

Mesoscale and Nutrient Conditions Associated with the Massive 2008 *Cochlodinium polykrikoides* Bloom in the Sea of Oman/Arabian Gulf

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Abstract *Cochlodinium polykrikoides* formed large blooms in the coastal waters of Oman from October 2008 through mid-January 2009, and satellite images from Aqua-MODIS and region-wide reports suggest that this bloom was found throughout the Arabian Gulf and Sea of Oman for more than 10 months. The unusual occurrence of this species appears to have supplanted the more regularly occurring bloom species, *Noctiluca scintillans*, in 2008–2009. For the first 2 weeks of the coastal Omani bloom, *C. polykrikoides* abundance was near monospecific proportions, with cell densities ranging from 4.6×10^3 to 9×10^6 cells L^{-1} and very high levels of chlorophyll *a* ($78.0 \mu g L^{-1}$) were also recorded. The regional progression of the bloom likely began with stronger than normal upwelling along the Iranian and northern Omani coasts during the southwest monsoon in late summer, followed by discharge of unusually warm coastal plume water along the coast of Oman with the reversal of monsoonal winds in late October. The occurrence and persistence of high densities of *C. polykrikoides* in Oman coastal water were also significantly influenced by an elevated nutrient load and warmer than normal temperatures. Concentrations of nutrients, especially NH_4^+ , urea, PO_4^{3-} , and organic nitrogen and phosphorus, were manifold higher than observed in the year prior or since. These findings suggest that mesoscale features were

important in bloom dynamics more regionally, but locally the bloom was sustained by nutrient enrichment supplemented by its mixotrophic capabilities.

Keywords Phytoplankton · *Cochlodinium polykrikoides* · Sea of Oman · *Noctiluca scintillans* · Harmful algal blooms

Introduction

In the past several decades, a massive expansion of dinoflagellate blooms has occurred in the Arabian Sea and Sea of Oman (formerly Gulf of Oman) (Parab et al. 2006; Al-Azri et al. 2007; Gomes et al. 2008; Harrison et al. 2011). These blooms were not observed during the Joint Global Ocean Flux Study (JGOFS) cruises of the 1990s (Gomes et al. 2008) but have expanded considerably, consistent with climate changes and atmospheric warming (Goes et al. 2005) and nutrient loading (Harrison et al. 2011). These recent blooms have been dominated by the heterotrophic dinoflagellate *Noctiluca scintillans* (Parab et al. 2006; Al-Azri et al. 2007; Gomes et al. 2008; Harrison et al. 2011). Blooms of *N. scintillans* are now recognized to be an offshore manifestation of eutrophication at least in some areas; increasing nutrients promote an increase in phytoplankton that, in turn, are the nutrient supply for this heterotrophic dinoflagellate (Harrison et al. 2011). However, even in this region where dinoflagellate blooms have increased, a unique *Cochlodinium polykrikoides* bloom occurred in late 2008–early 2009. During this event, *N. scintillans* blooms were not observed, raising the question of whether environmental drivers were different in 2008, in a region where many factors are rapidly changing.

The geographic expanse of the *C. polykrikoides* bloom in the Sea of Oman in 2008–2009 has been well documented to have been broad and to have caused massive fish kills especially in fish cages, to have impacted desalination plants and

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refineries, and to have had significant economic consequences (Pankrantz 2008; Richlen et al. 2010; Al Gheihani et al. 2012). In Oman alone, Al Gheihani et al. (2012) reviewed the progression of fish kills by date and location and reported that ~200 tons of fish, including 70 tons of caged fish, 70 tons of shellfish, and 60 tons of wild fish died in the period from October 2008 to March 2009. Furthermore, damage to coral reefs in the marine protected regions of the United Arab Emirates (UAE) was also reported to have resulted from this bloom (Berktaay 2011). The bloom required the closures of five desalination plants in the UAE due to clogging at the intake resulting in serious disruption to the potable water supply (Richlen et al. 2010; Berktaay 2011). Schools closed in the Muscat region due to intense odors from the methyl sulfide compounds produced by the bloom (Al Gheihani et al. 2012). It has been estimated that the bloom expanded along the western side of the Arabian Gulf in January 2009 where it proceeded to cover about 14,000 km², including 750 km of the Iranian coast and where it was responsible for additional fish and shellfish kills (Saeedi et al. 2011; Hamzei et al. 2012; Fatemi et al. 2012). In the broader Gulf region, more than an order of magnitude more fish kills were reported than those reported in Oman (Berktaay 2011). At the northern Strait of Hormuz, moreover, the bloom is estimated to have lasted 8–10 months from late 2008 into 2009 (Hamzei et al. 2012; Fatemi et al. 2012).

C. polykrikoides is among the many species of dinoflagellates which are increasingly adversely affecting fisheries, tourism, and economies around the world (Yuki and Yoshimatsu 1989; Guzman et al. 1990; Qi et al. 1993; Kim et al. 1999, 2004; Lee 2008; Gobler et al. 2008; Tomas and Smayda 2008; Anton et al. 2008; Mulholland et al. 2009; Morse et al. 2011; Howard et al. 2012). While previously most commonly observed in tropical systems (Steidinger and Tangen 1997), *C. polykrikoides* is now increasingly observed in temperate systems (e.g., Gobler et al. 2008; Kudela et al. 2008; Mulholland et al. 2009; Morse et al. 2011). As such, *C. polykrikoides* appears to be similar to many other harmful dinoflagellates undergoing global expansion (e.g., Heil et al. 2005; Glibert et al. 2005, 2006, 2008; Harrison et al. 2011). As an unarmored planktonic dinoflagellate, it is morphologically similar to *Gymnodinium catenatum* and *Gyrodinium impudicum* (Hallegraeff and Fraga 1996; Cho et al. 2001). While the precise mechanism of fish mortality by *C. polykrikoides* is still debatable, adverse effects, such as suffocation, hemolysis, and osmoregulatory alteration from reactive oxygen production, have been reported (Kim et al. 1999; Gobler et al. 2008; Dorantes-Aranda et al. 2009). Such blooms have been shown to be associated with elevated nutrients (Harrison et al. 1990) and may persist and reoccur because the species forms resting cysts (Kim et al. 2007; Kudela et al. 2008). However, Yang et al. (2000) have reported the occurrence of *C. polykrikoides* offshore in waters

receiving low nutrient submarine ground water as the primary nutrient source, raising the question as to whether the growth and persistence of many *C. polykrikoides* blooms are really a consequence of eutrophication.

While the identification and phylogeny of this bloom has previously been described (Richlen et al. 2010; Matsuoka et al. 2010), the environmental conditions associated with both the regional phenomenon and the local Omani conditions have not. We hypothesized that altered climatic conditions, combined with unusual nutrient conditions, were the factors leading to, or sustaining, this bloom. Here we report, using data from remote sensing and local sampling, the relationships of this *C. polykrikoides* bloom to physical features, monsoonal conditions, and nutrient concentrations both regionally and locally. Understanding nutrient sources may aid in developing strategies for its prevention.

Study Region

Oman, which sits on the southwest side of the Arabian Peninsula, is bordered by the UAE, Saudi Arabia, and Yemen. The northern tip of Oman juts out into the Strait of Hormuz, the entrance to the Arabian Gulf. The water exchange through the Strait is complex, in large part due to the shallow nature of the Arabian Gulf and the high evaporation rates due to elevated temperatures. This causes the Gulf to act, at least in large part, as an “inverse estuary,” with relatively fresher water from the Sea of Oman flowing into the Arabian Gulf, and relative saline waters exiting the Gulf at depth especially on the western (Omani) side (Pous et al. 2004) (Fig. 1). This Arabian Gulf water can result in a coastal plume affecting the coast of Oman. This coastal plume is typically maintained southward to the dominant promontory of Oman, Ras al Hadd (Fig. 1). Eddies and filaments form off of this coastal plume (e.g., Ezam et al. 2009).

