ARTICLE IN PRESS

Marine Environmental Research xxx (xxxx) xxx–xxx

Contents lists available at ScienceDirect

Marine Environmental Research

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

Potentially harmful microalgae and algal blooms in the Red Sea: Current knowledge and research needs

Zakaria A. Mohamed[1]

Department of Botany and Microbiology, Faculty of Science, Sohag University, Sohag 82524, Egypt

ARTICLE INFO

Keywords:
Harmful algae
Cyanobacteria
Red sea
Phycotoxins
Blooms

ABSTRACT

Harmful algal blooms (HABs) have increased throughout the world's coastal oceans during the last century mostly due to water eutrophication and climate change. These blooms are often accompanied by extreme extensive negative impacts to fisheries, coastal resources, public health and local economies. However, limited studies have reported HAB events in Red Sea coastal waters. This article reviews potentially harmful microalgae in the Red Sea, based on available published information during the last 3 decades. Five harmful algal blooms were recorded in the Red Sea; of which 3 blooms are formed by dinoflagellates (*Noctiluca scintillans*, *Pyrodinuium bahamense*, *Protoperidinium quinquecorne*), one by raphidophytes (*Heterosigma akashiwo*) and one by cyanobacteria (*Trichodesmium erythraeum*). Additionally, mangrove swamps in the Red Sea were occupied by cyanobacterial mats, which contain microcystin and saxitoxin-producing species. The existing data in this review could be a catalyst for the establishment of monitoring and management program for HABs and their toxins in Red Sea coastal waters. This review also identifies current research gaps and suggests future research directions.

1. Introduction

The Red Sea is a semi-enclosed narrow tropical sea separating northern Africa from the Arabian subcontinent (Western Asia), extending from (12.5°N) to about (30°N) over a distance of about 2250 km with an average width of 280 km (Acker et al., 2008). At the northern end, it separates into the Gulf of Aqaba (Eliat) and the Gulf of Suez, which is connected to the Mediterranean Sea via the Suez Canal. At the southern end, it is connected to the open Indian Ocean through the Gulf of Aden, and Arabian Sea via the Strait of Bab-el-Mandeb (Zhai et al., 2011). The Red sea is bordered by seven countries, namely Egypt, Sudan, Eritrea, Yemen, Saudi Arabia, Jordan and Israel. However, the region is sparsely populated, and no more than 5 million people are estimated to live along the coast. The Red Sea is considered as a region of high biodiversity, providing habitats for a wide range of marine organisms (Nassar et al., 2014). It is an oligotrophic sea without reverine inputs (Acker et al., 2008; Raitsos et al., 2015). The nutrients supply in the Red Sea occurs through water intrusion from the Arabian Sea via Bab-el-Mandeb (Churchill et al., 2014; Dreano et al., 2017), the subsurface mixing below the nutricline in the Northern Red Sea (Triantafyllou et al., 2014) or via dust deposition (Brindley et al., 2015). Generally, nutrient concentrations in the southern Red Sea are higher than those in the central and northern regions Acker et al., 2008). The southern part of the Red Sea, therefore exhibits the highest phytoplankton productivity. However, the distribution of nutrients in the entire Red Sea basin is predominantly controlled by eddy circulations pumping of nutrients from subsurface could sustain higher levels of production over a substantial spread of the Red Sea (Zhan et al. 2014; Wafar et al., 2016). Additional nutrients come from pollution caused by numerous industrial and domestic activities including oil spills and excessive loading of nutrients through addition of fertilizers and industrial wastewater and sewage into the Red Sea water (El-Tahera and Madkour, 2014; Nassar et al., 2014; Mustafa et al., 2016). This increase in nutrient concentrations (e.g. nitrate, ammonium, phosphate, and silicate) in seawater promotes the growth of phytoplankton to the extent that algal blooms may occur at the water surface (Raitsos et al., 2013). The rise in temperature due to climate change might also stimulate the proliferation of some phytoplankton species, particularly cyanobacteria (Rigosi et al., 2014; Chaidez et al., 2017). Based on remotely sensed sea surface temperature data from 1982 to 2006, the Red Sea has experienced rapid warming with average increase in annual temperature of 0.74 °C, comparable to the global average of 0.85 °C (Raitsos et al., 2011). Additionally, Chaidez et al. (2017) showed that the overall rate of warming for the Red Sea during the period 1982–2015 is 0.17 °C $decade^{-1}$. The climate warming in the Red Sea seems to be spatially heterogeneous, where the northern Red Sea, particularly the Gulf of Suez and Gulf of Aqaba, is warming faster (0.4 and 0.45 °C $decade^{-1}$) than central and southern regions ((0.1 and

E-mail address: mzakaria_99@yahoo.com.
[1] Tel.: +201141705691; fax: +20934601159.

https://doi.org/10.1016/j.marenvres.2018.06.019
Received 20 October 2017; Received in revised form 27 June 2018; Accepted 27 June 2018

Please cite this article as: Mohamed, Z.A., Marine Environmental Research (2018), https://doi.org/10.1016/j.marenvres.2018.06.019

