recognized to produce organic toxins, these blooms are still categorized as harmful due to their association with massive fish mortalities attributed to toxic levels of ammonia (Okaichi and Nishio, 1976). In addition, green *Noctiluca* is a voracious predator of diatoms, and thus competes with zooplankton, particularly copepods, thus having adverse impacts on the food chain and fisheries (Prasad, 1958). The decay phase of green *Noctiluca* blooms can result in the decline of dissolved oxygen levels in nearshore, subsurface regions, leading to fish mortality and evasion in the region of the blooms (Harrison et al., 2017).

Diatoms are believed to be the preferred diet of green *Noctiluca* because *Noctiluca* blooms often develop following diatom blooms (Kiørboe and Titelman, 1998; Dwivedi et al., 2015). This is the case in the Northern Arabian Sea, where blooms of green *Noctiluca* proliferate during the winter monsoon, from January to March. The strong winter convective mixing in this region, attributed largely to the evaporative cooling of surface water, entrains subsurface nutrients, and particularly silicate (Si), which, in turn, fuels high diatom production (Madhupratap et al., 1996). Anecdotally, this diatom bloom is observed to initiate in the western region of the Northern Arabian Sea and proceeds eastwards, followed by the development and spatial progression of green *Noctiluca* blooms, which likely are driven by prey availability and favourable winds (Kiørboe and Titelman, 1998; Dwivedi et al., 2006, 2015).

A recent study suggests that massive outbreaks of green *Noctiluca* in the Arabian Sea are caused by a shoaling of low oxygen waters from depth into the photic zone (Gomes et al., 2014). The authors suggested that a low oxygen preference of the *Noctiluca* endosymbiont leads to increased autotrophic production of green *Noctiluca*, which contributes to the intensity of the bloom. They concluded that the increased influx of low oxygen waters into the photic zone was related to anthropogenically-driven vertical expansion of the oxygen minimum zone due to the influence of major coastal cities in India. They also linked this expansion to a longer-term shift over the last decade from diatom-dominated to green *Noctiluca*-dominated plankton assemblages, potentially causing disruption to the diatom-supported fisheries in the Northwestern Arabian Sea (Gomes et al., 2014).

A combination of remote sensing data, shipboard observations, and biogeochemical (BGC)-Argo float measurements were used to examine the relationship between oxygen concentrations and the distribution/intensity of both green *Noctiluca* and diatom blooms in the Northeastern Arabian Sea. Temperature, salinity, chlorophyll-a (chl-a) and dissolved oxygen (DO) from two BGC-Argo floats are reported in the upper 200 m of the water column from the region. Remote sensing algorithms, developed for the detection of green *Noctiluca*, and able to distinguish between diatoms and green *Noctiluca* (Dwivedi et al., 2015), were validated using in situ data from several research cruises from 2009 to 2016.

2. Methods

2.1. Study area

The study was carried out in Northeastern Arabian Sea. The in situ measurements including shipboard (Fig. 1A) and BGC-Argo float (Fig. 1B) were taken within the geographical domain of 17–23° N and 63 to 70° E. The satellite data analysis was carried out over the spatial coverage of 10–31° N and 50 to 78° E.

2.2. Shipboard observations

In situ datasets of water quality parameters including DO, chl-a and phytoplankton cell abundance were collected onboard the

Table 1

Duration and geographical coverage of FORV Sagar Sampada cruises. Symbols corresponds to discrete locations shown in Fig. 1.

Cruise ID	Sampling Duration	Geographical Domain	Symbol
262	02/16/09 to 02/23/09	18.5–22.5°N and 64.0–70.0°E	●
263	03/01/09 to 03/11/09	18.0–22.5°N and 64.0–68.0°E	■
264	03/21/09 to 03/28/09	20.0–22.5°N and 64.0–69.5°E	◆
284	02/01/11 to 02/06/11	19.0–22.0°N and 66.0–69.0°E	●
285	02/22/11 to 02/25/11	21.0–22.0°N and 66.0–70.0°E	■
286	03/07/11 to 03/20/11	18.0–22.0°N and 66.5–69.5°E	◆
297	03/15/12 to 03/20/12	20.0–22.0°N and 65.0–70.0°E	●
298	03/30/12 to 04/04/12	19.0–22.0°N and 65.0–70.0°E	■
348	03/07/16 to 03/16/16	19.0–20.5°N and 66.0–67.5°E	●

FORV *Sagar Sampada* (SS) during several expeditions (Table 1) in the Northeastern Arabian Sea (Fig. 1A). All expeditions were conducted during the winter monsoon period between 2009 and 2016. In situ sampling was performed using Niskin bottles deployed at 12 standard oceanographic depths from 0 to 1000m. The present study uses shipboard DO and chl-a data up to 40 m while phytoplankton community composition data are from the surface. DO was analyzed by the Winkler's titrimetric method with final concentrations expressed in μM . Concentrations are given as the mean of duplicate analyses. Chl-a samples were extracted with 90% acetone and analyzed using the method described by Strickland and Parson (1965). Phytoplankton samples for taxonomy were fixed onboard and cell counting was carried out in the laboratory using standard identification keys. Live green *Noctiluca* samples were enumerated onboard the vessel. The dominance of green *Noctiluca* and diatoms was determined based on their contribution to the total phytoplankton count in assessing the performance of the satellite algorithm for accurate prediction at a particular station.

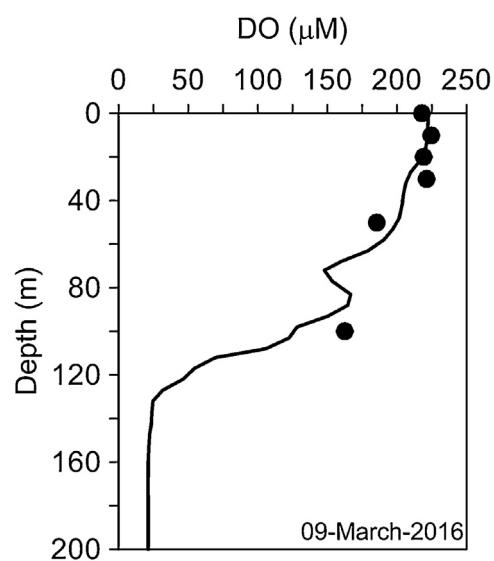


Fig. 2. Comparison of the vertical distribution of dissolved oxygen (DO) measured by the biogeochemical-Argo float (solid line) and from discrete water samples at various depths (●) at the nearest station on cruise SS-348 using the Winkler's titrimetric method.