Oman has an extensive coastline of 3,165 km that includes the Sea of Oman in the North and the Arabian Sea in the South. Biological characteristics of the ecosystem of the Sea of Oman are influenced by the hydrodynamics of the area driven mostly by monsoonal winds and by inflow and outflow of waters from the Arabian Gulf and the Arabian Sea. During typical years, the summer Southwest Monsoon (SWM) occurs from June to September and creates coastal upwelling and phytoplankton blooms (Brink et al. 1998). The winter Northeast Monsoon (NEM) occurs from November to February and creates eddies that transport phytoplankton blooms to the coast. These monsoonal changes are also associated with changes in phytoplankton community structure and abundance (e.g., Brock and McClain 1992). In recent years, due to climate change and increasing anthropogenic nutrient loading, these blooms have changed in magnitude and composition. For example, Goes et al. (2005) showed, using satellite

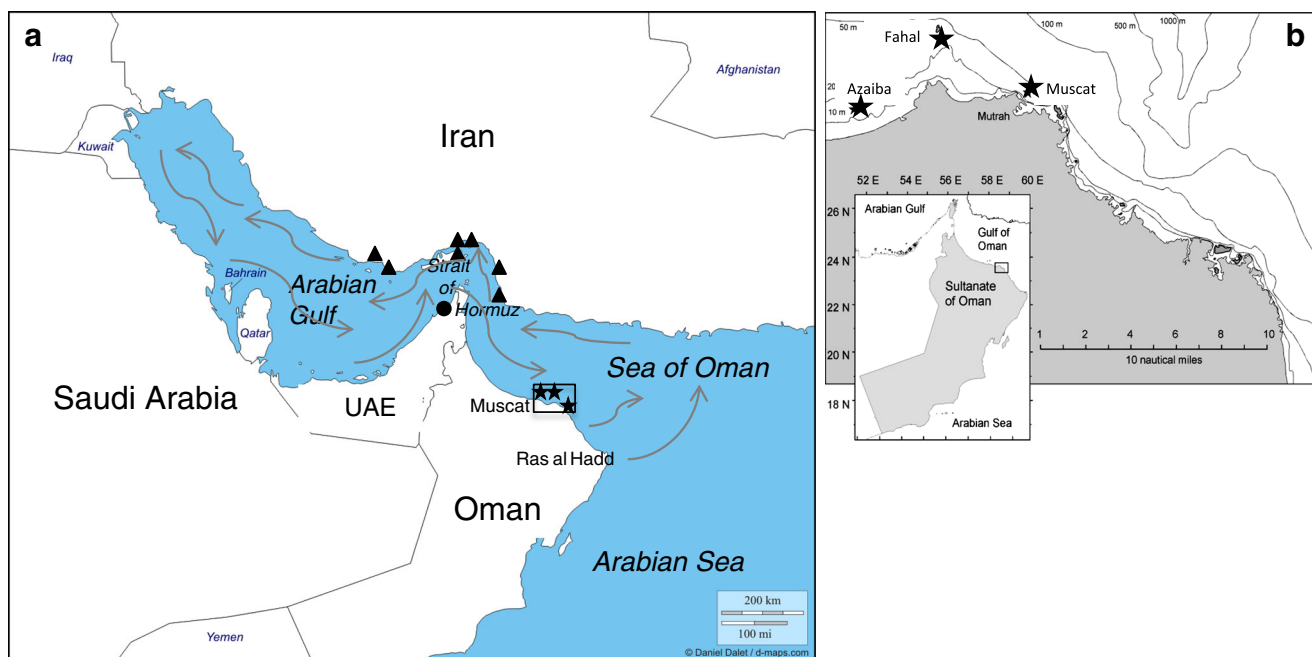


Fig. 1 **a** Region showing the Arabian Gulf, the Strait of Hormuz, and the Sea of Oman and the general circulation patterns (gray arrows). Triangles represent sites where *Cochlodinium polykrikoides* was positively identified during the period of late 2008–early 2009. The station indicated by a solid circle was the site where *C. polykrikoides* was reported by

Richlen et al. (2010), while triangles are locations of incidences reported by Fatemi et al. (2012) and stars are locations from this study. Base map modified from d-maps.com. **b** Greater detail of the sampling sites off the coast of Oman

data, that biomass appeared to be increasing during the SWM as a result of intensification of SWM winds and associated upwelling off Somalia, Oman, and Yemen. The Somali current is a major feature of these more southern coasts (Schott et al. 1990).

Materials and Methods

Sampling Sites

The current study was conducted at three stations (Muscat, Fahal, and Azaiba) in the Sea of Oman along the coastal region of the capital city of Oman, Muscat (Fig. 1), approximately midway from the northern tip of Oman to Ras al Hadd. The three stations were chosen for their ecological differences. Station Muscat with a maximum depth of 35 m (23°40′0.63″ N, 58°30′0.354″ E) is close to the Mina Al-Sultan Qaboos port and likely to be the most polluted, and Station Fahal is located close to Mina Al-Fahal (23°40′0.63″ N, 58°30′0.354″ E) and is characterized by high abundance of coral and a maximum depth of about 22 m. Station Azaiba (23°37′0.72″ N, 58°39′0.003″ E), with maximum depth of 12 m, is close to a desalination plant. These stations lie in the region of influence of the coastal plume described above.

Sampling and Hydrographic, Biological, and Meteorological Parameters

The three stations were sampled frequently from October 2008 to January 2009 from the *R/V Al-Hamor*, while station Fahal was also sampled for nutrients irregularly during the ~18 months prior to, and ~12 months following, the bloom event. At each station, water temperature and salinity profiles were measured with an Idronaut-Ocean Seven 316 CTD probe fitted with an additional sensor for measuring chlorophyll *a* (Chl *a*) by fluorescence. Laboratory measurements of Chl *a* using acetone extracts and a Turner 10 Designs Fluorometer (Knap et al. 1994) were conducted on selected samples for calibration of the sensor.

Subsurface water samples, representative of the mixed layer, were collected from 1 m depth with a clean 5-L Niskin bottle for subsequent analysis of NH_4^+ , $\text{NO}_3^- + \text{NO}_2^-$, urea, dissolved organic nitrogen (DON), and PO_4^{3-} , and dissolved organic PO_4^{3-} (DOP). For convenience herein, $\text{NO}_3^- + \text{NO}_2^-$ are simply referred to as NO_3^- . Inorganic nutrient samples were filtered (Whatman GF/F filters, aliquots of 100 mL), frozen at -20°C and later analyzed using a five-channel SKALAR Flow Access auto-analyzer. Urea samples were analyzed according to Revilla et al. (2005) and DON and DOP by persulfate oxidation (Solórzano and Sharp 1980; Bronk et al. 2000).

Phytoplankton samples were collected directly from the surface using a clean, acid-washed glass beaker. Samples were preserved with Lugol's iodine solution (Thronsen 1978) and stored at 4 °C in dark glass bottles. Samples were concentrated overnight by transferring into graduated cylinders to allow cells to settle to 20 mL prior to enumeration. Replicate 1 mL samples were transferred onto a Sedgewick-Rafter counting chambers and observed under a Zeiss inverted light microscope at $\times 200$ and $\times 400$ magnification. Identification was based on standard keys in most cases to the species level (Round et al. 1990; Sournia 1986; Tomas 1997).

For scanning electron microscopy, live samples from the field were fixed for approximately 1 h in 1 % O_5O_4 in growth medium (Anton et al. 2008). This was followed by rinsing the samples with distilled water to remove salt and then dehydrated in a graded ethanol series (30, 50, 70, 96, and 99.9 %). The samples were then coated with a layer of platinum–palladium. The images were taken using scanning electron microscope (LVSEM)—JEOL JSM-5600LV (voltage 30 kV, resolution—high vacuum 3.5 nm, low vacuum 5.0 nm, magnification $\times 18$ – $\times 300,000$, detectors SE and BSE).