0.2 °C $decade^{-1}$) (Chaidez et al. (2017). Climate warming may have a twofold impact on phytoplankton growth in tropical marine ecosystems including reduction in phytoplankton abundance and alterations in the timing of seasonal phytoplankton blooms (Gittings et al., 2018). In light of this, climate warming reduced phytoplankton abundance and shortened their bloom time in the northern Red Sea (Gittings et al., 2018). However, the rest of the Red Sea seems to experience higher biomass during warmer climate phases like El Nino (Raitsos et al., 2015). These conditions may favor HABs abundance, and add an extra pressure to the ecosystem especially during El Nino phases. Given that all coastal countries in the world can be affected by HABs (Villacorte et al., 2015), the Red Sea coasts are most likely plagued with HABs. Some of these blooms may be toxic leading to illness and death of marine organisms and humans as well (Anderson et al., 2012). Other blooms are non-toxic, but can cause ecological impacts such as oxygen depletion and damage of fishery resources, besides their impacts on commercial and recreational activities such as beach fouling and retardation of desalination plants (Anderson et al., 2012). There have been many studies concerning phytoplankton populations in the Red Sea. Most of these studies however, have provided information about phytoplankton species composition and community structure in relation to environmental factors (El-Tahera and Madkour, 2014; Ismael, 2015), and only a few studies have focused on harmful algal blooms in the Red Sea (Mohamed and Mesaad, 2007; Mohamed and Al-Shehri, 2012, Alkawri et al., 2016a,b; Banguera-Hinestroza et al., 2016). This paper reviews available information on the occurrence of potentially harmful and/or bloom-forming microalgae in the Red Sea (Fig. 1). This review also identifies research gaps and emphasizes the need for harmful algae monitoring programs in the Red Sea coastal waters.

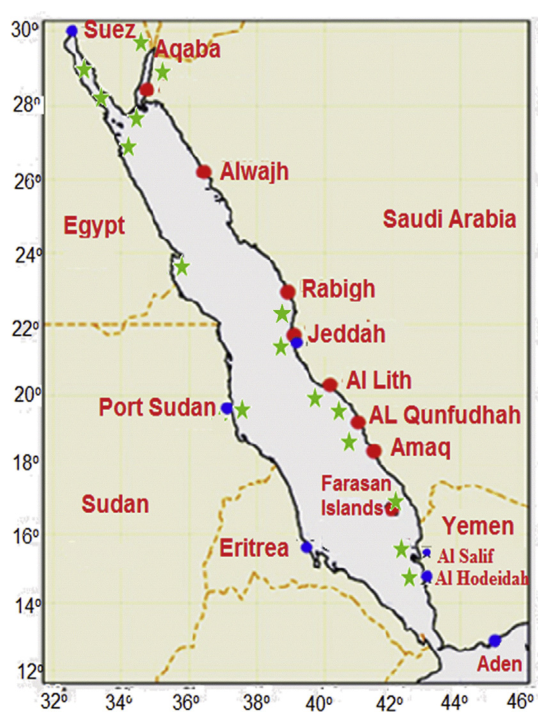

Fig. 1. Distribution map of potentially harmful microalgae in Red Sea coastal waters off different bordering countries. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

2. Occurrence of potentially harmful and bloom-forming microalgae in the Red Sea

2.1. In Egyptian Red Sea waters

Studies on phytoplankton and its productivity in the Red Sea have been carried out since 1900, and several species belonging to different groups (cyanobacteria, dinoflagellates, diatoms, chlorophytes, prymnesiophytes, rhaphidophytes) have been recorded (Ismael, 2015). Furthermore, the name of the Red Sea is attributed to the color of the water, which is thought to be due to red tides of *T. erythraeum* (Hoyt, 1912). Examination of published data from the literature about phytoplankton composition in the Red Sea has revealed the presence of species that have been confirmed as harmful and/or bloom-forming species elsewhere in the world. At Egyptian coasts, many of potentially harmful and bloom-forming species were recorded in the main body of the Red Sea, Gulf of Aqaba and Gulf of Suez. In the main body of the Red Sea, potentially harmful species of the dinoflagellates *Ceratium*, *Protoperidinium*, *Dinophysis* and *Gonyaulax* were recorded in considerable numbers (1–2x 10^3 cells L^{-1}) during spring 2008 at Hurghada and Sharm El-Sheikh coasts (Madkour et al., 2010, Table 1). The harmful diatoms *Pseudonitzschia, Chaetoceros* and *Thalassionema* also dominated phytoplankton population in these sites during winter 2007 (Madkour et al., 2010, Table 1). Recently, harmful species of diatoms (*Chaetoceros, Skeletonema, Proboscia*) and dinoflagellates (*Ceratium furca*) dominated phytoplankton population in Egyptian waters of the main body of the Red Sea at Al-Gemsha, Hurghada, Safaga and Al Qusir regions during winter and autumn 2013, respectively (Nassar et al., 2014). The abundance of such harmful species was correlated with high nutrient concentrations as well as low water salinity in these regions (Nassar et al., 2014). Additionally, potentially harmful dinoflagellates (*C. furca, Dinophysis caudata, Noctiluca miliaris*, *Peridinium cerasus*), Diatoms (*Chaetoceros decipiens, Rhizosolenia alata*) and cyanobacteria (*Oscillatoria limnetica*) were also reported in mangrove ecosystems of the Red Sea at the Southeastern Egypt (Halayib-Shalatin sector), but with low counts (15–117 individual L^{-1}) during summer 2001 (Abel Rahman and Nassar, 2005). Besides harmful dinoflagellates and diatoms, the main body of the Red Sea at Egyptian coasts showed a peak of the toxic cyanobacterium *T. erythraeum* (3×10^3 individual L^{-1}) in summer 2008 (Madkour et al., 2010).