2.3. Satellite data processing

Moderate Resolution Imaging Spectroradiometer [onboard Aqua satellite (MODIS)] Level-3 remote sensing reflectance (R_{rs}) data products with 4 km spatial resolution at wavelengths of 443, 488 and 531 nm were downloaded from the OceanColor Web (<http://oceancolor.gsfc.nasa.gov/cgi/l3>). Phytoplankton class products were generated, for the region encompassing in situ observation locations, using the algorithm developed by Dwivedi et al. (2015). The algorithm discriminates green *Noctiluca*, diatom

and non-bloom conditions. The pixel count of each class was calculated using ArcMap (version 10.3.0.4322).

2.4. Biogeochemical-Argo data processing

Water column salinity, temperature, DO and chl-a concentrations were obtained from the two BGC-Argo profiling floats (ID: 2902092 and 2902093). More details about the sensors onboard the floats, their data and quality control can be found at Schmechtig et al. (2015). A typical validation data set demonstrates

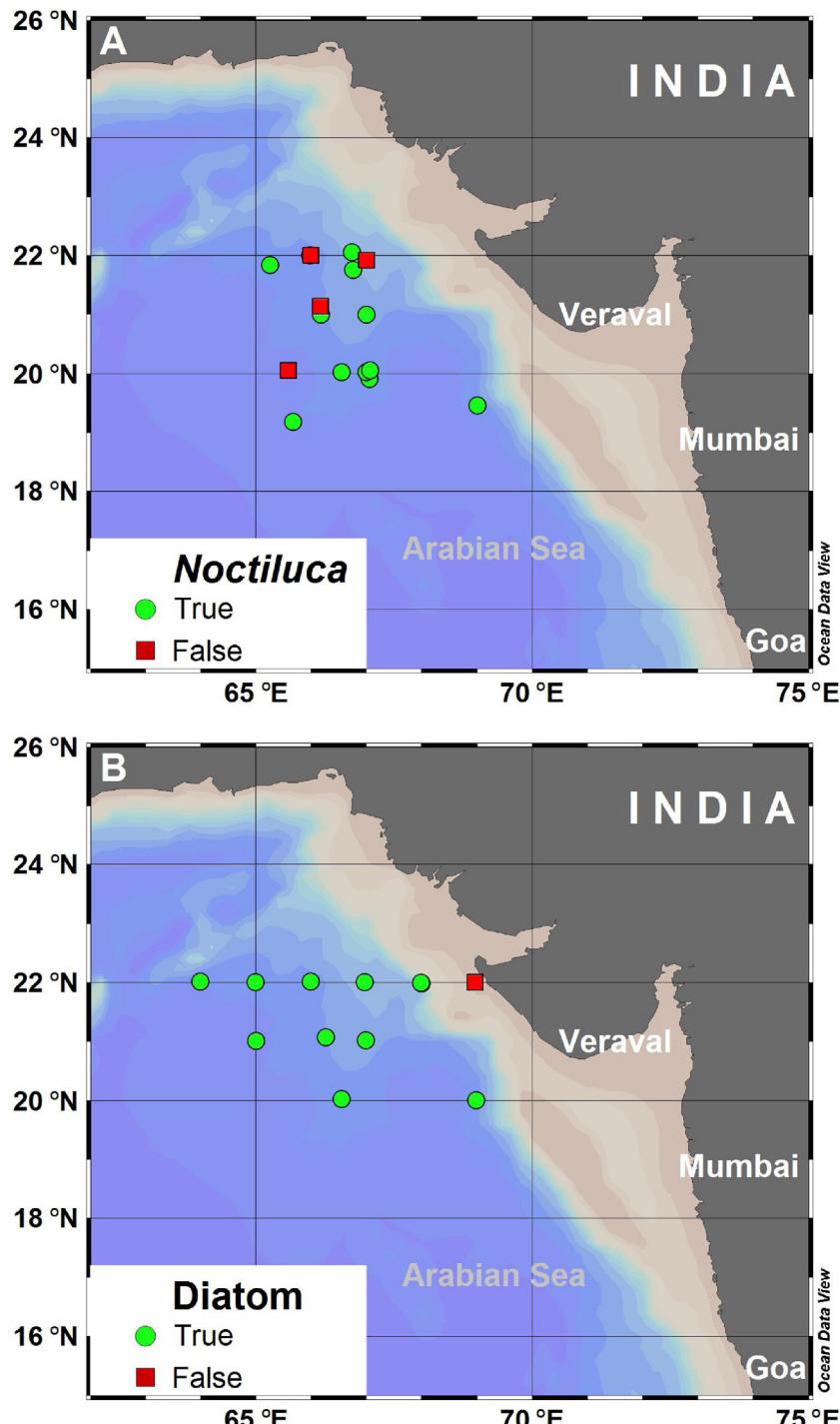


Fig. 3. Map indicating locations where satellite algorithms were compared with in situ abundance data. The agreement (green circles) or disagreement (red squares) of (A) green *Noctiluca* and (B) diatom are shown. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the close correlation of BGC-Argo-derived DO with in situ DO measured using Winkler's method on cruise-based samples from the same region (Fig. 2). BGC-Argo data from the upper 200 m of the water column were used from February 2013 to April 2016 to quantify the upper ocean thermohaline structure, mixing, hypoxia and phytoplankton biomass (i.e. chl-*a*).

3. Results

3.1. Satellite identification of green *Noctiluca* and diatom blooms

The algorithm developed by Dwivedi et al. (2015) is based on change in the spectral slope of R_{rs} due to the dominance of either green *Noctiluca* or diatoms. As a 16 km² pixel defines the smallest

