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Research Paper

Overview of decadal ecosystem changes in the Western Arabian Sea and the occurrence of algal blooms

[1]Paul J. Harrison, [2*]Sergey Piontkovski, and [2]Khalid Al-Hashmi

نظرة شاملة للتغيرات العِقدية في النظام البيئي لغرب بحر العرب وحدوث ظاهرة ازهرار الطحالب

بول ج هاريسون وسيرجي بوينتكوفسكي وخالد الهاشمي

Abstract. Gradual decadal changes have taken place in the Western Arabian Sea over the last 50 years. Here we syntheses available evidences and reveal the trends pronounced in directly measured and remotely sensed parameters. We show that decadal changes have affected wind speeds, atmospheric and sea surface temperature, thermohaline stratification, shoaling of the oxycline, and dust/iron inputs. A decrease in nitrate supply of the photic layer have caused an increase in annual frequency of harmful algal blooms and fish kills. Along with that, a decrease in diatom biomass and a shift from red *Noctiluca* to green *Noctiluca* during the northeast monsoon was observed during the last two decades, Even though these are the same species they have very different nutritional modes. The red one is a heterotroph with a preference for grazing diatoms, while the green one has a symbiont and thus it is a mixotroph. Recent results suggest that this shift may be caused by the shoaling oxycline since the green *Noctiluca* grows better under low oxygen because the symbiont produces oxygen for its host. The western Arabian Sea is temporally and spatially complex. With the recent advances in remote sensing of the ocean, a further understanding of the mesoscale spatial-temporal variability of *Noctiluca* blooms can be gained through analyzing frequent images with opportunistic ground-truthing.

Keywords: Sea of Oman; western Arabian Sea; monsoons; upwelling; nutrients; HABs

المستخلص: لقد طرأت تغيرات عقدية (كل عشر سنوات) تدريجية على غرب بحر العرب على مدى الخمسين سنة الماضية. هنا نقوم بتجميع الأدلة المتاحة وكشف أكثر الاتجاهات وضوحا في المتغيرات البيئية التي تم قياسها مباشرة وعن بعد. نوضح هنا أن التغيرات العقدية قد أثرت على سرعة الرياح ، ودرجة حرارة الغلاف الجوي ودرجة حرارة سطح البحر, وطبقات الملوحة ودرجة الحرارة ، وضحالة الطبقة المنخفضة الأكسجين , وعلى كمية امدادات الغبار / الحديد. وقد تسبب الانخفاض في امدادات النيترات للطبقة الضوئية في زيادة التكرار السنوي لازهرار الطحالب الضارة ونفوق الأسماك. بالأضافة الى انخفاض في الكتلة الحيوية للداياتومات وتحول ازهرار النكتيلوكا من اللون الاحمر الى اللون الاخضر اثناء الرياح الموسمية الشمالية الشرقية خلال العقدين الماضيين . على الرغم من أنها(النوكتيلوكا) هي نفس النوع الا انا لدى كل واحدة منهما وسائل غذائية مختلفة جدا. فذات اللون الأحمر تكون غيرية التغذية مع تفضيل الدياتومات ، في حين أن ذات اللون الأخضر فتحتوي بداخلها على طحالب تعايش ، وبالتالي تكون مختلطة التغذية. تشير النتائج الأخيرة إلى أن هذا التحول قد يكون ناجمًا عن ضحالة طبقة الماء المنخفضة الاوكسجين حيث أن النوكتيلوكا الخضراء تفضل النمو فو وسط منحفض الأكسجين بسبب ان الطحالب التعايشية تقوم بانتاج الأكسجين لمضيفها. إن غرب بحر العرب معقد من الناحية الزمانية والمكانية ولكن مع التطورات الحديثة في تقنيات الاستشعار عن بعد للمحيطات فانه يمكن الحصول على مزيد من الفهم للتقلبات الزمانية والمكانية لازهرار النوكتيلوكا من خلال تحليل الصور المتكررة والنتائج المأخوذه من البحر مباشرة

الكلمات المفتاحية: بحر عمان, غرب بحر العرب, الرياح الموسمية, التيارات الصاعدة,المغذيات, ازهرار

Introduction

Most areas of the ocean are already responding physically and biologically to anthropogenically induced impacts. Some of the small scale impacts such as eutrophication have occurred more quickly and are easier to understand and quantify in small scale coastal zone studies. However, the dual impacts of increased CO_2, which acidifies the ocean as well as warms the atmosphere and surface ocean are much more complex since they are large scale, evoke relatively slow changes and involve atmospheric as well as oceanic changes and impacts. Our review aimed to synthesize our current understanding of the relationship between long term ecosystem changes and the occurrence of algal blooms as well as other climatic changes that are occurring in the Sea of Oman and the western Arabian Sea.

How the Western Arabian Sea Ecosystem Functions

About 50 years ago, the International Indian Ocean Expedition was launched to explore one of the last great frontiers in the ocean. Yet 50 years later, the Indian Ocean remains one of the most poorly studied and

[2*]**Sergey Piontkovski** (✉) spion@squ.edu.om. [1]Dept. Earth & Ocean Sciences, Univ. British Columbia, Vancouver, BC, Canada V6T 1Z4.
[2]College of Agriculture & Marine Science, Sultan Qaboos University, Al-Khod 123, Oman

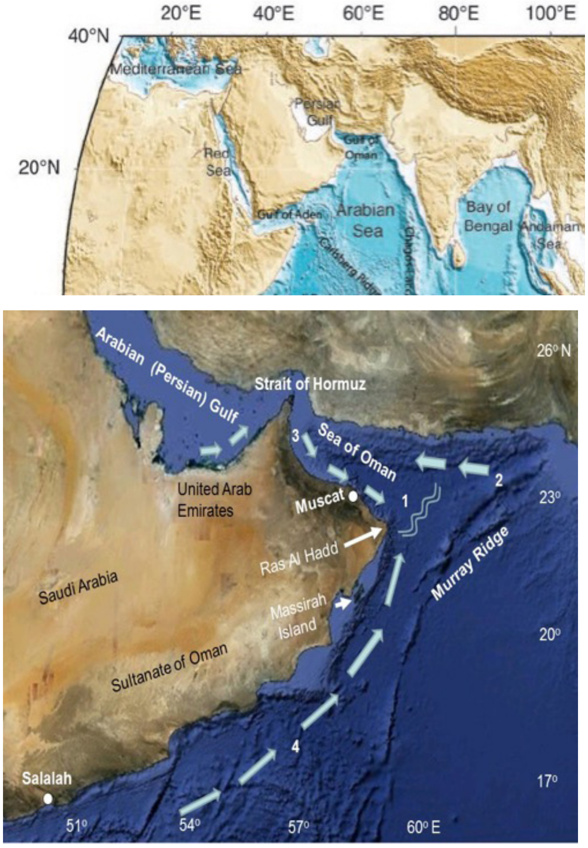

Figure 1. Top panel: Map of the Arabian Sea as a small NW section of the Indian Ocean, bounded by Oman and Somalia on the west and Indian on the east (from Etopo 2 bathymetry data from NOAA NGDG . Bottom Panel: The system of currents and water mass transport along the Omani coast. Background image: three-dimensional bathymetric map (www.earth.google.com). Two parallel lines: (1) demarcate the location of the Ras Al Hadd frontal zone formed by the confluence of currents (3 and 4). Arrows (2-4) indicate direction of the main currents in summer through the fall period. (2): inflow of the Indian Ocean Water mass, (3): outflow of the Arabian (Persian) Gulf Water mass, and (4): Oman Coastal Current.