Remote Sensing Data

Data on sea surface height (SSH) anomalies were retrieved from TOPEX/Poseidon, Jason-1 and Jason-2 altimeters through the Archiving, Validation and Interpretation of Satellite Oceanographic (AVISO) data center website (<http://www.aviso.oceanobs.com>). Satellite-derived (9 km spatial resolution MODIS Aqua) monthly level 3 products for sea surface temperature (SST) and Chl *a* (9 km spatial resolution SeaWiFS and MODIS Aqua) were obtained from the National Aeronautics and Space Administration (NASA) Ocean Color Group (<http://oceancolor.gsfc.nasa.gov>). Monthly time series data were acquired using the GES-DISC Interactive Online Visualization and Analysis Infrastructure (GIOVANNI) software as part of the NASA's Goddard Earth Sciences Data and Information Services Center. Nighttime sea surface temperatures (SSTs) for a site just north of Muscat were obtained from NOAA's Advanced Very High Resolution Radiometer (AVHRR) instrument on NOAA's Polar Orbiting Environmental Satellite (POES) (http://www.osdpd.noaa.gov/data/cb/time_series/all_Oman_Muscat). Satellite images (merged SeaWiFS and MODIS Aqua) were also obtained for Chl *a* for

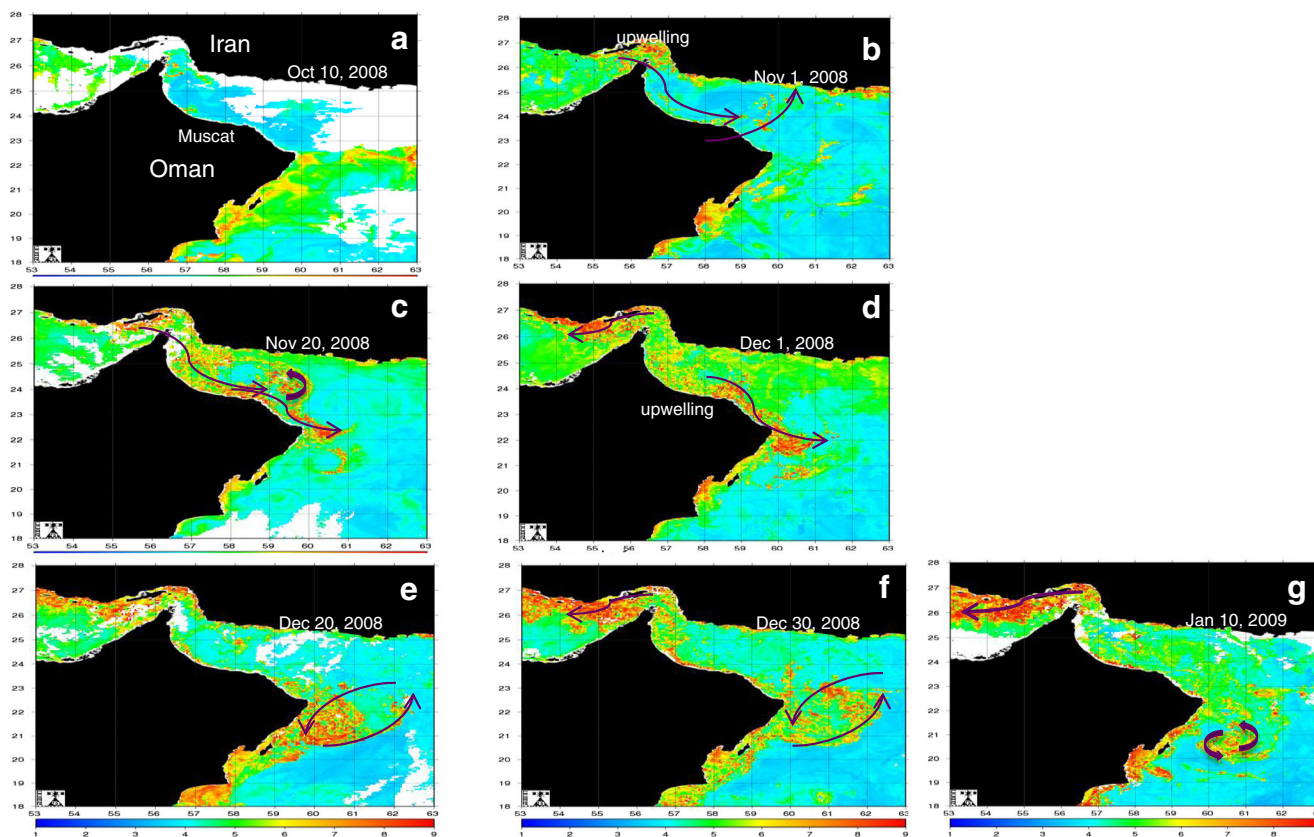


Fig. 2 a–g Satellite images showing the development of blooms in the Sea of Oman and Arabian Sea in 2008 and their dissipation in January 2009. The arrows superimposed on the images are intended to draw attention to the major mesoscale features and are not meant to imply

measured flow. The chlorophyll scale on the images is intentionally reported dimensionless to underscore the relative patterns, not absolute biomass accumulations

the period of the bloom (November 2008 to January 2009; see Gomes et al. 2008 for details on imagery and its calibration).

Results

Overview of Bloom Progression

Satellite images (Fig. 2a–g) illustrate the spatial and temporal scale of the bloom and convey a complex pattern of the spatial distribution of Chl *a* affected by mesoscale eddies (shown in the figure as blue and green gaps) caused by basin scale circulation. Accumulations of Chl *a* were evident in the Strait of Hormuz and along the coast of the UAE and northern Oman by early November 2008 (Fig. 2a, b). These high Chl *a* regions were identified to be dominated by *C. polykrikoides* (Richlen et al. 2010; Hamzei et al. 2012; Fatemi et al. 2012). From November through December, Chl *a* accumulations along the Omani coast were evident (as shown in the red

patches in Fig. 2c, d). In the later days of December, Chl *a* concentrations waned along the Omani coast, but intensified along the Iranian coast (Fig. 2e, f). This is seen not only in the satellite images, but also reported in field measurements by Hamzei et al. (2012) and Fatemi et al. (2012). Thus, although in situ Chl *a* concentrations are not available to validate the satellite observations for the entire region, these coastal observations confirm that the same species was occurring at multiple regions of the Sea of Oman and Arabian Gulf over the same period.

Fish kills due to *C. polykrikoides* were reported as early as the beginning of October in the northern waters of Oman (Al Gheihani et al. 2012). These events precipitated the intensive sampling that was carried out. In the first such sampling, on 29 October, Chl *a* levels of 78.16 $\mu\text{g L}^{-1}$ and cell densities of *C. polykrikoides* of 8.3×10^6 cells L^{-1} were documented at station Fahal (Fig. 3, Table 1). Cell counts at that station were maintained above 10^4 cells L^{-1} through the end of December (Fig. 3). The highest cell and Chl *a* concentrations attained at

Fig. 3 Comparison of abundance of dinoflagellates, diatoms, and *Cochlodinium polykrikoides* abundance (cells per liter) at three sites in Oman during the bloom. The broad line denotes concentration of *C. polykrikoides* in bloom proportions