For the Gulf of Aqaba, eutrophication from anthropogenic sources such as sewage and fish farms has contributed significantly to the abundance of potentially harmful algal and cyanobacterial species in the Gulf water (Stambler 2005). A bloom of the potentially toxic cyanobacteria *T. thiebautii* and *T. erythraeum* with $> 10^6$ colonies m^{-3} was detected in the coastal waters of the Gulf during fall 1997 (Post et al., 2002). Similarly, Al-Najjar et al. (2007) reported that *Trichodesmium* spp. showed an increase in the cell density reaching up to 4×10^4 cells L^{-1} during the summer/autumn 1999. In addition to *Trichodesmium*, *Synechococcus* sp. flourished in the Jordanian coasts of the Gulf of Aqaba with a peak (2×10^7 cells L^{-1}) obtained during early spring 1999. A strain of this species isolated from the Salton Sea has been confirmed as toxic with the capability of microcystin production (Carmichael and Li, 2006). Additionally, the prokaryotic *Prochlorococcus marinus* dominated phytoplankton population in the Gulf of Aqaba with concentrations around 2×10^7 cells L^{-1} during the stratified summer period 1999 (Stambler 2005; Al-Najjar et al., 2007). A strain of this species isolated from Sargasso Sea (Atlantic Ocean) was found to produce the neurotoxic nonprotein amino acid, *b*-N-methylamino-L-alanine (BMAA) (Cox et al., 2005). Some potentially harmful diatoms were also recorded in the Gulf water including *Thalassiosira* spp. which was prevalent throughout the year, with maximum concentrations in winter 1999 (1×10^5 cells L^{-1}), and *Chaetoceros* spp. which formed patchy blooms up to 1×10^5 cells L^{-1} in spring 1999 (Al-Najjar et al., 2007). The diatom *Proboscia alata* also dominated the phytoplankton community in the upper 10 m of the Gulf of Aqaba, with

Table 1
Potentially harmful and bloom-forming species of microalgae and cyanobacteria, and their highest recorded concentrations in the Red Sea waters.

Algal group	Country/Coordinates	Season of abundance	Species	Algal concentration (cells L^{-1})	Potential harmful effects	References
Dinoflagellates	Saudi Arabia, Al-Shuqaiq (19°65′N,42°18′E)	Winter 2004, 2005	*Noctiluca scintillans*	3×10^6 (*Bloom)	High biomass (fish kill)	Mohamed and Mesaad 2007
		Spring 2004	*Alexandrium sp.*	920	Saxitoxins, PSP	
			Dinophysis acuta	900	Okadaic acid, DSP dinophysistoxin	
	Saudi Arabia, Jeddah (21°40′N, 39° 10′E)	Spring 2004	*Ceratium dens, C. furca, C.fusus*	310	High biomass (hypoxia)	Touliabah et al., 2010
			Prorocentrum micans	145	Palytoxin	
	Saudi Arabia, Jeddah, lagoon (22°23.7′ N, 39°07.92′ E)	Fall 2013	*Pyrodinium bahamense*	9.9×10^4 (*Bloom)	Saxitoxins, PSP	Banguera-Hinestroza et al., 2016
	Saudi Arabia, inshore reefs (22°17.91′N, 38°58.05′ E)	Spring 2012, 2013	*Gambierdiscus belizeanus*	120 cells g^{-1} algae	Ciguatoxin	Catania et al., 2017
			Ostreopsis sp.	40 cells g^{-1} algae	Palytoxin	
	Egypt, Gulf of Suez (29°57′.2 N, 32°31′.8 E)	Spring 2015	*Ceratium furca*	400	High biomass	Nassar et al., 2016
			C. fusus	136		
		Summer 2014	*Protoperidinium cerasus*	278		
			Prorocentrum hentschelii	400		

*Bloom, indicates that bloom event occurred in the Red Sea coastal waters during that period. Algal concentrations are given in cells L^{-1}, unless otherwise specified. ND, not determined.

Algal group	Country/Coordinates	Season of abundance	Species	Algal concentration (cells L^{-1})	Potential harmful effects	References
Dinoflagellates	Egypt, Gulf of Suez (29° 52′N, 32° 29′E)	Fall 2012	*Ceratium furca*	50	High biomass	Nassar et al., 2015
			C. fusus	50		
			C. tripos	100		
			Prorocentrum micans	50	Palytoxin	
			P. minimum	50	Neurotoxins	
	(29°60′N, 32°31′E)	Fall 2014	*Katodinium* sp.,	ND	Potentially toxic	El Semary, 2016
			Gyrodinium sp.	ND	Potentially toxic	
			Gymnodinium sp	ND	Potentially toxic	
	Yemen, Al Hodeidah coast 15°26′N, 42°57′ E	Spring 2009	*Nictiluca. miliaris*	5.5×10^5 (*Bloom)	High biomass (Fish kill)	Alkershi and Nandini Menon, 2011
	(14°49′N,42°55‴E)	Summer 2012	*Protoperidinium quinquecorne*	14.3×10^6 (*Bloom)	Toxic/Fish kill	Alkawri et al., 2016a
			Gonyaulax verior	3.04×10^3	Yessotoxins	
			Prorocentrum micans	640	Palytoxin (Fish kill)	
	14°48′ N, 42°56′E	Summer 2013	*Pyrodinium bahamense* var. *bahamense*	3.3×10^5 (*Bloom)	Saxitoxins, PSP	Alkawri et al., 2016b
			Dinophysis caudata	650	Okadaic acid, DSP dinophysistoxin, DSP	
			D. acuminata	500	Azaspiracid toxins	
			Protoperidinium quinquecorne	7.7×10^3	Palytoxins	
			Prorocentrum micans	1.84×10^3	High biomass	
			Scrippsiella acuminata	195		

*Bloom, indicates that bloom event occurred in the Red Sea coastal waters during that period. Algal concentrations are given in cells L^{-1}, unless otherwise specified. ND, not determined.