overlooked regions in the world's ocean (Hood et al. 2015). Since the Arabian Sea is a relatively small basin in the northwest corner of the Indian Ocean bounded by Oman and Somalia on the west and India on the east it should be possible to intensify International efforts in the future (Fig. 1).

The Arabian Sea (AS) is one of the world's most productive oceanic areas, yet it is one of the least studied Large Marine Ecosystems (LEMs) (Naqvi et al. 2010; Hood et al. 2015; Piontkovski and Queste 2016). Therefore, it is difficult to obtain historical records of decadal time series of various parameters in order to assess climate change impacts. Oceanographic research in the Indian Ocean has lagged the Atlantic and Pacific Oceans. Yet, the AS has many unique characteristics such as intense upwelling, high productivity, predicable monsoon winds with reversing pattern, the world's largest scale hypoxia in deep waters and large dust inputs that deliver iron that make it ideal for testing various hypotheses. Wiggert et al. (2005; 2006) provide an excellent comprehensive historical review of the evolution of our understanding of monsoon-driven biogeochemical processes in the AS. Navqi et al. (2010) provide a summary of the biogeochemical processes during the late Southwest Monsoon (SWM) and Smith (2001) provides a summary of the 1994-96 Joint Global Ocean Flux Study (JGOFS) for the Arabian Sea region.

A small section of the northwest corner of the AS is called the Sea of Oman (or Gulf of Oman) (Fig. 1). Geographically, it is a strait connected to the Arabian Gulf (Persian Gulf) on the west and the western AS to the east and south. During the Northeast Monsoon (NEM) in winter (from December to March), surface waters are dominated by oceanic water which flows in along the Iranian coast accompanied with some upwelling. In contrast, in summer (in June to September), during the Southwest Monsoon (SWM) high salinity, low oxygen Arabian Gulf water flows out, producing a strong salinity front where this water meets the less saline surface water of the Sea of Oman and eddies are also produced (Piontkovski et al. 2012a). A frontal zone forms near the eastward promontory of the Ras Al Hadd in summer and roughly separates the Sea of Oman from the larger AS (Fig. 1).

The AS reverses its geostrophic circulation seasonally, due to the reversing monsoon wind which drives highly energetic currents and the formation of mesoscale eddies. The strength of the monsoon winds is regulated by the thermal gradient that develops from the differential heating of the land and ocean. During the SWM in summer, the heating of the Eurasian land mass produces a low pressure area and an accompanying high pressure over the ocean which gives rise to southwesterly winds which blow off Somalia, Yemen and Oman. These very strong winds are known as the Findlater jet and they produce intense upwelling off the central and southern coast of Oman. In addition to coastal upwelling, processes such as wind-mixing, lateral advection, Ekman pumping, mesoscale eddies and filaments also play an important role in supplying nutrients to the euphotic zone during summer (Piontkovski and Nezlin 2012; Piontkovski and Al-Jufaili 2013). The Ekman transport can transport chlorophyll offshore along with eddy formation. The most powerful current feature in the AS during the SW monsoon is an extension of the northward flowing Somali Current. At the eastern most point of Oman (Ras Al Hadd), this current veers abruptly offshore, forming the Ras Al Hadd jet or front (Fig. 1). At the northern boundary of a large anti-cyclonic eddy north of the Ras Al Hadd jet/front, a cyclonic eddy forms and it has higher concentrations of nutrients and chlorophyll (Piontkovski et al. 2012a, b: Piontkovski and Nezlin 2012). The counter-clockwise eddies are