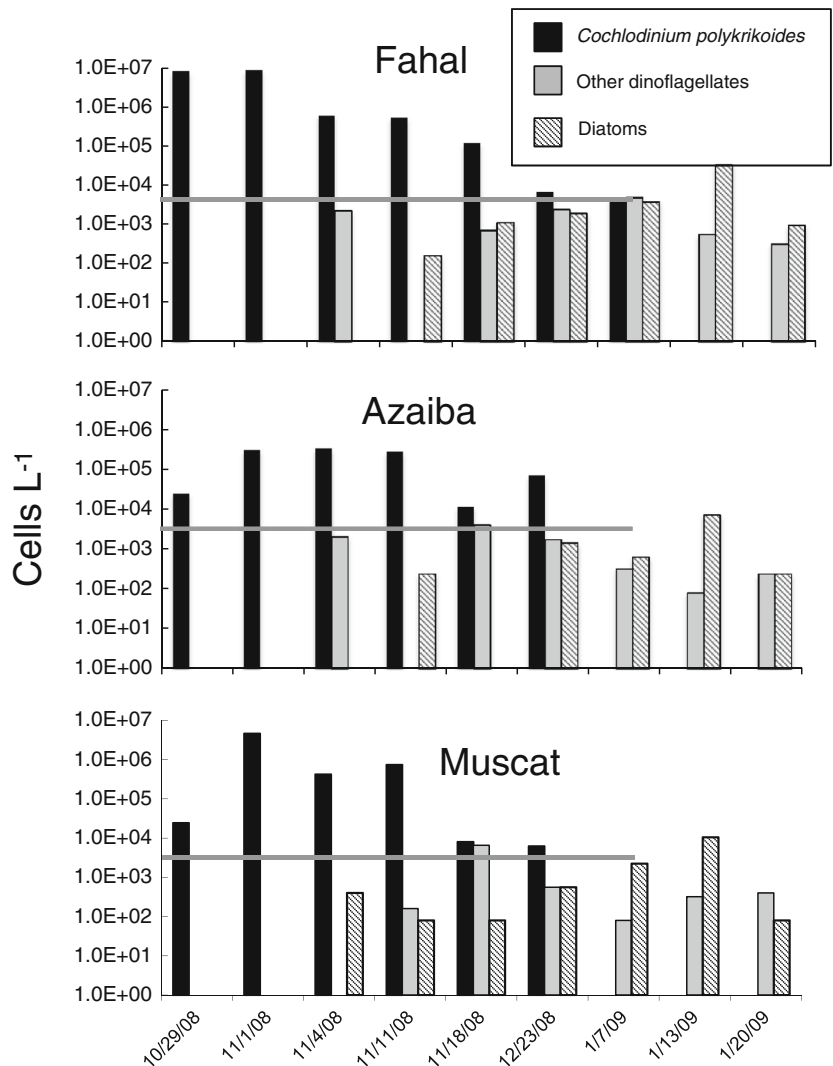
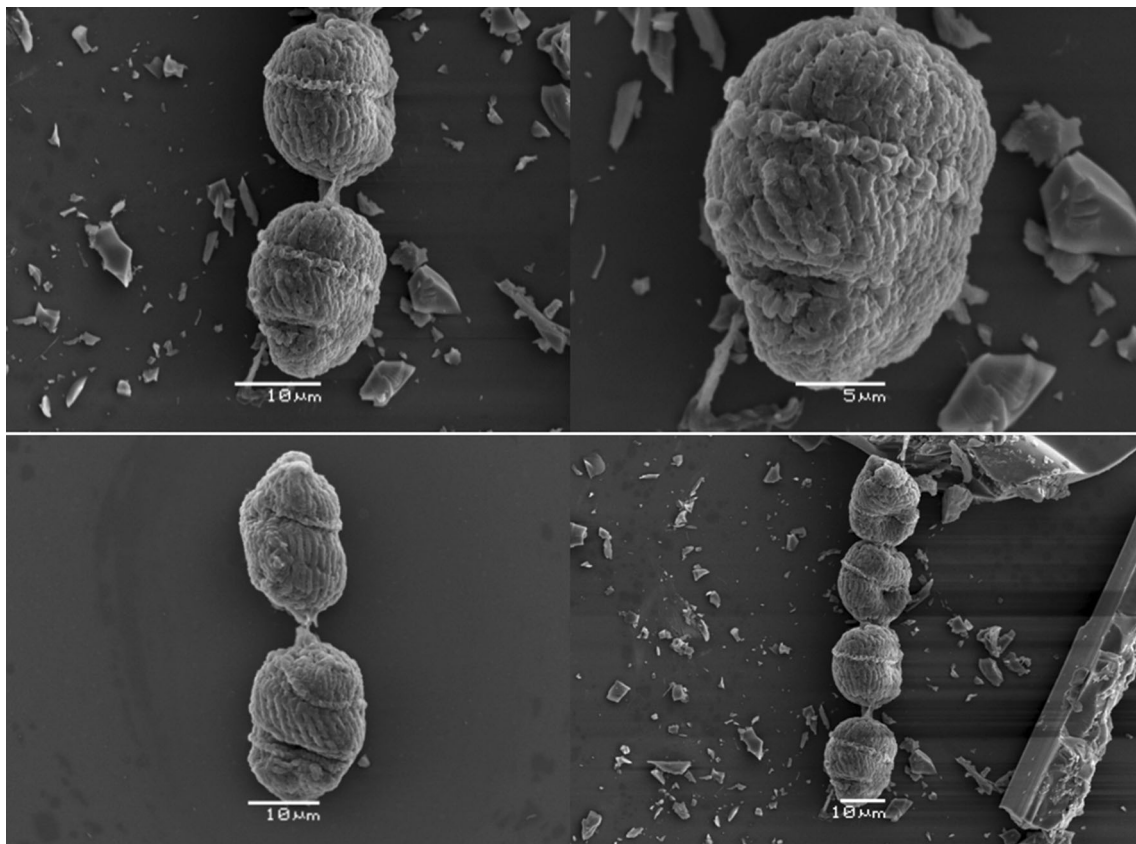


Table 1 Water column characteristics for the three stations sampled in Omani waters from October 2008 to January 2009

Station and parameter	October 29, 2008	November 1, 2008	November 4, 2008	November 11, 2008	November 18, 2008	December 23, 2008	January 7, 2009	January 13, 2009	January 20, 2009
Azaiba									
Temp (°C)	30.42	30.11	30.05	29.69	26.72	24.08	23.56	23.69	22.60
Salinity	37.12	37.30	37.35	37.37	36.88	36.58	36.62	36.60	36.47
Chl <i>a</i> (µg L ⁻¹)	0.40	1.64	34.81	24.35	19.07	1.08	1.23	2.55	0.54
Fahal									
Temp (°C)	30.70	30.11	29.87	28.69	26.70	24.23	23.73	23.73	23.13
Salinity	37.39	37.27	37.21	36.94	36.82	36.53	36.60	36.59	36.57
Chl <i>a</i> (µg L ⁻¹)	78.16	10.65	5.38	8.91	2.16	0.27	0.80	0.73	0.47
Muscat									
Temp (°C)	30.03	29.89	30.27	28.68	26.37	24.23	24.06	23.81	23.50
Salinity	37.12	37.07	37.22	36.82	36.78	36.54	36.52	36.58	36.58
Chl <i>a</i> (µg L ⁻¹)	14.99	36.34	10.05	2.30	14.01	1.40	0.96	1.01	0.62

the other two stations, Azaiba and Muscat, were found during the first week of November and were maintained above 10^3 cells L⁻¹ through the end of December or early January (Fig. 3). Ichthiotoxicity from *C. polykrikoides* has previously

been identified to occur at cell densities $>3.3 \times 10^3$ cells L⁻¹ (Gobler 2010). We thus use this as an operation “bloom” definition. Cell abundances recorded were thus sustained well within “bloom” proportion through the period from October to

**Fig. 4** SEM micrographs of *C. polykrikoides* collected from bloom waters off the coast of Oman

December in Omani waters (Fig. 3). Moreover, during the first weeks of sampling, the bloom was in near monospecific proportions. Light and scanning electron microscopy confirmed that the species was *C. polykrikoides* Margalef (Fig. 4).

Physical and Chemical Parameters

Preceding the bloom period, in late July 2008, there was a period of unusually cool temperatures, with as much as a -3 °C temperature anomaly, as reported by direct temperature observations from NOAA for a site just north of Muscat, using satellite nighttime SSTs (Fig. 5b). Such a pattern would be suggestive of strong upwelling in the late summer months, the period of the SWM.