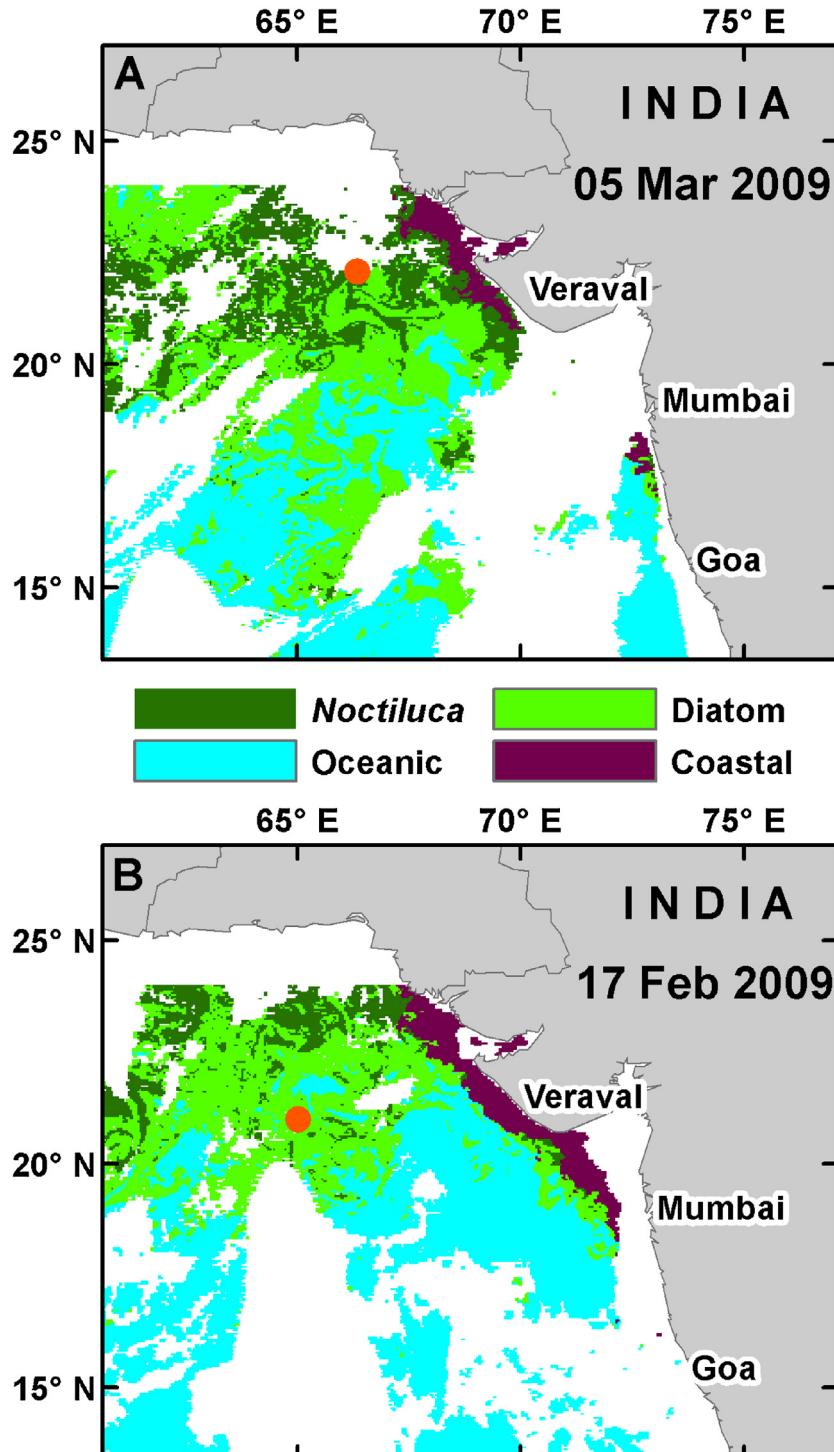


Fig. 4. Spatial distribution of green *Noctiluca*, diatom, non-bloom oceanic and coastal waters derived from MODISA data using Dwivedi et al. (2015) algorithm on 17 February 2009 and 05 March 2009. Red solid circles denote the confirmation of a (A) green *Noctiluca* bloom and (B) diatom bloom using in situ data. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

possible area in which satellite data can be resolved, it is possible that both green *Noctiluca* and diatoms co-exist in the same pixel. Hence, a sensitivity analysis was carried out for accuracy assessment of the algorithm in assignment of a pixel to green *Noctiluca* or diatom in the study area. Locations where the satellite derived algorithm matched the in situ microscopic analysis of cruise samples are shown in green circles and non-matching locations are marked in red squares for green *Noctiluca* (Fig. 3A) and diatoms (Fig. 3B).

Representative satellite images of green *Noctiluca*, diatoms, and non-bloom regions mapped using the Dwivedi et al. (2015) algorithms on days where the in situ samples were dominated by green *Noctiluca* (05 March 2009) and diatoms (17 February 2009) are shown in Fig. 4. The locations of confirmatory in situ data available on the same day are marked on the maps with a red circle. At locations where satellite data were available, with matching cruise stations (Fig. 1A), in situ green *Noctiluca* and diatom abundance was compared to the algorithm prediction (Fig. 5). Correct satellite algorithm attribution to green *Noctiluca* occurred when *Noctiluca* cell densities ranged from 8.3×10^2 – 4.5×10^6 cells/L (Fig. 5A) or were >40% of the total cell abundance (Fig. 5B). The pixels “incorrectly” assigned to *Noctiluca* based on cell abundance had *Noctiluca* densities between 1.7×10^2 and 1.4×10^3 cells/L, suggesting that the satellite algorithm reliably detects *Noctiluca*.

abundances $> 1.5 \times 10^3$ cells/L. The satellite algorithm correctly assigned a pixel to diatom when diatom abundance ranged from 3.8×10^2 to 1.0×10^4 cells/L and constituted at least 80% of the total cell abundance. However, when other phytoplankton species were most abundant, a pixel was incorrectly assigned to diatom (Fig. 5B) at a station close to shore (Fig. 3B). The validation of satellite algorithm with in situ data showed 76% accuracy for detection of green *Noctiluca* and 92% for diatom.

3.2. Water column environmental characteristics

The environmental characteristics of the water column during bloom (green *Noctiluca* and diatom) and non-bloom conditions were studied using BGC-Argo data collected from 2013 to 2016 (Figs. 6 and 7). Vertical profiles of water temperature, salinity, DO and chl-a concentration from the upper 200 m of the water column from two BGC-Argo floats (ID: 2092 and 2093) were analyzed. Both floats were in close proximity of the winter blooms in the Northeastern Arabian Sea described by the data (Figs. 5A; 6C; 7C). The phytoplankton types co-located with the BGC-Argo observations were identified from the satellite (MODISA) data using the Dwivedi et al. (2015) algorithm. Both floats showed similar variability in vertical distribution of environmental parameters during bloom and non-bloom conditions (Figs. 6 and 7).