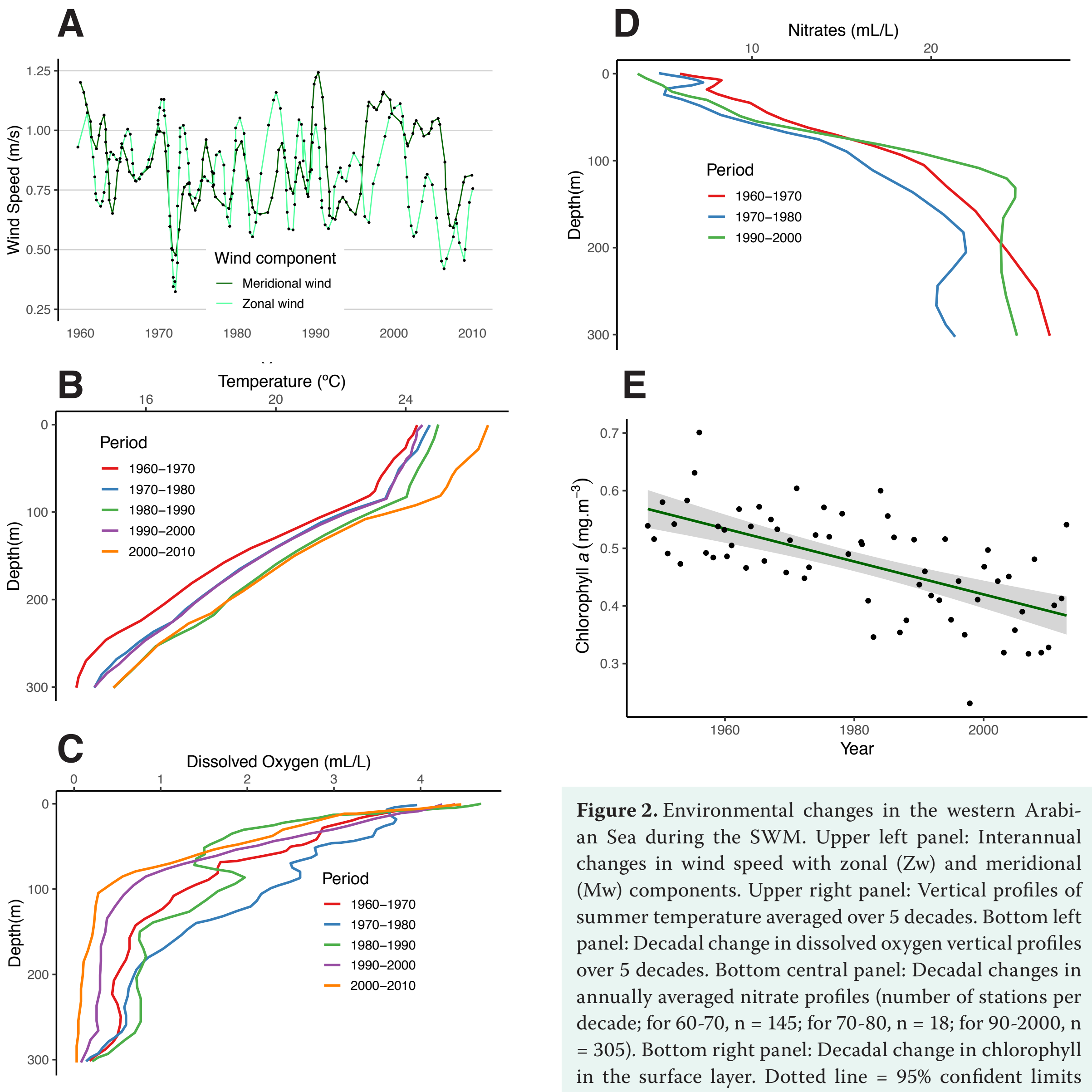

Figure 2. Environmental changes in the western Arabian Sea during the SWM. Upper left panel: Interannual changes in wind speed with zonal (Zw) and meridional (Mw) components. Upper right panel: Vertical profiles of summer temperature averaged over 5 decades. Bottom left panel: Decadal change in dissolved oxygen vertical profiles over 5 decades. Bottom central panel: Decadal changes in annually averaged nitrate profiles (number of stations per decade; for 60-70, n = 145; for 70-80, n = 18; for 90-2000, n = 305). Bottom right panel: Decadal change in chlorophyll in the surface layer. Dotted line = 95% confident limits (from Piontkovski and Queste 2016).

associated with offshore transport, while the clockwise eddies may transport blooms onshore. The injection of nutrients into the surface waters produce the highest chlorophyll concentrations during the year which gives rise to a rich fishery of small pelagics, in particular myctophids that escape predation by hiding in the oxygen minimum one during the day (Piontkovski et al. 2013). In winter, the Eurasian land mass cools and produces a high pressure area and consequently a switch to northeast winds. There is considerable interannual variability in the strength of the winds because when there is more snow cover, the pressure gradient between the land and the ocean increases and the winds are stronger (Goes et al. 2005). These cool dry winds are not as strong as the SEM winds, but the accompanying cooling of the surface waters promotes deep convective mixing of nutrients from depth and a subsequent increase in chlorophyll, but about 50% less than during the summer months (Piontkovski et al. 2011) During the spring inter-monsoon (March–May) these waters are largely oligotrophic with very low chlorophyll concentrations, whereas the fall inter-monsoon (September–November) represents the tapering phase of the very high summer chlorophyll concentrations (Piontkovski et al. 2011).

Decadal Changes in Ecosystem Drivers

Over the last several decades, the parameters that influence the functioning of the ecosystem have been changing. The AS is experiencing a regional climate shift, with substantial warming especially after about 1995. Surprisingly, Sarma et al. (2013) observed that the warming was more rapid off the southern Omani coast than in the

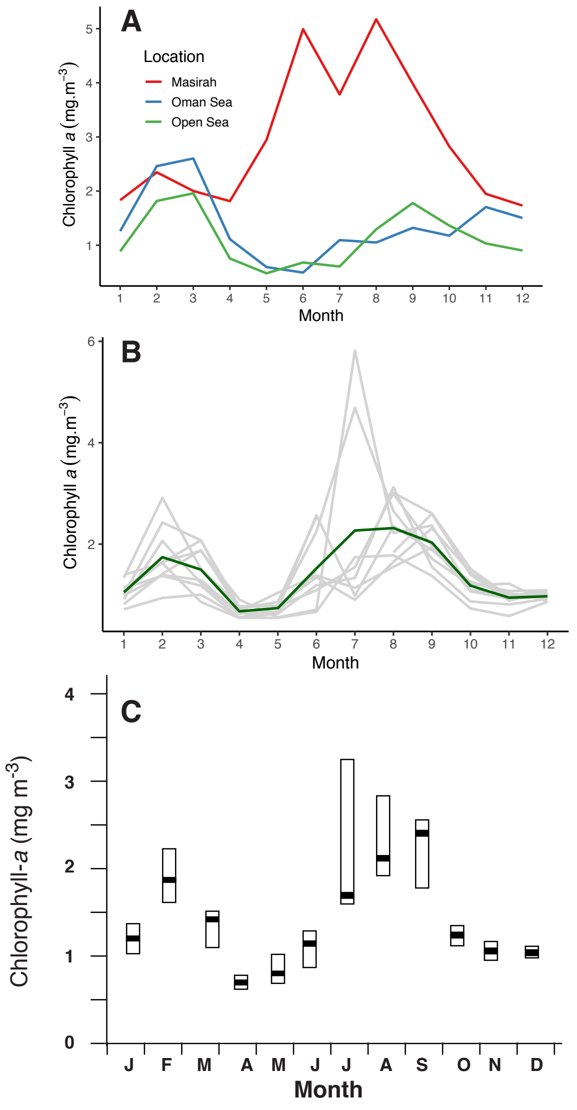

Figure 3. (A) Seasonal change in chlorophyll determined from SeaWifs data from 1998-2008. GOM = Gulf (Sea) of Oman; OS = open sea region; MS = Missirah (see Fig. 1). (from Piontkovski et al. 2011). (B) Interannual variability in the seasonal cycle of remotely sensed SeaWifs chlorophyll from 1998-2007 for the western Arabian Sea (mean is darker) and (C)averaged chlorophyll seasonal cycle (from Piontkovski and Nezlin 2012).