Algal group	Country/Coordinates	Season of abundance	Species	Algal concentration (cells L^{-1})	Potential harmful effects	References

(*continued on next page*)

Table 1 (*continued*)

Algal group	Country/Coordinates	Season of abundance	Species	Algal concentration (cells L^{-1})	Potential harmful effects	References
Dinoflagellates	Yemen, Al Salif, coast 15°19′ N, 42°40′E	Spring, Summer, Fall 2012–2013	*Akashiwo sanguine*	2×10^3	High biomass (hypoxia)	Alkawri 2016
			Alexandrium minutum	3×10^3	Saxitoxins, PSP	
			Dinophysis acuminata	115	Okadaic acid, DSP	
			D. acuta	133	Okadaic acid, DSP	
			D. caudata	1.3×10^3	Okadaic acid, DSP	
			Gonyaulax digitale	2.05×10^3	High biomass (hypoxia)	
			Kryptoperidinium foliaceum	2.26×10^6	High biomass (hypoxia)	
			Prorocentrum compressum	320	High biomass (hypoxia)	
			P.concavum	1.81×10^3	Okadaic acid, DSP	
			P. gracile	240	High biomass (hypoxia)	
			P. lima	96	Okadaic acid, DSP	
			P. micans	1.36×10^3	High biomass (hypoxia)	
			P. minimum	613	High biomass (hypoxia)	
			Protoperidinium quinquecorne	4.75×10^3	High biomass (hypoxia)	
			Scrippsiella acuminate	1.37×10^3	High biomass (hypoxia)	
	Sudan, Port Sudan coast 19°36‴N, 37°13′E	Fall 1986	*Ceratium, Gonyaulax, Peridinium, Prorocentrum*	1×10^5 (mixed species)	Potentially toxic/high biomass	El Hag and Nasr 1989
Diatoms	Egypt, Northern Red Sea harbors 29° 56′ N, 32° 34′ E	Winter 2015	*Asterionellopsis glacialis*	1×10^4	High biomass/hypoxia	Nassar et al., 2016
			Chaetoceros tortissimus	3.3×10^3		
		Autumn 2014	*Proboscia alata*	10×10^3		
		Spring 2015	*Thalassionema nitzschioides*	1.33×10^4		
			Pseudo-nitzschia pungens	1.4×10^3	Domoic acid toxin, ASP	
	Egypt, Gulf of Suez 29 °52′N, 32°29′E	Spring 2013	*Chaetoceros lorenzianus*	100-200 individ. L^{-1}	High biomass/hypoxia	Nassar et al., 2015
			Pseudo-nitzschia pungens	100-200 individ. L^{-1}	Domoic acid toxin	
			Skeletonema costatum	50 individ. L^{-1}	High biomass/hypoxia	
			Proboscia alata	> 200 individ. L^{-1}	High biomass/hypoxia	

*Bloom, indicates that bloom event occurred in the Red Sea coastal waters during that period. Algal concentrations are given in cells L^{-1}, unless otherwise specified. Individ., individual.

Algal group	Country/Coordinates	Season of abundance	Species	Algal concentration (cells L^{-1})	Potential harmful effects	References
Diatoms	Saudi Arabia, Jeddah 21°40′N, 39°10′E	Spring 2004	*Chaetoceros (C. curviselum, C. affine)*	168	High biomass/ hypoxia	Touliabah et al., 2010
			Thalassiossira (T. decipien, T. hyaline)	600		
	Saudi Arabia, Al-Shuqaiq 19°65′N,42°18′E	Spring 2004	*Thalassiossira rotula*	1.1×10^5	High biomass/ hypoxia	Mohamed and Mesaad 2007
			Pseudonitzschia sp.	70	Domoic acid toxin	
	19°80′N,42°18′E	Spring 2010	*Skeletonema* sp.	1.83×10^3	High biomass/ hypoxia	Mohamed and Al-Shehri 2012
	Jordan, Gulf of Aqaba 29°27′ N, 34 °57′	Spring 1999	*Chaetoceros* sp.	4×10^5	High biomass/ hypoxia	Al-Najjar et al., 2007
		Winter 1999	*Thalassiosira* sp.	1×10^5		
	Northeren tip of Gulf of Aqaba 29°28′N, 34°55′E	Summer 1996	*Proboscia alata*	30	High biomass/ hypoxia	Post et al., 2002
	Yemen, Al-Hodeidah coast 14°48′ N, 42°56′E	Summer 2013	*Lithodesmioides polymorphum*	2.93×10^3	High biomass/ hypoxia	Alkawri et al., 2016b
			Chaetoceros sp.	230		
			Rhizosolenia cochlea	1.42×10^4		
			Rhizosolenia setigera	6×10^3		
			Thalassiosira sp.	500		
	14°49′N,42°55′E	Summer 2012	*Lithodesmioides polymorphum*	630	High biomass/ hypoxia	Alkawri et al., 2016a
			Thalassionema nitzschioides	53		
	Sudan, Port Sudan coast 19°36′ N, 37° 13′E	Fall 1986	*Chaetoceros, Nitzschia, Rhizosolenia* (mixed species)	6.8×10^5-1.1×10^6	High biomass/ hypoxia	El Hag and Nasr 1989

*Bloom, indicates that bloom event occurred in the Red Sea coastal waters during that period. Algal concentrations are given in cells L^{-1}, unless otherwise specified.