In contrast, the 2008 fall period had unusually long SSH anomalies (Fig. 5a) that lasted from October until approximately March 2009, indicative of monsoon reversal to a NEM period. This SSH anomaly exceeded that of the previous 2 years in its duration by as much as 2–2.5 times (Fig. 5a). Such an anomaly is suggestive of a period of warm water temperatures. Negative temperature anomalies from October 2008 to ~March 2009 were smaller than those of previous

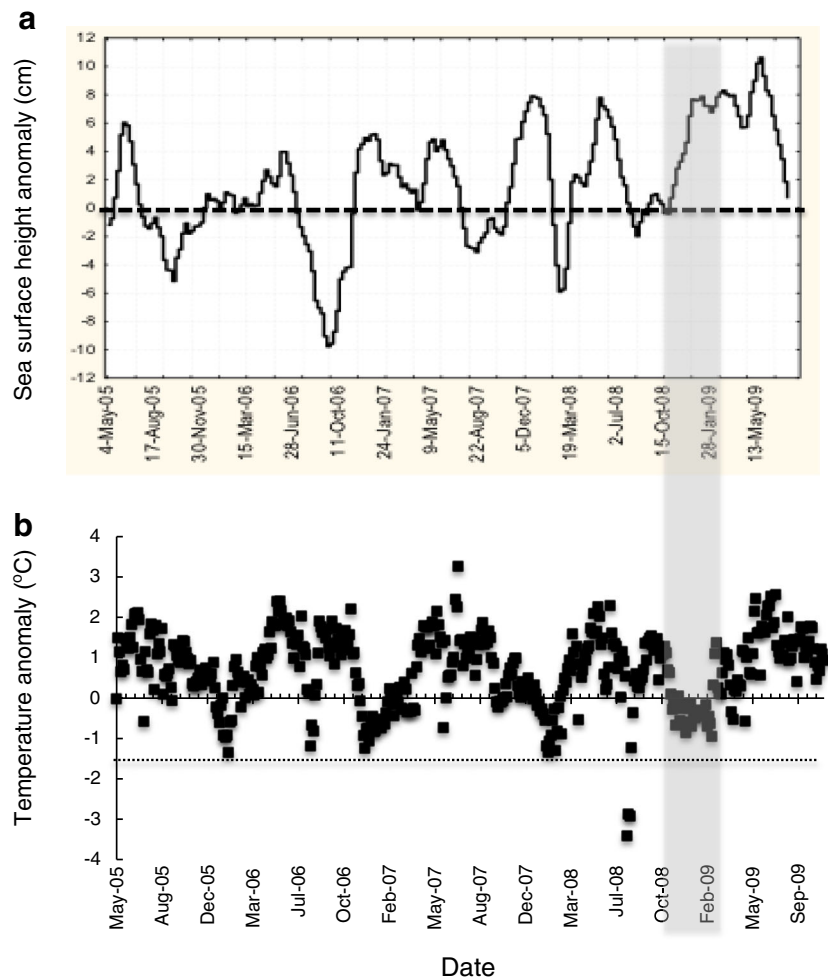
NEM periods, indicating warmer than normal temperatures (Fig. 5b).

Water temperature at all stations sampled off Oman suggested unusually warm water, >30 °C, during the first week of observation of the bloom (Table 1). Salinity at all stations showed less variation with values ranging from 36.82 to 37.39 (Table 1).

Nutrients

All forms of nutrients were elevated during the peak of the bloom compared to the following weeks (Fig. 6). NH_4^+ concentrations exceeded 6 μM at stations Fahal and Azaiba and 12 μM at station Muscat in late October and early November, but decreased below 1 μM at all stations in the following weeks (Fig. 6a–c). Urea-N concentrations were also elevated (above 4 $\mu\text{M-N}$) in early November at station Fahal (Fig. 6a). NO_3^- concentrations were low during the early weeks of the bloom, but rose at stations Fahal and Muscat in January (Fig. 6a, c). All sites also exhibited very high concentrations of DON in early November compared to the following weeks (Fig. 6d–f). The peaks in DON were comparatively short-

Fig. 5 **a** Weekly time series of SSH anomalies in the Sea of Oman for the area bounded by 23 – 26° N, 57 – 60° E. **b** Time series, from 2005 to 2009, of temperature anomalies for a site just north of Muscat based on NOAA-AVHRR data (details in text). The *gray panel* is intended to highlight the “general” period of the *C. polykrikoides* bloom. The *dashed line* in **b** is intended to draw attention to the “typical” anomalies attained in nonbloom years



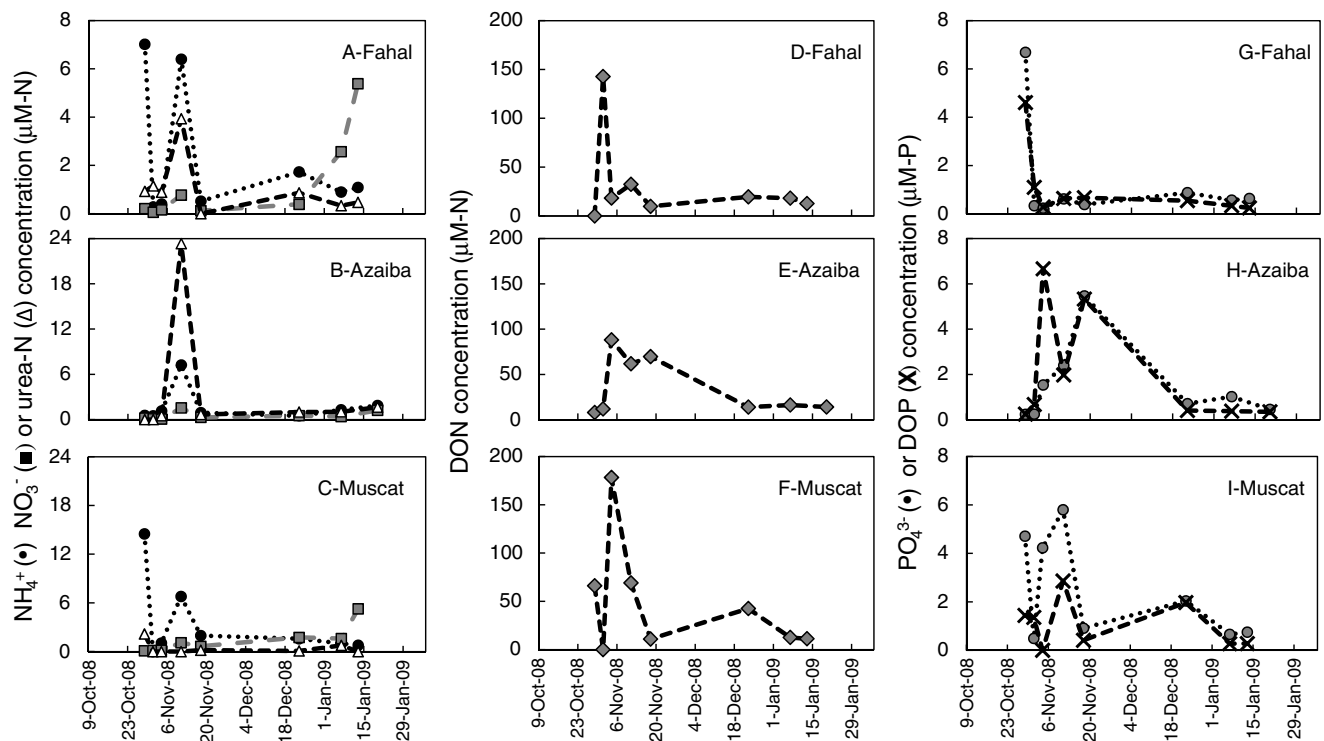


Fig. 6 Concentrations (micromolar) of ammonium (NH₄⁺), nitrate (NO₃⁻), urea (a–c), dissolved organic nitrogen (DON; d–f), and inorganic and organic phosphate (PO₄³⁻ and DOP; g–i) during the bloom (October 2008–January 2009) at three stations, Fahal, Azaiba, and Muscat

lived at stations Fahal and Muscat but were more sustained at station Azaiba (Fig. 6e). As with the nitrogenous nutrients, concentrations of both inorganic and organic P were significantly elevated during the early phase of the bloom compared to the following weeks (Fig. 6g–i).