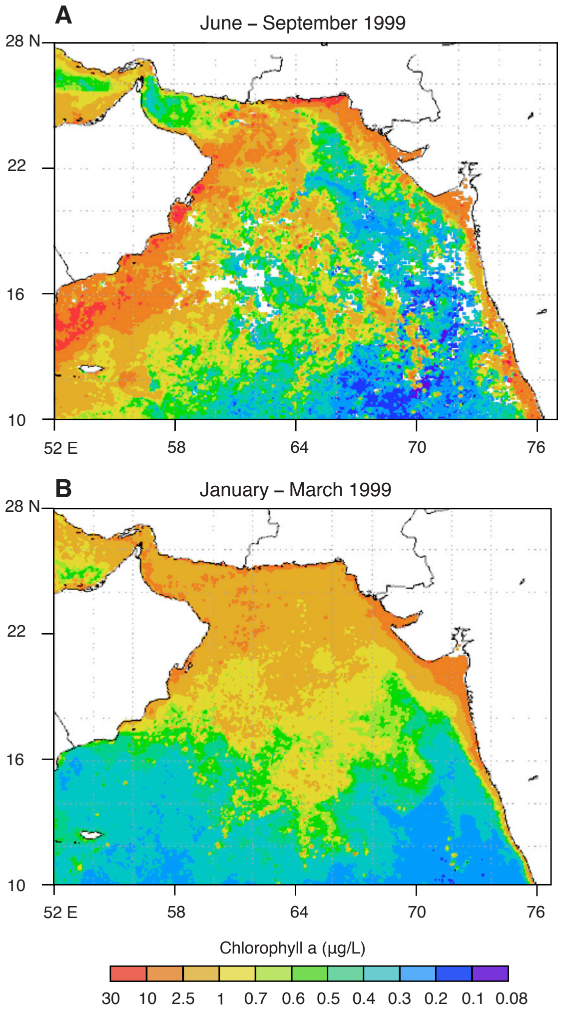

Figure 4. Satellite average chlorophyll concentrations for the months of (A) June to September (SWM) and (B) January to March (NEM) (from Piontkovski et al. 2013).

Sea of Oman from 1961 to 2010. There has been a 5-fold increase in intense cyclones (Kumar et al. 2007, 2010). Even though the AS has not been as well studied as many other areas, Piontkovski and Queste (2016) were able to find a relatively large amount of historical data. They obtained over 29,000 vertical profiles from mainly USA and UK cruises and determined many significant decadal changes over the last 50 years (1960-2010). They found that a decline in wind speed was influenced by the reduction in the Siberian High atmospheric anomaly (Fig. 2A). The increase in the atmospheric temperature caused an increase in the sea surface temperature (SST) of about 0.2°C/decade or 2.3°C from 1950 – 2010 and an increase in salinity in the top 300 m (Fig. 2B). This increase in thermohaline stratification due to surface warming resulted in a shoaling of the oxycline (Fig. 2C). The 1 ml L^{-1} oxygen concentration shoaled from 145 to 80 m (Banse et al. 2014; Piontkovski and Queste 2016). In addition, the Arabian Gulf water that enters the Sea of Oman at 150 to 300 m has less oxygen than in previous decade. The nitracline has shoaled and nitrate in the surface waters decreased by 30% (Fig. 2D). Changes in these physical and chemical parameters led to a decrease in chlorophyll Fig. 2E), a reduction in primary productivity, and a decline in sardine landings (Piontkovski and Queste 2016). Lower oxygen, partially due to warmer water, caused a nearly a 3 times increase in fish kills and likely some habitat compression due to the shoaling of the oxycline (Piontkovski et al. 2011; Harrison et al. in press). There was an increase in acidification, especially in the deeper waters, in part due to the decrease in pH of the deep water flowing in from the Arabian Gulf (Piontkovski and Queste 2016).

Since nitrate has shown a significant decadal decrease, it is possible that silicate may be decreasing also. Wyrtki (1971) noted that surface silicate concentrations were low compared to other oceans. Morrison et al. (2001) also suggested that Si may be limiting since N:Si ratios in the SWM water were often >2:1, whereas a 1:1 ratio indicates balance availability of N and Si. Similarly N:P ratios were frequently <16:1 suggesting that N availability was less than P, possibly because the intense oxygen minimum zone is a major sink for nitrate via denitrification. Because of the interest in denitrification in the Arabian Sea, the main focus of nutrient measurements has been on nitrate and nitrite and much less effort on Si (Naqvi et al. 2010; Ward et al. 2009; Banse et al. 2014). Therefore, more N and Si measurements are needed to determine if N and Si play a dual role in the regulation of diatom blooms. Unfortunately, Piontkovski and Queste (2016) did not determine decadal changes for silicate along with nitrate. Silicate is supplied by the intense summer upwelling over a 200 km band off the Omani coast and is taken up diatoms, the main group of primary producers during the summer upwelling season. However, silicate is exported more rapidly out of the photic zone than nitrogen due to its slower regeneration rate. Nair et al. (1989) reported that biogenic silica collected in moored sediment traps in the northern Arabian Sea, contributed up to 40% of the particle flux in July, primarily as frustules of *Guindardia (Rhizosolenia).* In contrast, in the eastern basin off India, the sediments are relatively devoid of diatom frustules, suggesting that Si may be limiting in this area perhaps due to less intense upwelling. Modeling and measurements of silicate during the JGOFS expedition in the 1990s, also indicated potential silicate limitation, mainly in the eastern basin east from ~66ºE to the western coast of India (Young and Kindle 1994).

Another driver of productivity is iron that is delivered to the ocean as dust (Wiggert and Murtugudde 2007). The canonical thinking that the northern Arabian Sea is invariably iron replete is now being challenged by both model results and recent observational studies (Wiggert and Murtugudde 2007; Moffett et al. 2015). Results indicate that the low iron concentrations (0.3 to 0.5 nM) are strongly modulated by the specific composition of the aeolian mineral deposition. Thus, climate and/or land use influences dust mobilization and composition and may explain the large interannual variability in algal blooms that is frequently observed (Moffett et al. 2015). Dust-enhanced blooms result in a more pronounced shift toward netplankton, and an increase in export flux of up to a 20% during the SWM Monsoon and possible regulation of diazotrophic blooms such as *Trichodesmium* which could be a source of new nitrogen (Moffett et al. 2015)

Moffett et al. (2015) found that the Fe concentration is relatively high in the eastern AS due to the oxygen minimum zone where the reduced form of iron, Fe(II), is dominant. In contrast, in the western Arabian Sea, Fe is low and often limiting during the SWM. The upwelling of nutrients and subsequent advection offshore during the SWM and accompanying Fe addition by dust can represent a large scale fertilization event with increased production up to 1000 km from the coast. In Fe enrichment incubations at sea, chlorophyll increased up to 6-fold for some areas in the central Arabian Sea (but there were no Fe additions for the western AS) with rapid growth of the flagellate *Phaeocystis,* thus confirming Fe limitation for these areas (Moffett et al. 2015). The enhanced depletion of Si relative to N is one of the diagnostics of Si limitation (Takada et al. 2005). Nutrient concentrations during the SWM showed preferential depletion of Si relative to N during the advection of the upwelled water further offshore (Morrison et al. 1999). Takeda et al. (1995) determined that at the beginning of the Northwest Monsoon (NWM), phytoplankton were co-limited by Fe and nitrogen. As the NWM continues, nitrate builds up and the phytoplankton become Fe-limited and therefore, a dust storm could stimulate bloom formation.