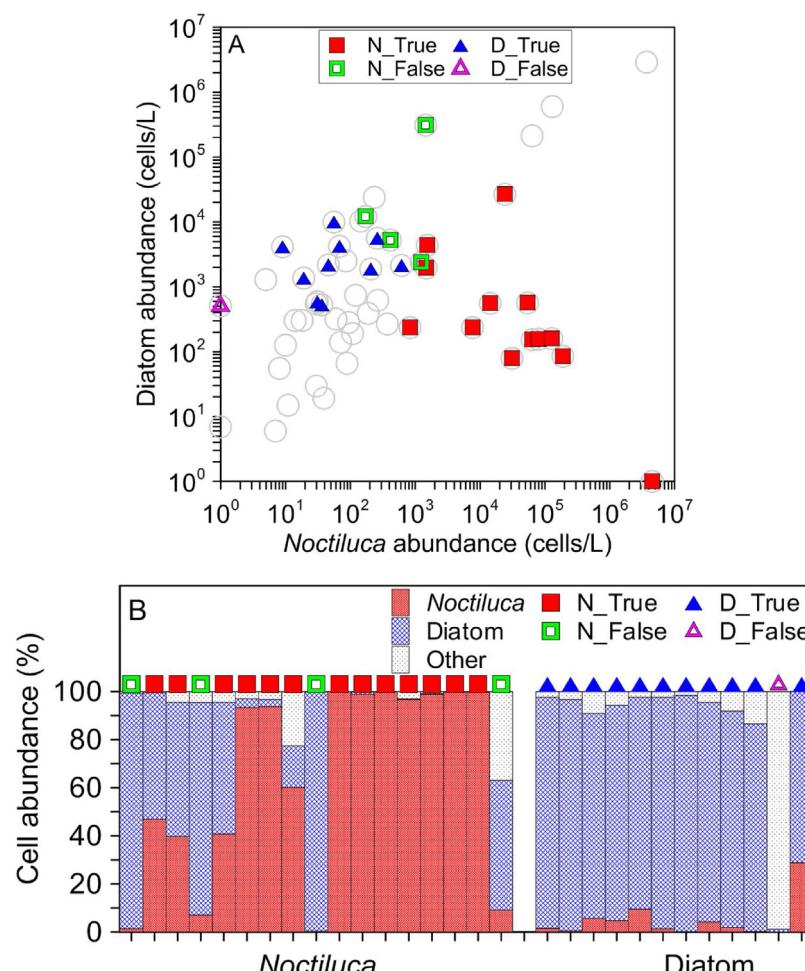


Fig. 5. (A) Total green *Noctiluca* and diatom abundance at cruise stations showed in Fig. 1. The ability of the satellite algorithm to match the in situ abundance for green *Noctiluca* or diatom was indicated as true (red filled squares for green *Noctiluca*, N_True; blue filled triangles for diatom, D_True) or false (green open squares for green *Noctiluca*, N_False; magenta open triangles for diatom, D_False). The empty circles indicate non-availability of concurrent satellite data. (B) in situ abundance (%) of *Noctiluca*, diatom and other phytoplankton (hatched bars) compared to the assignment of a pixel to *Noctiluca* or diatom using the satellite algorithms. Symbols on top of bars indicate the validity of the algorithm as true or false using the same color notations and abbreviations as in (A). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

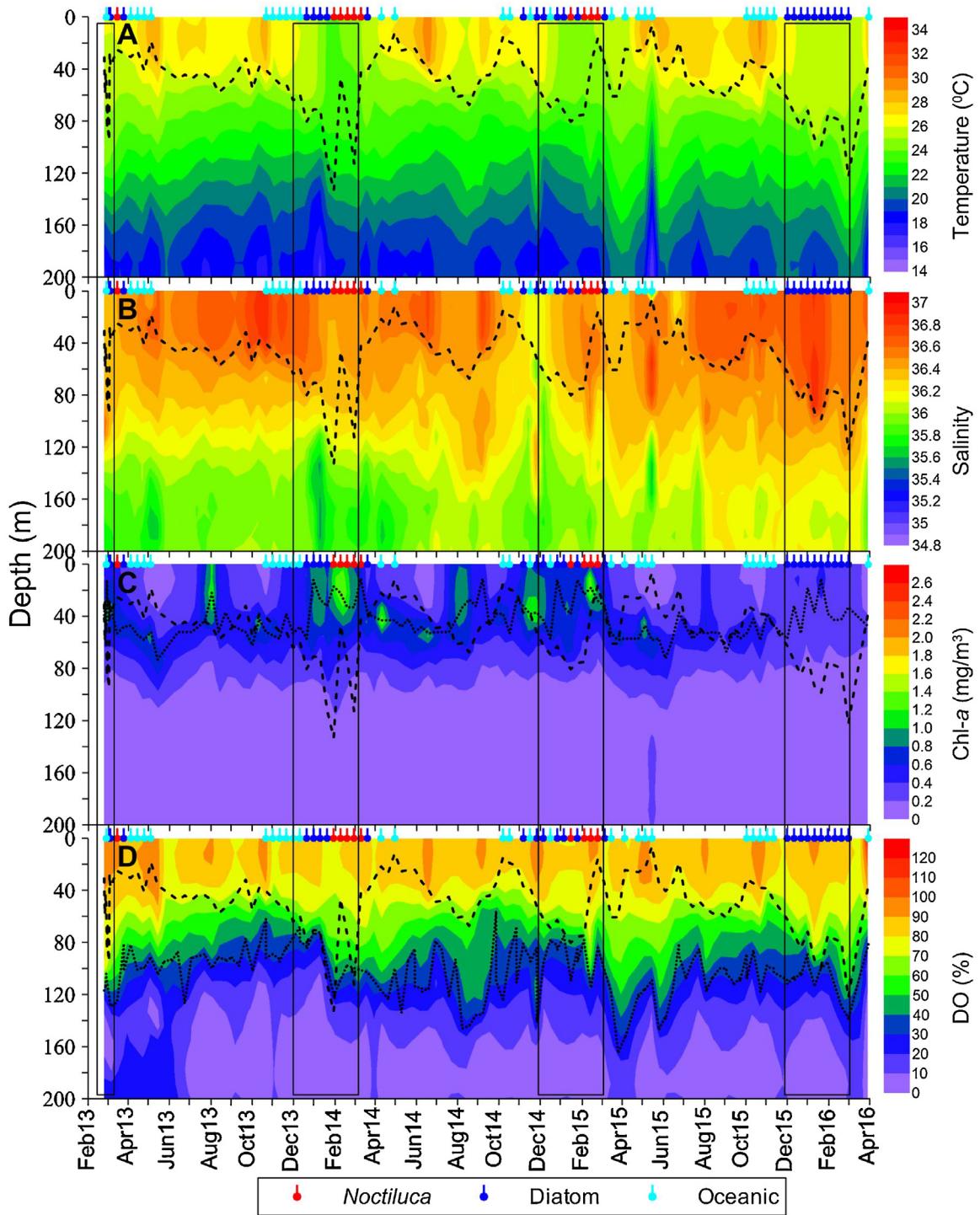


Fig. 6. Vertical profiles of temperature, salinity, chlorophyll-*a* (chl-*a*) and dissolved oxygen (DO) saturation measured by biogeochemical-Argo float 2092 (locations shown in Fig. 1B). The dashed line in all panels corresponds to mixed layer depth (MLD). The dotted line in panel “C” corresponds to deep chlorophyll maxima (DCM) and in panel “D” corresponds to 60–65 µM DO concentration. The annual winter monsoon period (e.g. “bloom” period) is designated by a box from December – March in each year.