The time series of nutrient concentrations from station Fahal beginning ~18 months before the bloom and extending a year past the bloom suggests that these high levels of NH₄⁺, urea, and PO₄³⁻ during October 2008 were unusual, at least

for the available data. It was also noted that elevated levels of NO₃⁻ occurred a few months after the observed peaks in the other nutrients (Fig. 7).

From October 2008 to January 2009, with the exception of one point, all ratios of dissolved inorganic N to inorganic P (DIN/DIP) at all sampled stations were less than classical Redfield proportions, in some cases <5 on a molar basis (Fig. 8a). However, molar ratios of the organic forms of N and P were significantly greater than 16:1 proportions (Fig. 8b).

Fig. 7 Ammonium (NH₄⁺), urea, phosphate (PO₄³⁻), and nitrate (NO₃⁻) concentrations at station Fahal over the extended time series from February 2007 to November 2009. Note the temporal offset in the peaks of NO₃⁻ relative to those of the other nutrients

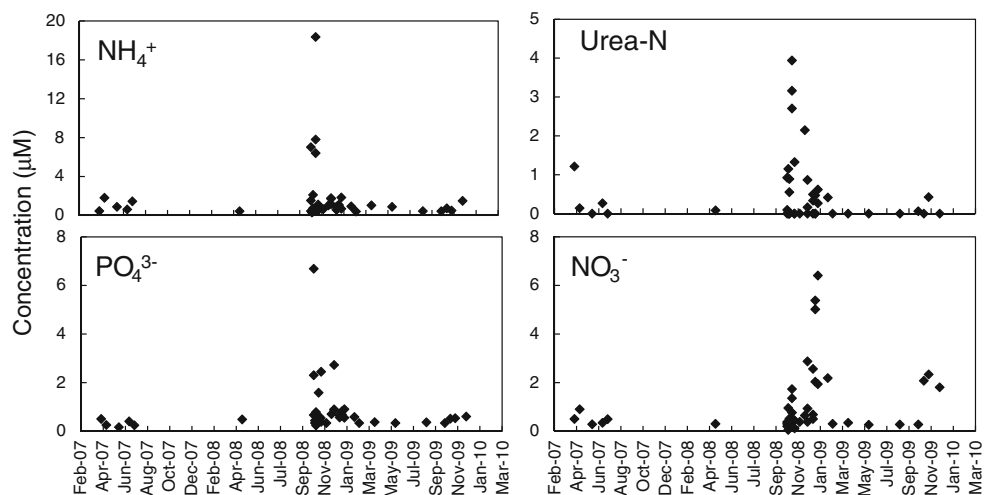
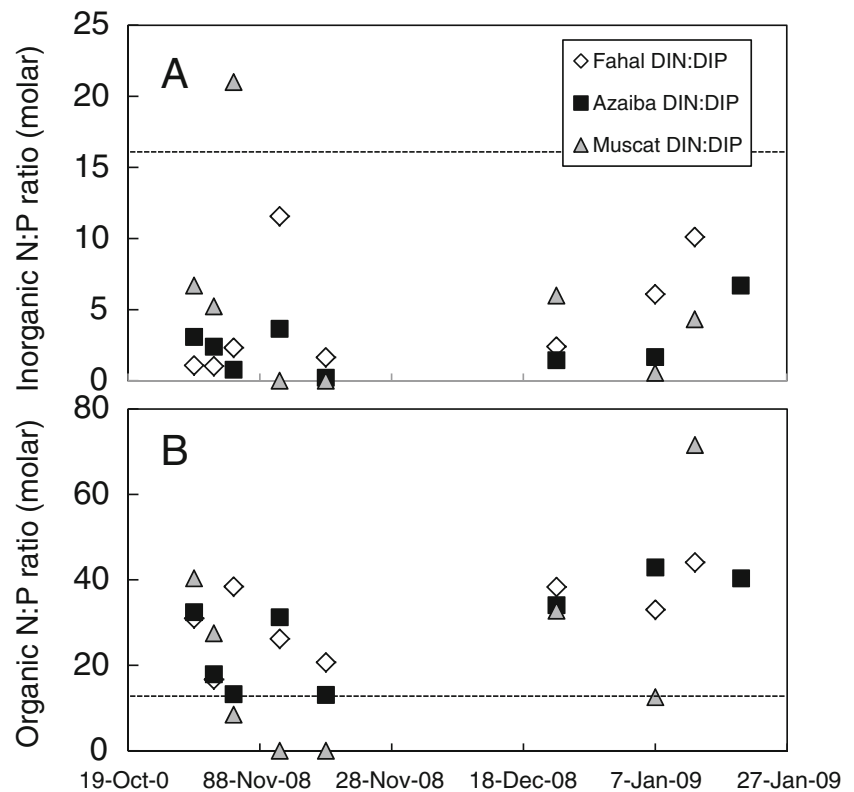


Fig. 8 Molar ratios of inorganic N/P (a) and organic N/P (b) during the *C. polykrikoides* bloom in Omani waters in 2008. The dashed line is the Redfield ratio, 16:1



Discussion

Occurrences of harmful algal blooms (HABs) in the coastal waters of the Sultanate of Oman have been reported with increasing frequency over the past three decades. Barwani (1976) reported the first incidence of “red tide” and mass mortality of fish along the Salalah coast of southern Oman. Since then, HAB events have continued to occur in coastal and nearshore Omani and Arabian Gulf waters and have been attributed to multiple species of diatoms and dinoflagellates, including *Prorocentrum* sp., *Chaetoceros* sp., *Karenia selliformis*, *Ceratium* sp., *Alexandrium* sp. as well as *N. scintillans* (Thangaraja 1990; Subba-Rao and Al-Yamani 1998; Heil et al. 2001; Glibert et al. 2002; Glibert 2007; Thangaraja et al. 2007; Al-Azri et al. 2007). Fish kills have long been noted in the region and have been attributed to many causes, not just HABs (e.g., Claereboudt et al. 2001).

The unusual occurrence of *C. polykrikoides* in Omani waters was confirmed throughout the greater Gulf region. Richlen et al. (2010), who confirmed the species identification off the UAE, found cell counts as high as $1.1\text{--}2.1 \times 10^7$ cell L^{-1} in October 2008. In the Strait of Hormuz during the same month, cell counts of this species were 2.6×10^7 cells L^{-1} and Chl *a* reached values of $32 \mu g L^{-1}$, where normally in the same month of a nonbloom year, concentrations are $<1 \mu g L^{-1}$ (Fatemi et al. 2012). These previous reports have also made note of the numerous fish kills that occurred coincident with the bloom on both shores of the Sea of Oman and Arabian Gulf as

well as the associated economic losses to fisheries and desalination facilities (Berktaý 2011). Thus, there is no question that the bloom was expansive and destructive, encompassing much of the entire Gulf region.

Cell densities throughout the region were on par with blooms of this species that have recently occurred in the temperate estuaries of the east coast of the USA as well as in the Gulf of California, Mexico, and along the coast of California (e.g., Gárate-Lizarrága et al. 2004; Gobler et al. 2008; Curtiss et al. 2008; Mulholland et al. 2009), all of which resulted in fish kills and other disruptions to ecological processes. In Korean waters, *C. polykrikoides* blooms reach similar cell densities in regions of intense aquaculture (e.g., Cho et al. 2001; Kim et al. 2004).