Since dust storms and their delayed effects on productivity are difficult to detect due to ship-scheduling uncertainties, various types of satellite data may provide daily information on chlorophyll as well as dust storms. Although episodic dust events are more prevalent in the summer because of the high winds, cloud cover limits satellite observations. Therefore, Banerjee and Kumar (2014) focussed on the winter NWM when nutrients are entrained by convective cooling and deepening of the mixed layer. However, during the NWM, the dust levels are lower than the SWM period, but some dust deposition can still occur in winter due to the Shamal NW winds. They tracked 45 dust storms during the NWM from 2002-2011 and found that only 8 storms produced enhanced chlorophyll. Wiggert and Murtugudde (2007) examined satellite images from the central Arabian Sea (CAS) and concluded that even though the CAS supports low levels of Chl biomass during the winter, the influence of episodic events like dust depositions that supply DFe can periodically turn the CAS into a productive system and account for a large part of the interannual variability within this region. Kumar et al. (2010) examined both summer and winter monsoons and they found little increase in chlorophyll during the summer, but during Sept to the winter, the increase in chlorophyll was more pronounced. Barnali and Mishra (2013) examined satellite data from 2002 to 2012 from Modis Aqua and Tera and SeaWifs and found that after most dust storm events there was an increase in chlorophyll and thus an indication of Fe limitation by phytoplankton in various areas of the AS. So in general, the strength of dust storms might be considered as one of potential drivers of productivity in the region.

Decadal Chlorophyll Responses to Environmental Changes

There are several major upwelling areas in the global oceans that were investigated by the JGOFS program. The AS was a relatively unique site for JGOFS' biogeochemical investigations because of its predictable reversing monsoon winds, intense upwelling, deep convective mixing and their subsequent effect on algal blooms during these two seasonal monsoon periods (Barber et al. 2001; Marra and Barber 2005). The JGOFS group concluded that primary productivity during the SWM off Oman was controlled mainly by mesozooplankton grazing and secondarily by episodic nitrogen limitation and that Fe and light were not limiting. As expected, the SWM period was the most productive at ~123 mmol C m^{-2} d^{-1}, but did not reach its capacity because of the active grazing that kept chl at ~3 mg m^{-3}, nevertheless the chlorophyll-specific productivity was high at >10 mmol C mg Chl^{-1} d^{-1}. The Northeast Monsoon (NEM) productivity was higher than expected at 112 mmol C m^{-2} d^{-1}. The spring intermonsoon productivity was also surprisingly high at 86 mmol C m^{-2} d^{-1}, considering the more oligotrophic conditions and the dominance of picoplankton such as *Synechococcus* and *Prochlorococcus.* In 1995, the annual mean primary productivity was 111 mmol C m^{-2} d^{-1} and was about equal to the North Atlantic spring bloom (Barber et al. 2001).

More recent studies in the coastal upwelling area of the western AS near Massirah Island, found that the seasonal cycle of chlorophyll has two peaks, high concentrations in Aug-Sept and a lesser peak in Feb-Mar which corresponds the end of the SWM and NEM respectively (Fig. 3) (Piontkovski et al. 2011; Piontkovski and Nezlin 2012). In the Sea of Oman, the highest chlorophyll peak of >2 mg m^{-3} occurred during the convective mixing of the NEM, while a smaller peak of 1 mg m^{-3} occurred in the SWM (Fig. 3) (Al-Azri et al. 2010; Piontkovski et al. 2011). In the western Arabian Sea, satellite images of chlorophyll clearly show the higher spatial variability during the SWM (Piontkovski et al. 2013; also see their Table 1) due to upwelling, eddies and filaments compared to the NEM with much less pronounced spatial variability (Fig. 4).

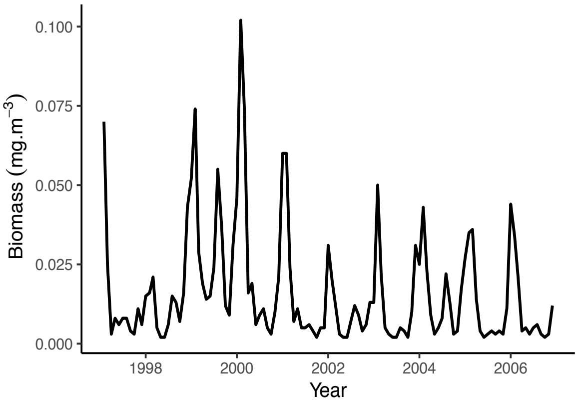

Figure 5. Interannual change in diatom biomass in the Sea of Oman from NOAA Ocean Biogeochemical model (from Piontkovski et al. 2012a).

Goes et al. (2005) suggested that the Arabian Sea was becoming more productive due to the warming of the Eurasian landmass due to the decrease in the snow cover in the Tibetan-Himalayan plateau due to a general warming trend. This was linked to a strengthening of the SWM winds and a subsequent increase in upwelling, increased nutrients and an increase in phytoplankton blooms in the western AS (Gomes et al. 2008; 2010). The increase in chlorophyll reported by Goes et al. (2005) was partially ascribed to a large increase in the abundance of green *Noctiluca scintillans* (*N. miliaris* is no longer the accepted name: see WoRMS website). The increase in chlorophyll was based on a correlation between the increase in sea surface temperature (SST) and chlorophyll during the SWM between 1997 and 2004. However, Goes et al. (2005) only selected a 5º square region (52-57ºE, 5-10ºN), which is only a small section (~1%) of the whole Arabian Sea. Their report stimulated Prakash and Ramesh (2007) to determine if there was a similar increase in chlorophyll in the eastern part of the Arabian Sea between 1997 and 2005, by deriving chlorophyll from monthly SST data. They did not find an increase in the eastern AS and suggested that the increase reported by Goes et al. (2005) was not due to global warming and the heating of the Eurasian land mass. They concluded that any change in the monsoonal intensity because of a contrast in land-sea temperature should affect the NE Arabian Sea more strongly because of its closer proximity to the Himalayan region compared to the southwest AS. In a follow up to the Prakash and Ramesh (2007) analysis, Piontkovski and Claereboudt (2012) analyzed the SST, chlorophyll, and wind speeds during 1997-2009 (12 years) for the whole AS by sub-dividing it into 61, two degree grids. On a basin-wide analysis, chlorophyll did not show the increase that was observed in the single 5o region in the southwest AS that was reported by Goes et al. (2005). This basin-wide analysis agreed with the findings of Prakash and Ramesh (2007) for the northeastern basin of the AS that there was no significant increase in chlorophyll, but there was more interannual variability in the chlorophyll concentration compared to the eastern region (Piontkovski and Claereboudt 2012).