The vertical distribution of water temperature showed a similar pattern with depth over ~3 years. However, marked variability over seasonal time scales was observed (Figs. 6A and 7A), particularly in the upper 100 m. Sea surface temperatures (SST) varied within 30–33 °C and the mixed layer depth was 40–45 m during the summer monsoon (June–September) and intermonsoon periods (October–November and April–May). A deep extension of the thermocline (150–155 m) also was generally observed during these times. During the winter monsoon

(December–March), SST decreased to 24–25 °C and the water column became isothermal to ~100–120 m depth. The base of the thermocline extended to ~120–140 m during the winter monsoon.

The salinity sections also showed variability on seasonal time scales (Figs. 6B and 7B). Surface salinity ranged from 36.0 to 37.0 over annual cycles, while salinity ranged from 35.3 to 36.9 in the mixed layer during the summer monsoon, and 36.1–36.9 during the winter monsoon. The halocline also shifted significantly between the summer and winter monsoons, becoming deeper

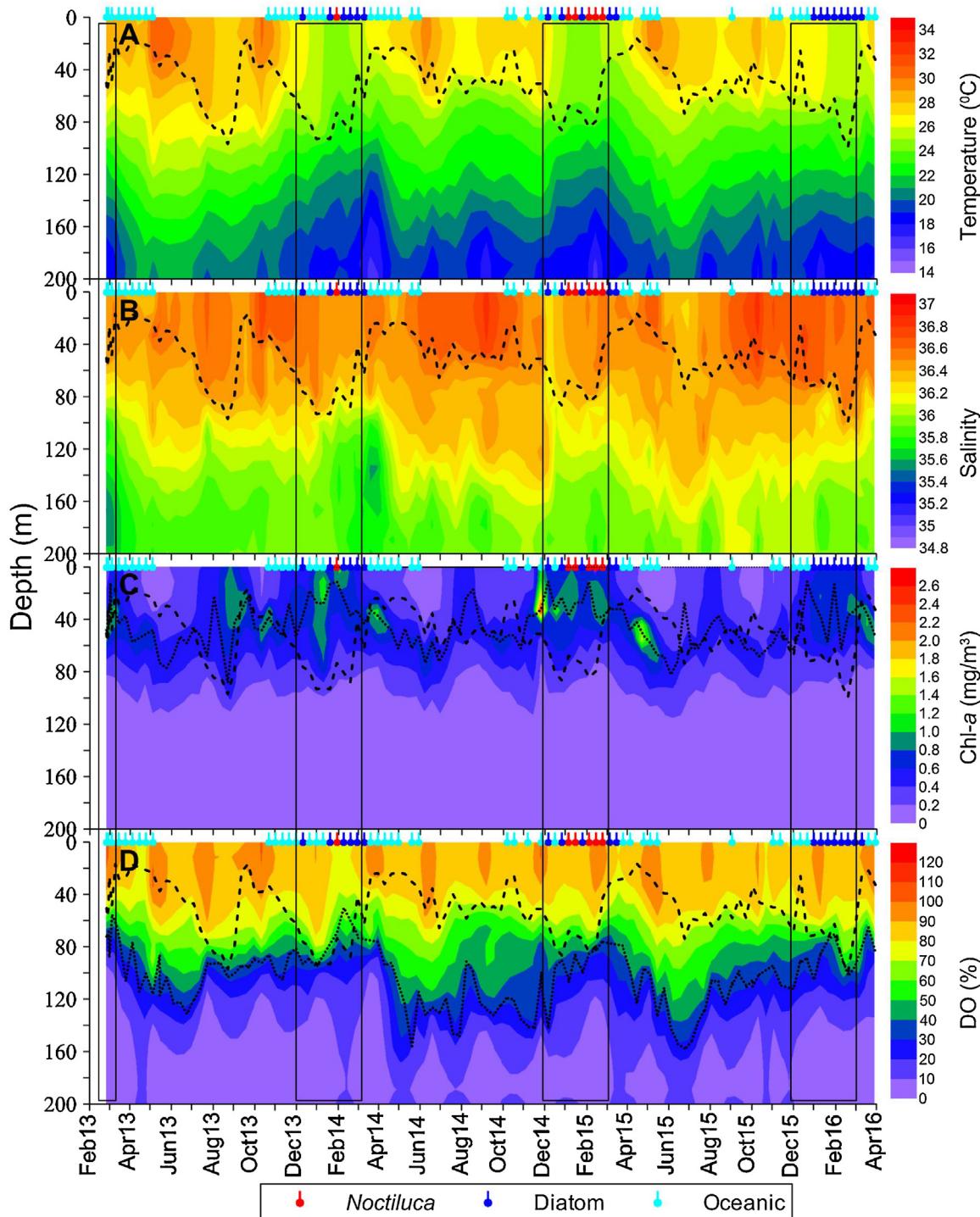


Fig. 7. Vertical profiles of temperature, salinity, chlorophyll-a (chl-a) and dissolved oxygen (DO) measured by biogeochemical-Argo float ID: 2093 (locations shown in Fig. 1B). The dashed line in all panels corresponds to mixed layer depth (MLD). The dotted line in panel “C” corresponds to deep chlorophyll maxima (DCM) and in panel “D” corresponds to 60–65 µM DO concentration. The annual winter monsoon period (e.g. “bloom” period) is designated by a box from December – March in each year.

(~140–145 m) during summer, and shallower (~90–120 m) during the winter monsoon.