Algal group	Country/Coordinates	Season of abundance	Species	Algal concentration (cells L^{-1})	Potential harmful effects	References
Raphidophytes	Saudi Arabia, Al-Shuqaiq 19°80′N,42°18′E	Spring 2010	*Heterosigma akashiwo*	4.6×10^7 (*Bloom)	Brevetoxins/fish kill	Mohamed and Al-Shehri 2012
			Chattonella sp.	142	Brevetoxins/fish kill	

(*continued on next page*)

Table 1 (*continued*)

Algal group	Country/Coordinates	Season of abundance	Species	Algal concentration (cells L^{-1})	Potential harmful effects	References
Cyanobacteria	Saudi Arabia, Jeddah 21°40′N, 39° 10′E	Summer 1978 Spring/summer 2004	*Trichodesmium* spp. *Trichodesmium erythraeum, T. hiebautti*	1.6×10^4 4×10^5 3.5×10^5	Saxitoxins	Shaikh et al., 1986 Touliabah et al., 2010
	Saudi Arabia, Al-Shuqaiq 19°65′N,42°18′E	Spring 2011	*Aphanothece elabens* *Calothrix breviarticulata* *Lyngbya majuscula* *Leptolyngbya tenuis* *Oscillatoria accuminata* *O. tenuis*	2.9×10^4 cells cm^{-2} 9×10^3 cells cm^{-2} 1.55×10^4 cells cm^{-2} 2.64×10^4 cells cm^{-2} 1.1×10^4 cells cm^{-2} 2.34×10^4 cells cm^{-2}	Toxic/high biomass	Mohamed and Al-Shehri 2015
	Saudi Arabia, Farasan islands, Jazan 16°40′N,42°00′E	Spring 1990/ Winter2004	*Lyngbya majuscula*	Large mats	Lyngbyatoxins/skin irritants	Hussain and Khoja 1993; Al-Shehri and Mohamed 2007
	16°31′N,42°07′E	Fall 2011	*T. erythraeum*	Bloom patches	Saxitoxins	Kürten et al. (2015)
	Jordan, Gulf of Aqaba 29°28′N,34°55′E	Fall 1997	*T. erythraeum, T. thiebautii*	10^3 individ. L^{-1}	saxitoxins	Post et al., 2002

*Bloom, indicates that bloom event occurred in the Red Sea coastal waters during that period. Algal concentrations are given in cells L^{-1}, unless otherwise specified.

Algal group	Country/Coordinates	Season of abundance	Species	Algal concentration (cells L^{-1})	Potential harmful effects	References
Cyanobacteria	29°27′ N, 34 °57′E	Summer/Fall 1999	*Trichodesmium* sp	4×10^4	Saxitoxins	Al-Najjar et al., 2007
		Early spring 1999	*Prochlorococcus* spp. *Synechococcus* spp	1×10^7 2×10^7	Potentially neurotoxic ND	Al-Najjar et al., 2007
	Egypt, Northern Red Sea harbors 29° 56′ N, 32° 34′ E	Spring 2015	*Oscillatoria* sp.	436 individ. L^{-1}	Neurotoxins/ microcystins	Nassar et al., 2016
	Egypt, Gulf of Suez 29° 52′N, 32° 29′E	Summer 2013	*Trichodesmium erythraeum* *Pseudoanabaena limnetica* *Oscillatoria tenuis* *Lyngbya majuscula*	> 200 individ. L^{-1} > 200 individ. L^{-1} 50-100 individ. L^{-1} 100-200 individ. L^{-1}	Saxitoxins Microcystins Microcystins Lyngyatoxins	Nassar et al., 2015
	Yemen, Al-Hodeidah Coast (14°49′N,42°55‴E	Summer 2012	*Trichodesmium erythraeum*	3.8×10^3	Saxitoxins	Alkawri et al., 2016a
	14°48′ N, 42°56′E	Summer 2013	*T. erythraeum*	1.65×10^4	Saxitoxins	Alkawri et al., 2016b
	Sudan, Port Sudan coast 19°36′ N, 37° 13′ E	Fall 1986	*Trichodesmium* spp.	3.33×10^5	Saxitoxins	El Hag and Nasr 1989

*Bloom, indicates that bloom event occurred in the Red Sea coastal waters during that period. Algal concentrations are given in cells L^{-1}, unless otherwise specified. Individ., individual.

densities of 1×10^5 cells m^{-3} during early spring 1996 (Post et al., 2002). It has been suggested that warmer temperature and increase in nutrient concentrations are the main factors contributing to the dominance of these species in the Gulf water (Post et al., 2002; Al-Najjar et al., 2007). The dinoflagellates, *Dinophysis, Neoceratium* and *Protoperidinium* were found with low concentrations in association with *Trichodesmium* sp. blooms in the Gulf of Aqaba during fall 1997 (Post et al., 2002).