The finding of Goes et al. (2005), has stimulated other satellite oriented investigations for the same period and to consider the effect of the 1998 El Niño and the 1999 La Niña. Liao et al. (2014) found that chlorophyll was lower during the El Niño because of surface warming, increased rainfall and a decrease in winds which weaken Ekman pumping and transport offshore, leading to reduced nutrient supply. Examining data after 2000, Naqvi et al. (2010), Prakash and Ramesh (2007) and Liao et al.

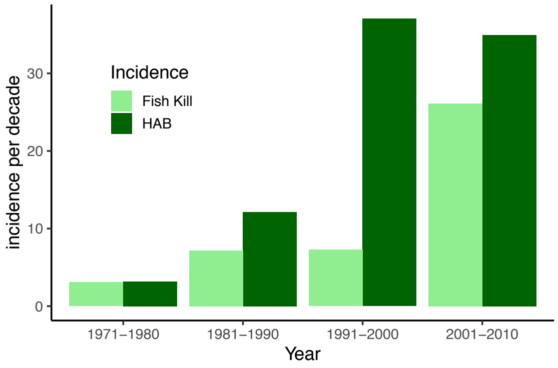

Figure 6. Decadal frequency and relationship between HAB occurrences and fish kills in the Sea of Oman (from Piontkovski et al. 2012a).

(2012) all found a decrease in winds and hence no increase in chlorophyll in the Oman upwelling area during 2004-09, in disagreement with Goes et al. (2005) who found an increase in chlorophyll after 1997. Patra et al. (2007) suggested that the anomalous NE winds during the decline of El Niño reduced the atmospheric input of dust/Fe which could have reduced chlorophyll. Roxy et al. (2016) examined a larger area that included more open ocean (50-65°E and 5-25°N) than Goes et al. (2005) who examined a smaller more coastal area (47-55°E and only 5-10°N) and found a 20% decrease in chlorophyll over the last 6 decades due to surface warming and increased stratification.

Decadal Changes in Harmful Algal Blooms (HABs) Due to Environmental Changes

Piontkovski et al. (2012a) observed a decrease in diatoms and an increase in dinoflagellates (not shown) from 1997- 2006 in the Sea of Oman (Fig. 5) and this change occurred about the same time as the decrease in red *Noctiluca*. More HABs have been observed to occur along the northern area adjacent to the Gulf of Oman possibly because more research has been conducted in this area (Thangaraja et al. 2007; Al-Azri et al. 2012; Al-Gheilani et al. 2012). Another plausible explanation is that bloom development is initiated in the Arabian Gulf and then cells are exported into the Gulf of Oman where further growth occurs. It is not surprising that HAB occurrences peak during the NE and SW monsoon periods due to the injection of nutrients into the surface during the convective mixing in winter and upwelling in summer. The annual frequency of HABs have increased from 1970s to 2010 along with fish kills (Fig. 6).

There are more than a dozen HABs and they are mostly dinoflagellates, but two HABs, red and green *Noctiluca scintillans* and the ichthyotoxic dinoflagellte *Cochlodinium polykrikoides*, make up the bulk of the reports (Al-Azri et al. 2012). There was a huge long-lived *Cochlodinium* bloom in 2008 that caused extensive fish kills, closure of desalination plants and a reduction in tourism in the western Arabian Gulf and the Sea of Oman (Richlen et al. 2010; Piontkovski et al. 2011; Al-Azri et al. 2014). It is surprising that since 2008, large blooms of this species have not re-occurred. This is similar to Korean waters where large annual blooms of Cochlodinium occurred from 1995 to 2007 and since 2008 there has been a sharp decrease in blooms of this species for unknown reasons (Lee et al. 2013). Occasionally the large nitrogen-fixing cyanobacterium *Trichodesmium erythraeum*, the dinoflagellates, *Karenia selliformis* and *Prorcentrum arabianum* and some diatoms also contribute to the blooms (Al-Gheilani et al. 2012).

Red *Noctiluca* is a neritic, heterotrophic dinoflagellate that can often replace copepods as the primary grazer on phytoplankton and has a preference for diatoms, small copepods and even fish eggs (Harrison et al. 2011). *Noctiluca* is less harmful than most HAB species, and any fish kills are usually due to low oxygen during the decomposition of the bloom. *Noctiluca* does have relatively high intercellular NH_4, ranging from 8 nmol per cell (Pithakpol et al. 2000) to 20 mM (Nawata and Sibaoka (1976), but when the bloom decomposes, the NH_4 concentration in the ambient waters ranges from 36 to 80 µM (Montani et al. 1998; Pithakpol et al. 2000), but only in a very thin 5 cm surface layer which is not toxic for most organisms. Hence, previous claims that *Noctiluca* is toxic because of its high intracellular NH_4 concentrations are unfounded. Red *Noctiluca* is generally considered a temperate to sub-tropical species and its optimum temperature range is 17-25°C. Previous to the mid-1990s, the red form of the dinoflagellate *Noctiluca* was abundant and formed frequent blooms in the Sea of Oman and western AS (Al-Azri et al. 2007). Red *Noctiluca* has been observed in the Arabian Sea in the Indus shelf region of Pakistan (Saifullah and Chaghtai, 1990) and on both the east and west coasts of India (Subrahmanyan, 1954) and it geographically overlaps with green *Noctiluca*, but they appear in different seasons (e.g. red *N. scintillans* in winter) or in different water masses as discussed below. In the coastal waters of the northern part of the Arabian Sea bordering Pakistan, red *Noctiluca* occurs during a short period in late winter (Feb and Mar) when water temperatures are 22-24°C. Compared to the Baluchistan shelf west off Karachi, the blooms are more frequent off the Indus Delta shelf due to eutrophication and the subsequent higher productivity and more algal biomass (food supply) in this area (Saifullah & Chaghtai, 1990).