Previous taxonomic analyses, including partial analysis of the rRNA gene sequences of this *C. polykrikoides* bloom, confirmed that this species is identical to isolates from the northeastern USA to Mexico and Malaysia (Richlen et al. 2010). Matsuoka et al. (2010) reported that the species in the Arabian Gulf belongs to the American/Malaysian ribo-type. Ballast water introductions have been suggested as one mechanism of introduction (e.g., Richlen et al. 2010), but that does not explain its regional expansion, nor its sudden appearance.

As previously noted, phytoplankton dynamics in the Sea of Oman is largely driven by the monsoon winds (Wiggert et al. 2010; Al-Azri et al. 2010) that are strong and seasonally reversing, i.e., SWM winds from June to September and NEM winds from November to February (Schott et al. 1990;

Brock and McClain 1992). The SWM winds have classically been associated with the persistence of the coastal upwelling, as well as coastal mixing and advective transport. These processes may contribute to nutrient availability and other physical factors that may be conducive for phytoplankton blooms in general (Brock and McClain 1992; Barber et al. 2001; Banse and Piontkovski 2006; Gomes et al. 2008; Al-Azri et al. 2010). Specifically in 2008, it appears that there was a period of intense upwelling off Oman in summer as suggested by the $-3\text{ }^{\circ}\text{C}$ temperature anomaly (Fig. 5b). Upwelling alone, however, is not the only factor contributing to the proliferation of this extensive bloom. The bloom actually was at its highest abundance in Omani waters during the reversal from SWM to NEM and was sustained during the NEM period when temperature anomalies were less than in prior years. Thus, the bloom maintenance period was out of phase with upwelling.

Given the extent and longevity of the bloom in the Sea of Oman, Strait of Hormuz, and Arabian Gulf (Fig. 2), it is likely that its development and dispersal were influenced by multiple co-occurring factors. An anticyclonic eddy (or eddies) may have been the physical mechanism that pushed the bloom closer to both shores (west and east sides of the Sea of Oman) and magnified its strength in the coastal regions. The expansion of the bloom appeared to occur under the impact of anticyclonic eddies which extended from the Southern Sea of Oman (Ras al Hadd) and spanned the central part of the Gulf in November. The highest recorded density of *C. polykrikoides* in Omani waters (Fig. 3) occurred at a salinity of >37 and a temperature of $>30\text{ }^{\circ}\text{C}$ (Table 1). Interestingly, in Iranian waters, the highest cell abundance was observed over a broad temperature range from $28.9\text{ }^{\circ}\text{C}$ in October 2008 to $21.8\text{ }^{\circ}\text{C}$ in November 2008 (Fatemi et al. 2012). It has been previously reported that *C. polykrikoides* has the ability to tolerate wide range of temperature and salinity (Kim et al. 2004; Kudela et al. 2008). These favorable conditions of high salinities and a wide range of temperature likely contributed to an environment that sustained growth. Interestingly, temperatures $>30\text{ }^{\circ}\text{C}$ are generally not supportive of blooms of *N. scintillans*, the species which now typically dominates this time of year in the Sea of Oman. Blooms of *N. scintillans* are generally found at temperatures $<26\text{ }^{\circ}\text{C}$, although many exceptions have been noted (Harrison et al. 2011). It is therefore entirely conceivable that warm Arabian Gulf waters together with ambient nutrients created favorable conditions for *C. polykrikoides* to grow, but these conditions were too warm for *N. scintillans* to do well.

While mesoscale features may have contributed to the time and position of the bloom along the coast, the pulsed nature of outbreaks at different times and the size of the bloom in the different localized regions are highly suggestive that local environmental conditions also contributed to the bloom development and persistence. One of the features of the

environmental conditions during this bloom off Oman was the elevated concentrations of nutrients, especially NH_4^+ , urea, PO_4^{3-} , DON, and DOP at the time that the bloom was first noticed (Fig. 6). Concentrations of NH_4^+ and/or urea exceeded $10\text{ }\mu\text{M-N}$ at all sites in the early phase of the bloom. In fact, at least for station Fahal, where a longer record of nutrient concentrations exists (Fig. 7), concentrations at the start of the bloom were manyfold higher than observed in the previous year or in the year following the bloom. Although the time series is incomplete, the observed concentrations, especially of NH_4^+ and PO_4^{3-} , are far higher than previously observed during the same time of year during the year following the bloom. The time series of nutrients at station Fahal shows that NH_4^+ , urea, and PO_4^{3-} concentrations were clearly elevated when the bloom was first observed in October 2008. NO_3^- started to increase following the decline of NH_4^+ reaching maximum values in January 2009, suggesting nitrification or potentially a new upwelling event. It thus appears that while upwelling may have driven the physical dynamics of the broader region, localized nutrient inputs either accelerated or sustained the bloom.

Some nutrient data are also available for the Iranian coast during this bloom event. In the stations sampled in the Strait of Hormuz, cell density exceeded $2 \times 10^7\text{ cells L}^{-1}$, a value ~ 2 orders of magnitude higher than that considered to define a “bloom” (e.g., Gobler et al. 2008). Concentrations of NO_3^- there ranged from 10 to $17.9\text{ }\mu\text{M-N}$ and PO_4^{3-} concentrations ranged from 6.3 to $15.5\text{ }\mu\text{M-P}$ (Fatemi et al. 2012). In contrast, for these same stations during nonbloom periods, NO_3^- concentrations averaged a factor of 2 lower, and PO_4^{3-} concentrations averaged factors of 3–10-fold lower (Fatemi et al. 2012). Also, blooms dissipated in Iranian waters when nutrient levels began to decline (Fatemi et al. 2012). Ratios of DIN/DIP during the bloom periods in Iran were <2 on a molar basis and more than 2-fold lower than observed during nonbloom periods (Fatemi et al. 2012). It should be noted that NH_4^+ data are not available for the Iranian coast, and if concentrations were elevated and included, would tend to further depress the DIN/DIP ratio.

Previous studies have demonstrated that this species is often associated with elevated levels of PO_4^{3-} (reviewed by Gárate-Lizarraga et al. 2004) and the findings of this study are consistent with such a conclusion. The data set for Long Island embayments (Gobler 2010) further confirms, in a comparison of bloom versus nonbloom sites, that in all bloom cases, PO_4^{3-} concentrations were on average 50–100 % higher than in nonbloom sites, and all concentrations were $>1\text{ }\mu\text{M-P}$. The Gobler (2010) findings are therefore similar to the findings reported here and of the Iranian coast (Fatemi et al. 2012) mentioned above.

A comparison of DIN/DIP ratios for the Sea of Oman bloom period with those reported for numerous other blooms of *C. polykrikoides* (Fig. 9) shows that this species commonly

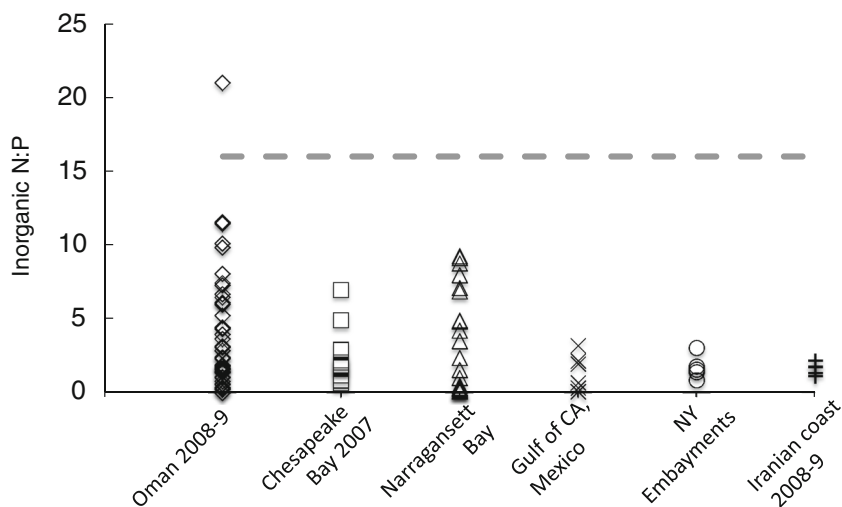


Fig. 9 Comparison of the ambient, inorganic molar ratios of N/P during *C. polykrikoides* blooms in Omani waters in 2008–2009 with those previously reported during similar blooms in Chesapeake Bay (Mulholland et al. 2009), Narragansett Bay (Tomas and Smayda 2008), Gulf of California, Mexico (Gárate-Lizarrága et al. 2004), New York (NY) embayments (Gobler 2010), and the Iranian coast during 2008–