The Gulf of Suez is increasingly exposed to different sources of pollution including agricultural, industrial and domestic wastes, and oil exploration and ship ballasts (Nassar et al., 2015). This pollution increases nutrient concentrations in the Gulf water which eventually accelerate the growth of phytoplankton and harmful algal bloom formation. The phytoplankton community structure in the Gulf of Suez was investigated by several authors who showed variable biodiversity of species to different ecological conditions and different spatial and temporal scales (Nassar et al., 2015). The results of these studies also revealed the presence of potentially harmful algal species in the Gulf water. The potentially harmful dinoflagellates, *Ceratium* sp and *Prorocentrum* sp. (Table 1) were found in both eastern and western coasts of the Gulf with highest densities recorded in Autumn 2006 (Nassar, 2007) and autumn 2012 (Nassar et al., 2015). Meanwhile, the harmful diatoms, *Chaetoceros* spp., *Pseudo-nitzschia pungens, Skeletonema* spp. and *Proboscia* spp. have also flourished in the water of Suez Gulf during spring 2006 and 2013 (Table 1; Nassar, 2007; Nassar et al., 2015). Harmful species of cyanobacteria also showed frequent abundance in the coastal water of the Gulf of Suez. Among these species, *T. erythraeum* showed a peak (7×10^3 individuals L^{-1}) in eastern Gulf coasts during summer 2008 (Madkour et al., 2010, Table 1), but recorded with low counts in summer 2013 (Nassar et al., 2015, Table 1). Other potentially toxic species of cyanobacteria (e.g. *Lyngbya majuscula, Oscillatoria agardhii, O. tenuis, O. formosa, Pseudoanabaena lymnetica*) have also been investigated in both eastern and western coasts of the Gulf of Suez (Nassar, 2007; Nassar et al., 2015, Table 1).

More recently, a study by Nassar et al. (2016) revealed the presence of potentially toxic and bloom-forming dinoflagellate species (*C. furca, C. Fuscus, Protoperidinium cerasus, Prorocentrum hentscheli*) with cell densities ranging from 136 to 400 cells L^{-1} in different harbors along this Gulf. The dominance of these species correlated with high temperature in summer 2014, and with the increase in nutrient concentrations resulting from treated sewage discharge into the Red Sea waters of Suez Bay. In addition to dinoflagellates, harmful diatoms including fish killing non-toxic species (*Asterionellopsis glacialis, Chaetoceros tortissimus, P. alata, Thalassionoema nitzschioides)* and toxic species (*P. pungens*) were also found in these harbors (Nassar et al., 2016). These diatom species showed high abundances (1400–13333 cell L^{-1}, Table 1) in autumn 2014 and spring 2015, in association with highest values of dissolved nitrate (0.170–1.262 μmol L^{-1}). The noxious blooms of nontoxic diatoms cause fish mortality due to anoxic conditions resulting from high cell densities of these species (López-Cortés et al., 2015). Otherwise, these species, even in low densities, may cause obstruction and injuries in fish gills, which stimulate mucus production in the respiratory epithelium, leading to suffocation (Smayda, 2006). On the other hand, domoic acid (DA) toxin produced by diatoms has no toxic effects on fish, but can accumulate in fish tissues with potential transfer to higher trophic levels including humans and causes amensic shellfish poisoning, ASP (Lefebvre et al., 2012). Cyanobacteria were also present in the Gulf of Suez harbors and represented mainly by potentially toxic *Oscillatoria* spp. which has dominated in spring 2015 in correlation with high temperature and high nutrient concentrations (Nassar et al., 2016). In addition to planktonic species, potentially harmful benthic dinoflagellates (*Katodinium* sp., *Gyrodinium* sp. and *Gymnodinium* sp.) were also investigated in the northwestern part (29^0 60\` N and $32^0$ 31\` 67\`\` E) of the Gulf of Suez (Ain Sokhna) (El Semary, 2016). Although the author did not test the toxicity of these species, such benthic dinoflagellates are known to be potentially toxic (Tester et al., 2014). Seven cases of ciguatera poisoning were reported in a costal Egyptian city (Port Said), in which populations may consume fish as a major part of their diet (Abd Elhaleem and Abd Elkarim, 2011). Ciguatera Fish Poisoning (CFP), the most commonly reported seafood nonbacterial disease in the world (Fleming et al., 1998) is due to the accumulation of toxins produced by the benthic dinoflagellate *Gambierdiscus* in fish tissues. Nevertheless, the study of Abd-Elhaleem and Abd-Elkarim (2011) did not define CFP–causing dinoflagellates in coastal waters at this region.