The distribution of green *Noctiluca* appears to be much more restricted and is limited mainly in tropical Asian waters and parts of the AS, Sea of Oman and the Red Sea. In the late 1990s, green *Noctiluca* became dominant off the Omani coast, while red *Noctiluca* declined in abundance (Al-Azri et al. 2012). Even though they are the same species, green *Noctiluca* has a symbiont inside called *Pedinomonas noctiluca*, belonging to the class *Prasinophyceae* (Sweeney 1976). It has its optimum growth rate at a pH of 4.5 to 5.5, which is the intracellular pH of *Noctiluca*. *Noctiluca* has unusually high intracellular NH_4 concentrations (Furuya et al. 2006a; Harrison et al. 2011) and therefore it is not surprising that as a unialgal culture, growth of *Pedinomonas* in the laboratory is fast on NH_4. The amount of the symbiont inside *Noctiluca* varies (Hansen et al. 2004). When the symbiont is abundant, *Noctiluca* is mainly autotrophic and its growth rate in laboratory cultures is lower (~ 0.2 µ d^{-1}), compared to the more mixotrophic/heterotrophic 'feeding strain' that has a higher growth rate of > 0.3 µ d^{-1} (Furuya unpubl. results). These growth rates of green *Noctiluca* fall well below the maximum for most phytoplankton species and its temperature optimum is ~30°C, compared to ~25°C for red *Noctiluca*.

While the appearance of green *Noctiluca* was relatively rapid along the Omani coast, coastal waters of Pakistan (Chagntai and Saifullah 2006), and the western AS (Katti et al. 1988; Prakash et al. 2008; Gomes et al. 2008) in the early 2000s, there were similar reports of its relatively sudden appearance in other tropical/sub-tropical areas. Green *Noctiluca* was first discovered in the Gulf of Thailand in the early 1970s (Sweeney 1976), but in the early 1990s it appeared as massive blooms in Manila Bay, Philippines and in the Gulf of Thailand (Lirdwitayaprasit et al. 2006). In Manila Bay, it replaced the two previously dominant HABs, *Pyrodinium bahamense and Gymnodinium catenatum* and since 2001, it has persisted (Azana and Miranda 2001; Furuya et al. 2006b). In the Gulf of Thailand, there are massive blooms of green *Noctiluca* along with *Ceratium* at the north end of the gulf (Furuya et al. 2006b). It is unknown why massive blooms of green *Noctiluca* appeared in the early 2000s in these three geographically separated areas, but it suggests that there could be a common factor among these three widely separated areas, such as surface warming. In Manila Bay and the Gulf of Thailand, excessive eutrophication may play a role in algal bloom development (Furuya et al. 2006b), but obvious eutrophication impacts are less pronounced along the Omani coast.

Vertical Distribution of HABs: the Overlooked Dimension in Their Distribution

Many algal blooms are only noticed due to marked coloration of the surface waters and then often subsequently sampled to determine the species. Similarly in Hong Kong waters, the government counts the HAB ('red tides) occurrences by confirming fishermen's reports of coloured surface water. Of course this leads to under reporting since sub-surface populations are not detected and in addition, some HABs occur in relatively low concentration at the surface and go undetected (Harrison et al. 2010). George et al. (2013) and Ravichandran et al. (2012) observed a deep chlorophyll maximum at 40-80 m in the AS and suggested that cells in this layer could seed the surface layer along with nutrient enrichment when mixing occurs during the convective overturn during NEM.

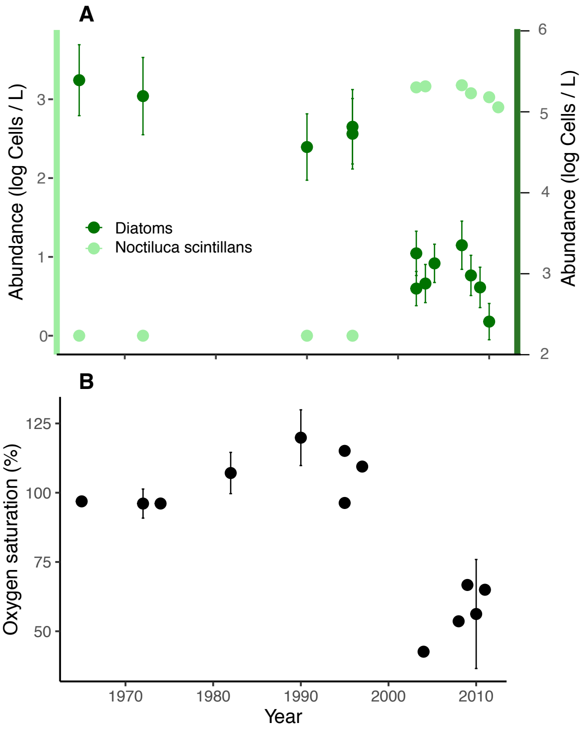

Figure 7. Abundance of *Noctiluca scintillans* and diatoms from 1965 to 2010 in the section of the Arabian Sea from 19-23°N to 64-69°E. B) Percent O_2 saturation in upper 40 m. Bars represent +/- 10% s.e. (from Gomes et al. 2014).

Recent field surveys using sea gliders deployments showed that *Noctiluca* dominated the biomass in the subsurface algal blooms at 25-55 m, which persists throughout inter-monsoon seasons. They may form a seed population and therefore link the chlorophyll maximum to algal blooms that are subsequently initiated during the SW and NE monsoons (Piontkovski et al., submitted). Sampling this subsurface bloom showed a net decrease in *Noctiluca* cell size that is indicative of an actively growing population and illustrated a shift towards a deep chlorophyll maximum adapted community, but no increase in its endosymbiont. Therefore, while HABs may not 'bloom' in the chlorophyll maximum, they do provide a viable seed population that can account for subsequent blooms when they are mixed to the surface during the monsoon periods.

The Arrival of New HABs and Environmental Changes

The most dramatic new arrival is green *Noctiluca*. Until about the mid-1990s, the red heterotrophic *Noctiluca* was dominant, but there has been a gradual shift from the early 2000s to dominance of green *Noctiluca*, a mixotroph with a photosynthetic symbiont called

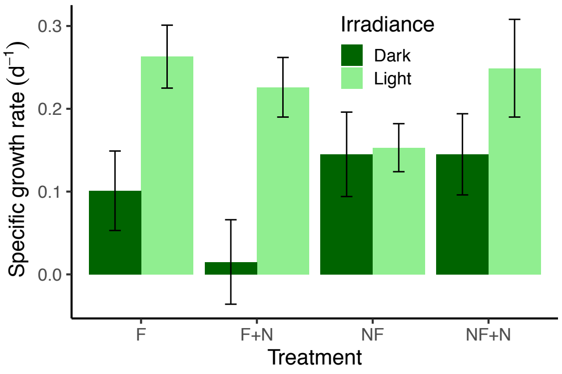

Figure 8. Specific growth rates of *Noctiluca scintillans* incubated for 96 h with food (F) and no food (NF), with or without nutrients (N) in the light and dark. Bars = +/- 1 SD and n = 3 to 8. (from Gomes et al. 2014).