The chl-a depth distributions also varied significantly over seasonal time scales (Figs. 6C and 7C), with most phytoplankton concentrated at depths shallower than 80–100 m. Concentrations of chl-a during the summer monsoon (non-bloom period) were comparatively low (0.2–0.8 mg/m³), and the deep chlorophyll maxima (DCM) generally occurred between 50 and 55 m. Ephemeral higher chlorophyll events were observed during

the summer monsoons of 2013 and 2014, although the spatial extent of these anomalies was unclear because satellite data were not available during this season. Conversely, high chl-a concentrations were observed during the time of deep convective mixing in the winter monsoon, with values ranging between 0.8–1.6 mg/m³. Diatoms and green *Noctiluca* blooms dominated during this period, and there was little evidence of a DCM.

The surface DO concentrations in the upper water column averaged near saturation (>90%) during most of the year, with little

substantial change over inter-annual time scales (Figs. 6D and 7D). There were periods where oxygen saturation dropped to close to 70%, particularly in the region of BGC-Argo float (ID: 2092), but these were limited to very short intervals. The transition from oxygen-saturated surface waters to hypoxic (60–65 µM DO, or <30% saturation) subsurface waters occurred between 60 and 150 m over the observation period, but these changes were not clearly associated with any particular seasonal phase. During the winter monsoon, DO saturation decreased but remained >70% within the photic zone, i.e., well above hypoxia, including during all periods of green *Noctiluca* blooms (Figs. 6 and 7).

To complement the DO data from BGC-Argo, in situ DO data, analyzed from water samples with Winkler's method, from cruises during February and March 2009, 2011, 2016 are detailed in Fig. 8. Oxygen saturation during these cruises, ranging from 17 to 30 days in length, was never below 80% in the upper 40 m of the water column and was always at 100% in the upper 20m. The March 2009 and 2011 cruises overlap the same time period of the apparent low DO observations in Gomes et al. (2014).

3.3. Spatio-temporal distribution of green *Noctiluca*, diatoms, and dissolved oxygen

The relative occurrence of green *Noctiluca* and diatom-dominated surface phytoplankton communities in the Northern Arabian Sea were quantified from 2003 to 2013, using MODISA data, where the total daily pixel count was determined along with

those pixels showing green *Noctiluca* or diatom dominance. The average dominance in the Northern Arabian Sea between 01 February and 31 March from 2003 to 2015 is shown in Fig. 9A. In general, diatoms dominated relative to the spatial distribution of green *Noctiluca*, and there were no specific trends over the past thirteen years (2003–2015). It is important to recognize that the remote sensing data are restricted to only the upper regions of the photic zone, so it may not accurately reflect the integrated water column phytoplankton composition. However, these patterns corresponded well with the averaged in situ phytoplankton composition measured by microscopy (Fig. 5A). The cyclical inverse relationship of these blooms is shown for 01 February to 31 March 2015 (Fig. 9B), where diatom abundance was maximal during early February, when green *Noctiluca* was at a minimum. Green *Noctiluca* subsequently began to increase while diatoms showed a decreasing trend in the study area.

The annual average in situ concentrations of green *Noctiluca* and diatoms are shown in comparison to average DO concentrations in Fig. 10. Green *Noctiluca* cell density ranged by three orders of magnitude, from 8.6×10^2 to 1.4×10^5 cells/L, similar to the range observed for diatom abundance (7.4×10^2 – 1.4×10^5 cells/L). The DO concentrations over this period varied from 190.8 to 243.9 µM, or ~200% over the hypoxia threshold of 64 µM (Turner et al., 2005). There was no significant temporal trend in DO concentrations (Fig. 10), and no observed relationship between the average annual cell density of green *Noctiluca* or diatoms and DO concentrations.

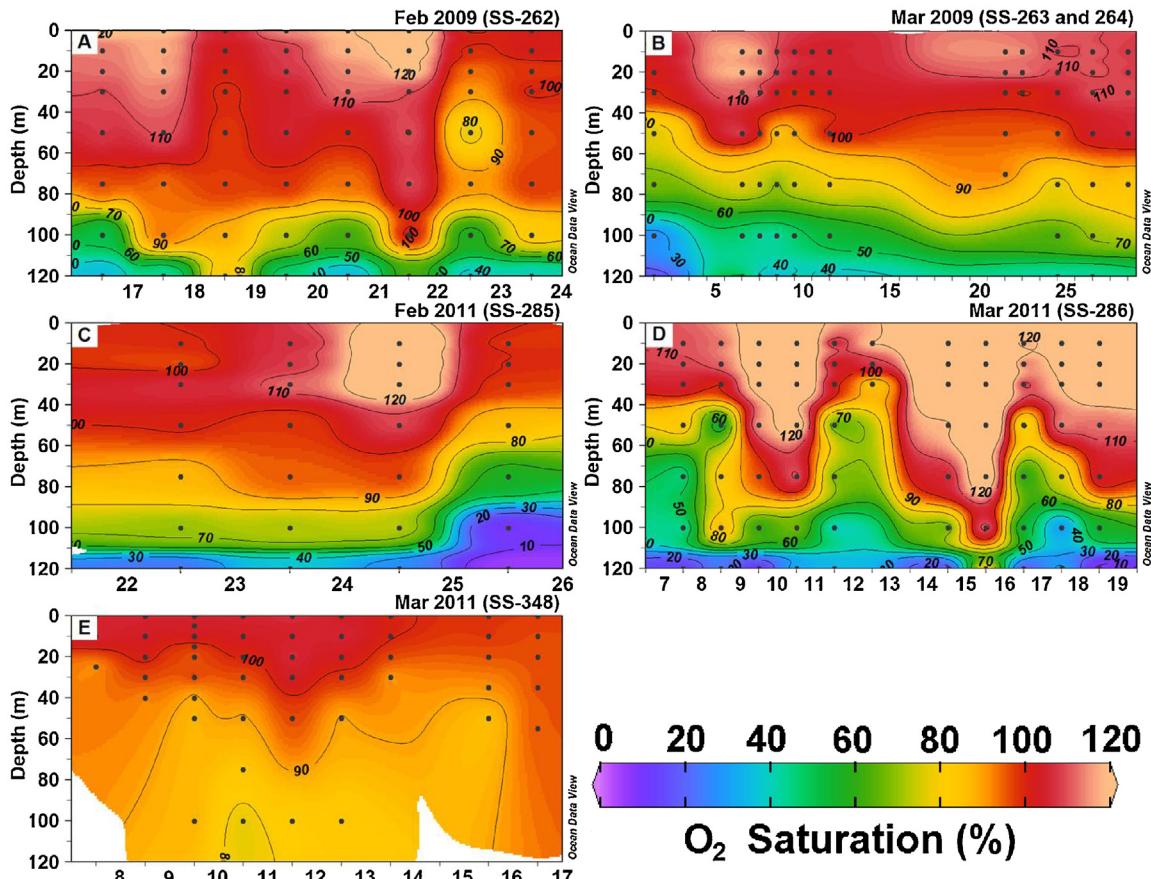


Fig. 8. Vertical distribution of dissolved oxygen (DO) saturation (%), measured using Winkler's titrimetric method from water samples collected using Niskin bottles at several depths (●) onboard various cruises (see Table 1 for cruises and Fig. 1A for cruise locations) during (A) February 2009 (SS-262), (B) March 2009 (SS-263, SS-264), (C) February 2011 (SS-285), (D) March 2011 (SS-286) and (E) March 2011 (SS-348) plotted in Ocean Data View software (Schlitzer, 2016). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