2.2. In Saudi Red Sea waters

The abundance and species composition of phytoplankton in the Red Sea coasts off Saudi Arabia have been largely explored by many authors (Ismael, 2015), but little information is available on harmful algal blooms in this region. The first bloom of dinoflagellates in Saudi Red Sea coasts was observed at southern regions (Al Shuqayq and Gazan) in February 2004 and caused by *N. scintillans* (Mohamed and Mesaad, 2007). The highest cell density of this bloom (3×10 cells L^{-1}) was recorded during February 2004. This species, being heterotrophic, did not correlate with high nutrient concentrations, but such high nutrient concentrations increased the growth of autotrophic phytoplankton which *Noctiluca* may feed on. Therefore, the authors suggested that the increase in *Noctiluca* abundance could be linked to increasing eutrophication, possibly caused indirectly by an increase in prey abundance (Mohamed and Mesaad, 2007). In addition to *N. scintillans*, other potentially harmful phytoplankton species including the diatom *T. rotula*, and the dinoflagellates (*Alexandrium* sp., *Ceratium* sp., *Dinophysis* sp., *Prorocentrum* sp.) were also found in this region (Table 1). These species were abundant in the absence of an *N. scintillans* bloom, but their densities decreased sharply upon the appearance of an *N. scintillans* bloom (Table 1). The negative relationship between the abundance of *N. scintillans* and that of some of the phytoplanktonic species during the present study is indicative of predation by *N. scintillans* on these species, which was confirmed by the presence of cells of these species in the food vacuoles of *Noctiluca* (Mohamed and Mesaad, 2007). At Jeddah coast, the harmful dinofalgellates, *C. furca, C. fusus, C. dens* and *Prorocentrum micans* dominated the spring peak of phytoplankton in 2004 (Touliabah et al., 2010). In addition to dinoflagellates, Jeddah coastal waters exhibited flourishing of the harmful diatoms, *Chaetoceros affine* and *Thalassiossira decipiens* during spring 2004 (Touliabah et al., 2010, Table 1). The high nutrient concentrations due to sewage runoff were the main reason for the dominance of dinoflagellate and diatom species in this area. Banguera-Hinestroza et al. (2016) recorded a bloom of the harmful dinoflagellate *P. bahamense* in a Red Sea lagoon north of Jeddah, Saudi Arabia (22° 23.700 N, 39°07.924 E). The peak of this bloom was recorded in November 2013 (8×10^4 cells L^{-1}), correlating with high temperature at that time of the year. Those authors also demonstrated that *P. bahamense* bloom can produce saxitoxins, and the highest toxin production coincided with the peak and culmination of *P. bahamense* bloom. The potentially harmful algae, *Dinophysis miles* and *Gonyaulax spinifera*, were also encountered, but with low numbers (19500, 3033 cells m^{-3}) in southern Red Sea coasts in the vicinity of the aquaculture facilities at Al Lith area (Kürten et al., 2015, Table 1). More recently, Catania et al. (2017) demonstrated the presence of the toxic benthic dinoflagellates *Gambierdiscus belizeanus* and *Ostreopsis* spp. On *Turbinaria* and *Halimeda* macroalgae in coral reefs off Saudi Red Sea coasts. These species were observed at low cell densities (< 200 cells g^{-1} wet weight algae) and were negatively correlated with seawater salinity. The authors confirmed *G. belizeanus* as a ciguatoxin (CTX) producer, with a maximum toxin content of 6.50×10^{-5} pg $cell^{-1}$, but they did not test the toxicity of *Ostreopsis* sp. However, *Ostreopsis* species were found to produce palytoxin (PTX), and a number of deaths directly associated with the ingestion of PTX contaminated seafood elsewhere in the world (Faimali et al., 2012). Besides dinoflagellate blooms, southern Red Sea coasts of Saudi Arabia have witnessed a large bloom of the harmful raphidophyte *H. akashiwo* during May and June 2010 (Mohamed and Al-Shehri, 2012). The formation of *Heterosigma* bloom was linked to nutrient discharge from a nearby shrimp farm into the study site (Al Shouqiq area). Specifically, the intensity of *H. akashiwo* bloom correlated with high nutrient concentrations, a rise in temperature (up to 24 °C) and a decrease in salinity to below 30‰ at this site (Mohamed and Al-Shehri, 2012). The authors found that only the raphidophyte *Chattonella* was found in association with *H. akashiwo*, while phytoplankton from other groups disappeared during the period of *H. akashiwo* bloom, suggesting that the presence of *H. akashiwo* bloom might have an inhibitory allelopathic activity against other phytoplankton leading to biodiversity loss. Additionally, *H. akashiwo* bloom was found to have haemolytic activity (as determined by erythrocyte lysis assay (ELA) that may cause ichthyotoxicity and mortality in fish in the Red Sea and in shrimp aquacultures (Mohamed and Al-Shehri, 2012). In addition to dinoflagellates and raphidophytes, harmful cyanobacteria were also recorded in the Red Sea at Saudi coasts. *Trichodesmium* spp. dominated phytoplankton at Jeddah coasts and peaked in summer 1978 at the time of maximal stratification and minimal surface water nutrient levels (Shaikh et al., 1986). *T. erythraeum* and *T. thiebautti* have flourished again in Jeddah coastal waters, and attained two peaks in spring and summer 2004 (Touliabah et al., 2010, Table 1). *Trichodesmium* spp. were also found at southern coasts of Saudi Arabia (Al- Shouqiq area) but with low cell numbers (54 cells L^{-1}) at the time of the absence *Heterosigma* bloom in May 2010 (Mohamed and Al-Shehri, 2012). Recently, extensive surface bloom patches of *T. erythraeum* were observed in southern Red Sea of Saudi Arabia, including Al-Lith, Doga and Farasan islands (Kürten et al., 2015). However, the cell densities of this species in these areas were low (91000, 122727, 79268 cells m^{-3}, respectively) because they were calculated based on total water volume (12 m^{-3}) filtered by phytoplankton net towed horizontally parallel to the reef through the surface mixed layer for 10–15 min. Furthermore, Mohamed and Al-Shehri (2015) demonstrated that mangrove swamps in the Red Sea off the southern coast of Saudi Arabia are occupied by cyanobacterial mats residing on plant pneumatophores and surrounding sediments. These mats harbor saxitoxin-producing species (e.g., *L. majuscula*, *Leptolyngbya tenuis* and *Oscillatoria accuminata*) and microcystin-producing species (e.g., *Aphanothece elabens*, *Oscillatoria tenuis* and *Calothrix breviarticulata*) (Table 1).