Pedinomonas noctilucae (i.e. carbon fixation plus prey ingestion). During peak blooms, chlorophyll reached 25 mg^{-3} and C-fixation rates of 2 g C m^{-3} d^{-1} at the surface and 12 g C m^{-2} d^{-1} (Gomes et al. 2014). In some large blooms, green *Noctiluca* has replaced the traditional diatom-dominate bloom during the NEM (Fig. 7A). As discussed previously, there are many factors that have changed in the last few decades such as changes in atmospheric pressure, wind speed, warming of the SST, increased stratification, N and especially Si availability/limitation, and iron deposition by dust. Gomes et al. (2008) hypothesized that cyclonic cold core eddies bring up nutrients and low oxygen during the NEM and these factors are responsible for promoting green *Noctiluca* blooms. They observed, along with others that the oxycline was shoaling and thus O_2 was lower in near surface waters Figs. 2C & 7B) (Gomes et al. 2014, Banse et al. 2014; Piontkovski and Al-Oufi 2015; Piontkovski and Queste 2016). In a series of laboratory experiments, Gomes et al. (2014), tested if *Noctiluca*'s symbiont P. *noctilucae* could fix carbon more efficiently under low O_2 than other phytoplankton. In shipboard experiments, these authors observed that green *Noctiluca* had significantly higher C-fixation rates in low O_2 water than other phytoplankton in the size class of <100 μm (see Fig. 4 in Gomes et al. 2014). Gomes et al. (2014) also tested green Noctilca's dual nutrition strategy of photosynthetic C-fixation and facultative heterotrophy (i.e. prey ingestion). They found that growth rates via photosynthetic C-fixation were greater than by phagotrophy (food ingestion in the dark) (Fig. 8). Hence, phagotrophy is a reserve/supplemental mode of nutrition when nutrients and/or light are limiting. Since phagotrophy involves a preference for the ingestion of diatoms, the combined results of faster growth at low O_2 and phagotrophic ingestion of diatoms may explain how *Noctiluca* has been able to replace the previously dominant diatom blooms. Therefore, capturing a symbiont has the dual advantage of having its own organic carbon factory (Hansen et al. 2004) that can operate efficiently under low O_2 because the photosynthetic symbiont can produce O_2 and hence green *Noctiluca* is not as sensitive to low ambient O_2 concentrations as the red *Noctiluca*. A similar symbiont strategy is used by the large diatom *Guiardia (Rhizosolenia)* to cope with oligotrophic conditions in the Equatorial Pacific by hosting a cyanobacteria that fixes N_2 and subsequently providing ammonium for this very large diatom (Villareal 1998).

The massive bloom of the ichthyotoxic dinoflagellate *Cochlodinium polykrikoides* in the Sea of Oman and western AS in 2008 was unexpected since it had not been previously observed in the area (Al-Azri et al. 2014). It had been a regular problem for fish farms off the coast of Korea in the 1990s and early 2000s, in a different temperate environment vs. the tropical Sea of Oman. Kudela et al. (2008) suggested that it appears to be expanding globally. In the Sea of Oman, it was able to outcompete the regularly occurring *Noctiluca*. It has many of the ideal characteristics that allow it to outcompete other phytoplankton. It swims, produces cysts in order to survive adverse conditions, grows slowly (reduced nutrient demand), is a mixotroph (prefers NH_4 and utilized dissolved organic nitrogen), tolerates high temperatures up to ~30ºC and it is not readily grazed (Kudela et al. 2008; Richlen et al. 2010; Kudela and Gobler 2012: Koch et al. 2014; Al-Azri et al. 2014). The suggested environmental conditions that promoted the bloom was the much stronger than normal upwelling (much lower SST) along the Iranian and Omani coasts during the SWM in late summer accompanied by elevated inorganic and organic nutrients. In late October, the discharge of unusually warm surface water that enhanced stratification and setup the optimum conditions for the bloom to form (Al-Azri et al. 2014; Al-Hashmi et al. 2015) and with its mixotrophic capacity, the bloom lasted for many months. Anti-cyclonic eddies have been suggested to have concentrated the bloom by pushing it closer to the shore in the Sea of Oman due to the reversal of the wind direction during the NEM. It is likely that *C. polykrikoides* was able to outcompete *Noctiluca* because it can tolerate temperature to ~30ºC compared to ~25ºC for *Noctiluca*.

Conclusions

The AS is a large physically and biogeochemically complex area to attempt to monitor short and long term changes over large spatial scales. Fortunately, rapid advances have been made in satellite technology and have made it cost-effective to monitor winds, sea surface temperature and a estimation of nutrient inputs from upwelling and mixing, sea surface height anomalies (eddies), aerosols (dust), and chlorophyll (with an estimation of primary productivity) with ground-truthing carried out by HPLC and microscopy (Parab et al. 2006).

Imaging from space offers great potential for determining environmental conditions that trigger algal blooms. These images can complement local in situ measurements (ground-truthing) and provide larger spatial and temporal coverage. The Coastal Zone Color Scanner (CZCS) (Banse and English 2000) and SeaWifs (Banzon et al. 2004) provided images from the late 1970s to 2010. Further advances have been made and Moderate Resolution Imaging Spectroradiometer (MODIS)-Aqua and Terra and well as Medium Resolution Imaging Spectroradiometer (MERIS) provide better resolution of blooms down to 300 m (Zhao et al. 2015). Recently, Cochlodinium blooms have been distinguished from diatoms, *Noctiluca* and *Trichodesmium* blooms using the integration of MERIS fluorescence and particle backscattering data in the Arabian Gulf and the Sea of Oman (Zhao et al. 2015) and Tholkapiyan et al. (2014) and Dwivedi et al. (2015) detected the green *Noctiluca* bloom along the west coast of India. However, phytoplankton biomass and estimates of the AS productivity may be greater than estimated previously through remote sensing observations due to the persistence, intensity, and vertical extent of the deep chlorophyll maximum layer which cannot be accurately measured remotely. Autonomous instruments such as ARGOS profiling floats and/or gliders with physical, chemical and biological sensors have been used to obtain information over large spatial, temporal and vertical scales (George et al. 2013; Ravichandran et al. 2012) and may be necessary for ground-truthing satellite measurements and assessing vertical chlorophyll distribution.

The most intriguing change in HABs has been the shift from red to green *Noctiluca* that forms a massive bloom in the western AS during the NEM. It has been suggested that this shift may be due to the shoaling oxycline. Further studies on long-term succession of the phytoplankton community are needed since keystone species like *Noctiluca* scintillans play an important role in the formation of the trophic structure of a pelagic ecosystem in this region.

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