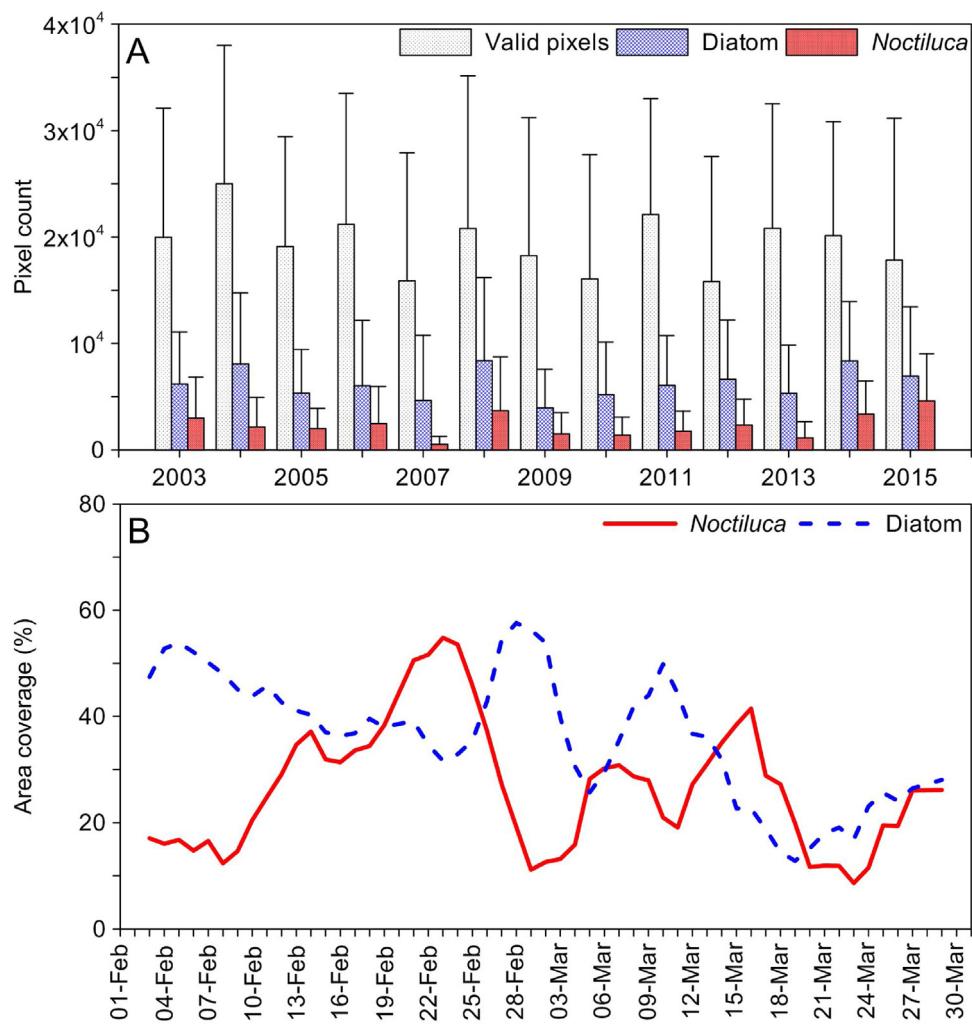


Fig. 9. (A) The distribution of green *Noctiluca* and diatom calculated from processed daily satellite (MODISA) data and averaged from 01 February to 31 March. Vertical bars show the standard deviation, (B) variability in area coverage in distribution of green *Noctiluca* and diatoms during 2015 in Northern Arabian Sea (10 to 31°N and 50 to 78°E), as a percentage of total valid pixels retrieved from satellite (MODISA), using the Dwivedi et al. (2015) algorithm. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

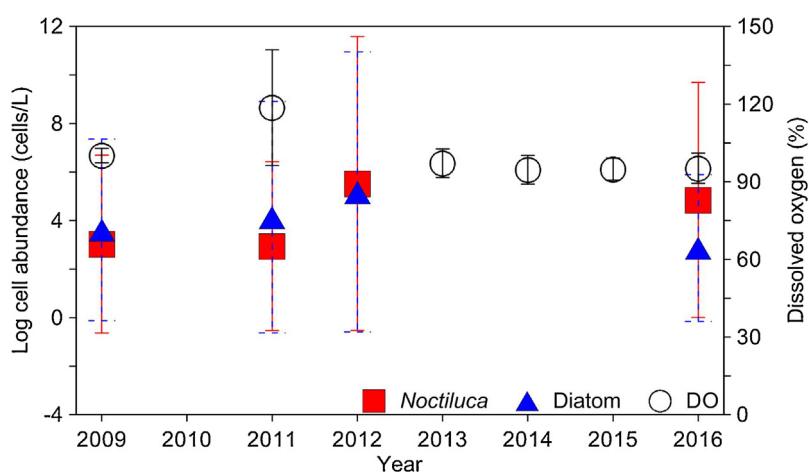


Fig. 10. Mean annual abundance of in situ measured green *Noctiluca* and diatom cell density and dissolved oxygen (DO) saturation in upper 40 m for the stations shown in Fig. 1. Vertical bars show the standard deviation. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

There is evidence that the planktonic system in the Northern Arabian Sea has shifted over the last decade, from diatom-dominated communities to progressively more prevalent blooms of the mixotrophic, green variant of the dinoflagellate *Noctiluca* (Parab et al., 2006; Al-Azri et al., 2007; Gomes et al., 2008, 2009, 2014). This transition potentially has major ramifications for fisheries, which are not believed to be supported energetically by green *Noctiluca*, and for biogeochemical processes, because it is likely that the export of carbon to deep waters by declining *Noctiluca* blooms will be less efficient than that from the production of large fecal pellets by copepods (Prasad, 1958; Prakash et al., 2008). Understanding the mechanisms underlying this change are important not only for forecasting future conditions in the Northern Arabian Sea, but because these changes might presage planktonic shifts in other productive oceanic systems.