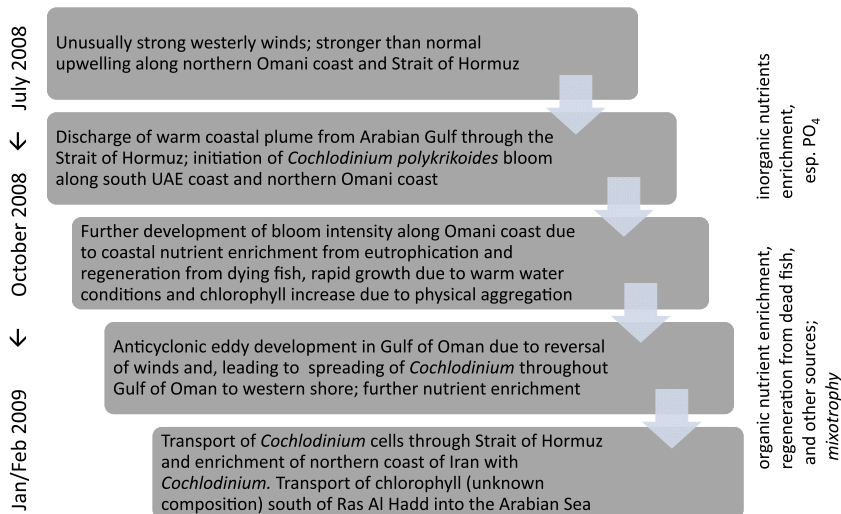
2009 (Fatemi et al. 2012). Note that the Oman, Chesapeake, Narragansett, and NY data include NH_4^+ as well as NO_3^- , while the others only include NO_3^- as the estimate of inorganic N. [Inclusion of NH_4^+ or those sites for which data is unavailable would only serve to further depress the reported ratios]. The dashed line is the Redfield ratio

appears to be associated with waters that are elevated in P but comparatively deficient in inorganic N, especially NO_3^- . Not only do all of these reports show that blooms are associated with nutrients comparatively rich in P, but that their deviation from Redfieldian proportions is considerable. With the exception of one data point, all DIN/DIP ratios in waters from throughout the world were <10 , and in some cases <5 (Fig. 9). The ratios of inorganic N/P during the bloom were, with a single exception, well below Redfield proportion (Fig. 8a), while the molar ratios of organic N/P were generally above 16:1 (Fig. 8b). This would suggest that organic forms of N may have also contributed to the nutrition of the bloom.

While this species has a broad range of capabilities for taking up a range of forms of N, including organic (Mulholland et al. 2009), all comparative data sets that have

reported different forms of N availability (e.g., Tomas and Smayda 2008; Mulholland et al. 2009; Gobler 2010) demonstrate that when blooms are associated with high inorganic N levels, those are in the form of NH_4^+ , not NO_3^- . Moreover, its mixotrophic properties have long been known (Larsen and Sournia 1991; Jeong et al. 2004). Its growth rate has been shown to increase by almost a factor of 2 when growing mixotrophically compared to autotrophically (Jeong et al. 2004). It is thus possible, if not likely, that *C. polykrikoides* was deriving some of its nutrition mixotrophically during the period of its progression. Mixotrophic nutrition is now the “default expectation for photosynthetic protists living in illuminated water” (Flynn et al. 2013) and nutrient or light deficiency is not a prerequisite for this mode of nutrition to be employed (Burkholder et al. 2008; Glibert and Burkholder

Fig. 10 Conceptual schematic of the progression of the *C. polykrikoides* event in 2008–2009 in the Sea of Oman and the Arabian Gulf based on the findings reported herein as well as previous reports (Richlen et al. 2010; Hamzei et al. 2012; Fatemi et al. 2012). The right-hand text suggests potential changes in nutrition that may have occurred during this progression



2011). Moreover, HABs that may be initially promoted by, or associated with upwelling, exhibit mixotrophy and osmotrophy (Kudela et al. 2010). Due to the suite of physical factors at the time, we suggest that *C. polykrikoides* may have been the warmer water substitute for *N. scintillans* which is also strongly mixotrophic, and both may be coastal or offshore manifestations of eutrophication, supplementing their nutrition with nutrients that come “prepackaged” in the form of phytoplankton or other particulates (Harrison et al. 2011).

There is currently very little information on nutrient loads to this coastal region. Yet, it is known that the area is under the influence of a variety of environmental pressures and pollutants that contribute to eutrophication, such as desalination plants, sewage discharge, refineries, and fertilizer factories. Reactive nitrogen deposition over the northern Indian Ocean and Arabian Sea is now recognized to be among the highest in the world (Duce et al. 2008; Naqvi et al. 2010). Locally, dead and dying fish and extensive nutrient regeneration may also have contributed to the high concentrations of NH_4^+ and urea. Little is known of the potential sources of elevated PO_4^{3-} found throughout the region during this extended event and these findings underscore the need for further study on eutrophication of the region. While upwelling may be an important nutrient source for the Sea of Oman during this, and more typical years, the elevated levels of NH_4^+ , urea, and PO_4^{3-} along the Omani coast suggest that nutrients were available in levels that could support eutrophic conditions (Fig. 7).

In conclusion, it is likely that the development of the bloom of *C. polykrikoides* in the coastal waters of Oman was likely facilitated by the mesoscale forcing towards the coastal region-driven reversal of monsoonal periods, while the occurrence and persistence of high densities of *C. polykrikoides* was significantly influenced by an elevated nutrient load and warmer than normal temperatures. We speculate that the progression of this regional event began with stronger than normal upwelling from the SWM along the Iranian coast and northern Omani coast in the Strait of Hormuz (Fig. 10). This was likely followed by discharge of warm coastal plume water from the Arabian Gulf, and together with nutrient discharge (which included enrichment of PO_4^{3-}), the *C. polykrikoides* cells were able to grow rapidly and accumulate along the Omani coast. These blooms intensified, but were also carried in an anticyclonic direction back to the Iranian shore following wind reversal in late October/November and the onset of the NEM. There, they were transported into the Arabian Gulf through the Strait of Hormuz where they affected the coast of Iran for several months into 2009 (as reported by Hamzei et al. 2012; Fatemi et al. 2012). Export of Chl *a* to the Arabian Sea also apparently occurred by January 2009, as seen from the satellite images, but the community composition of this high phytoplankton biomass is not known. Nutritional strategies of these cells, while not investigated herein, but well documented from the literature (e.g., Larsen and Sournia

1991; Jeong et al. 2004; Mulholland et al. 2009), likely included inorganic nutrient uptake, organic nutrient uptake, and mixotrophy as the bloom progressed (Fig. 10).

This study supports the growing conclusion that increasing numbers of blooms of *C. polykrikoides* are associated with nutrient loading, and the diversity of nutritional mechanisms appears to allow them to not only establish under conditions of high nutrient loads, but to be sustained for long periods of time. There is much yet to be understood, however, with regard to the long-term, large-scale patterns of phytoplankton change in the Gulf region, and specifically when and why *C. polykrikoides* can displace *N. scintillans* as the major bloom-former of this region and the sources of nutrients that support these blooms, as well as the differential factors leading to growth of one dominant species over another.

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