Gomes et al. (2014) suggested that this trajectory in the planktonic community composition is a direct consequence of an increased influx of hypoxic subsurface waters into the oceanic photic zone; a change that ultimately stems from increased anthropogenic nutrient inputs from burgeoning coastal populations. There is a plethora of literature on the association of intense blooms of green *Noctiluca* with cultural eutrophication in coastal waters, but the suggestion by Gomes et al. (2014) that this linkage also can extend far out into oceanic waters is questionable. The present findings refute their conclusion by demonstrating that there is no correlation between the presence and abundance of green *Noctiluca* and low oxygen content in surface waters of the Northeastern Arabian Sea. This assessment is based in large part on in situ microscopy measures of phytoplankton community composition and DO profiles collected on nine cruises over eight years and is extrapolated to the broader Northern Arabian Sea region using algorithm-derived estimates on abundance of green *Noctiluca* and diatoms. This remote sensing product correlates well with in situ measurements (Figs. 3–5), which increases confidence in the spatial assessment of phytoplankton community composition. Combining these data with those from two BGC-Argo floats (Figs. 6 and 7) and DO data from five cruises (Fig. 8) confirms that there was no near-surface hypoxia from 2009 to 2016. There also were no consistent seasonal or pulsed fluctuations in the oxycline that correlated with the measured (cruise) or estimated (satellite) green *Noctiluca* abundance in the region. Indeed, surface oxygen never dropped below 70% saturation (Figs. 6–8), and even then, fluctuations in DO concentrations did not correlate with the switch between diatom and green *Noctiluca*-dominated phytoplankton communities (Fig. 9). The absence of a link with hypoxia is clearly illustrated by the high variability in annual abundances of diatoms and green *Noctiluca* relative to uniform DO concentrations in surface waters (Fig. 10).

How can the difference between the present findings and those by Gomes et al. (2014) be reconciled? The substantial change in oxygen saturation between 2004 and 2009, relative to 1974–1997, that was highlighted by Gomes et al. (2014, Supplementary Fig. 2d and e) coincided with a change in sensor equipment. DO measurements in the 1980s and 1990s were done chemically using the standard Winkler's method, as used with the shipboard sampling here, while the more recent oxygen data obtained by Gomes et al. (2014) used an oxygen sensor that was not well described. It is likely that this instrumental change contributed to the inferred change in oxygen concentrations. Regardless, DO profiles from the two BGC-Argo floats deployed in the same region at the time of the green *Noctiluca* blooms described by Gomes et al. (2014, see red box in Supplementary Fig. 1) and from five cruises, including two cruises that overlapped in time with theirs (Fig. 8),

show that oxygen saturation remained above 70% in the upper 40 m (Figs. 6D and 7D). The present finding invalidates the hypothesis that extension of cultural eutrophication into the oceanic realm is responsible for the increasing frequency of green *Noctiluca* blooms in the Northeastern Arabian Sea. There are clear linkages between harmful, high biomass green *Noctiluca* blooms and cultural eutrophication in coastal waters (Harrison et al., 2011), however, extension of these effects into oceanic waters requires more evidence than has been presented to date.

What other factors might have contributed to the shifting trajectory of Northeastern Arabian Sea phytoplankton community composition? Phytoplankton production in these waters is fueled during the winter monsoon by enhanced convective mixing, which erodes the nutricline and thereby injects nutrients into the photic zone (Madhupratap et al., 1996). Prakash et al. (2017) showed that the silicate to nitrate ratio (Si:N) climatology has strong latitudinal variability in February, being much lower in the Western Arabian Sea compared to the eastern region. This suggests that the Western Arabian Sea becomes "silicate stressed" during the latter part of the winter monsoon, which conceivably could trigger the initiation of green *Noctiluca* blooms that later spread toward the east. Prakash et al. (2017) also suggest that intensity of the convective and wind-driven mixing plays an important role in this observed community shift. The silicocline in Northern Arabian Sea is deeper than the nitrocline, which implies that stronger mixing intensities could generate higher Si:N ratios in surface waters, thereby supporting stronger diatom blooms. On the other hand, weaker mixing could lead to lower Si:N ratios and facilitate an earlier community transition from diatoms to green *Noctiluca*. The striking inverse relationship between diatom- and *Noctiluca*-dominated communities over time (Fig. 9) might reflect the cycling between bottom-up and top-down regulation of diatoms. In this scenario, the vertical infusion of nutrients in winter initially drives diatoms to flourish, but lowered Si:N ratios in this influx ultimately leads to Si stress conditions for diatoms, but not green *Noctiluca*, which could utilize the remaining NO₃ and graze upon the diatoms. This trend could then be reversed by wind-driven events that infuse new N and Si into surface waters, diluting *Noctiluca*, thereby diminishing grazing efficiency, and stimulating diatom growth. The cycle could then keep repeating, depending on the frequency of periodic wind-driven mixing: a scenario analogous to the classic predator:prey interaction theory in terrestrial ecosystems. The present study lacks the necessary stratification and wind intensity data needed to test this hypothesis, however such data will provide a viable mechanism that may explain the long-term increase in *Noctiluca* abundance in the Northeastern Arabian Sea.

It is also possible that climatic warming of surface waters (Kumar et al., 2009) has contributed to increasing green *Noctiluca* abundance. Warming would increase the intensity of the pycnocline, reduce nutrient flux to the photic zone, and lead to more rapid onset of nutrient stress for large nanophytoplankton during the winter season. This change, in turn, would decrease the abundance of the optimal prey for copepods. Mixotrophs such as the green *Noctiluca*, on the other hand, might still flourish under these reduced nutrient conditions and lower abundances of nanophytoplankton.

Regional changes in planktonic systems can arise from both climatic and global change pressures, namely the combination of direct (e.g., cultural eutrophication) and indirect (i.e., climate change) factors. The present findings show no evidence that cultural eutrophication has contributed to the decadal scale shifts in plankton composition in the Northeastern Arabian Sea. Instead, the lessons that are learned here may help to forecast the effects that climate change may have in other productive oceanic ecosystems.

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