2.3. In Yemeni Red Sea waters

In the past few decades, harmful algal blooms have been observed and increased drastically in Yemeni coastal waters (Alkershi and Nandini Menon, 2011; Alkawri et al., 2016a). This could be due to high nutrient concentrations received from intermediate water inflow through the Gulf of Aden in the summer (Churchill et al., 2014; Dreano et al., 2016), besides the discharge of large quantities of nutrients from domestic, industrial and agricultural wastes. However, limited scientific studies have documented harmful algal blooms in the Red Sea off Yemeni coasts. The first bloom in Red Sea Yemeni coasts was caused by *Noctiluca miliaris* at Al-Hodeidah during March 2009 (Alkershi and Nandini Menon, 2011). The highest density of this bloom

(5.5×10^5 cells L^{-1}) was recorded at a station where large amounts of remains of slaughtered fishes and wastes from fishing boats are discharged. The second bloom was observed in June 2012 in Khor Al-Khateeb lagoon at the coast of Al Hodeidah. The dinoflagellate *Protoperidinium quinquecorne* contributed most to this bloom, with highest cell number of 1.4×10^7 cells L^{-1} (Alkawri et al., 2016a, Table 1). The *P. quinquecorne* bloom was accompanied by a massive die-off sardine fish (*Sardinella* sp.) observed along Al Hodeidah coast (Alkawri et al., 2016a). The third bloom was caused by the toxic dinoflagellate *P. bahamense* var. *bahamense,* and has been witnessed along the coast of Al-Hodeidah City in August 2013 (Alkawri et al., 2016b). The highest cell density of this bloom (3.3×10^5 cell L^{-1}) was recorded when water temperature was 32 °C and salinity was 37‰. In addition to *P. bahamense* bloom, other toxic and potentially toxic species were also present in Al-Hodeidah coastal waters during the period Nov. 2012–Sep.2013. Among these species, the dinoflagellates (*Dinophysis caudata*, *D. acuminata, P. quinquecorne, Scrippsiella acuminata* and *P. micans)*, the diatoms (*Lithodesmioides polymorphum*, *Cyclotella* sp., *Cocconeis* sp. and *Diploneis* sp.) and the red tide-forming cyanobacterium, *T. erythraeum* were prevalent (Alkawri et al., 2016b, Table 1). It is interesting that these species were found in few cell numbers during *P. bahamense* bloom compared to their higher cell counts in absence of this bloom, suggesting the inhibitory allelopathic activity of *P. bahamense* against other phytoplankton species. Such antagonistic properties of *P. bahamense* may eventually lead to loss of biodiversity in this region. Recently, Alkawri (2016) identified 20 harmful dinoflagellate species in Yemeni waters of the Red Sea at Al Salif coast during the period 2012–2013. Twelve of these species have been assigned as toxin producers (Table 1). The abundance of these species showed seasonal variation, as the lowest values were obtained in winter and the highest ones were in spring. Among toxic dinoflagellates, *Alexandrium* species are known to produce saxitoxins responsible for paralytic shellfish poisoning, PSP (Bazzoni et al., 2015), and *Prorocentrum* species are producers of okadaic acid and its derivatives, responsible of diarrhetic shellfish poisoning, DSP (Sahraoui et al., 2013).

2.4. In Sudanese Red Sea waters

The surface seawaters in Sudanese part of the Red Sea are characterized by high temperature and salinity, weak currents, lack of upwelling and limited freshwater (Triantafyllou et al., 2014; Ali et al., 2018). However, seasonal rainfall can form short-lived streams (Khors). These seasonal streams along with rapid population growth combined with economical and industrial developments represent nutrient inlets into Sudanese coastal waters (Beyer et al., 2015). These conditions favor the growth of harmful microalgae in this region. Nevertheless, a few studies have been made on distribution and abundance of harmful phytoplankton species in Sudanese Red sea coasts. El Hag and Nasr (1989) recorded high population densities of potentially harmful phytoplankton species including the dinoflagellates (*Ceratium* sp., Gonyaulax sp*., Peridinium sp.* and *Prorocentrum* sp.), diatoms (*Chaetoceros* and *Nitzschia*), and cyanobacteria (*Trichodesmium* spp.). Dinoflagellates and diatoms contributed to the highest phytoplankton peaks recorded at most sites studied, but *Trichodesmium* established the highest peaks attained at one site during summer period. In a recent study, Ali (2015) registered potentially toxic phytoplankton species in the Red Sea off Port Sudan coast. The most abundant species in this study are belonging to some genera of dinoflagellates (*Ceratium, Dinophysis, Peridinium, Prorocentrum*), diatoms (*Chaetoceros, Nitzschia, Rhizosolenia*) and cyanobacteria (*T. erythraeum*).

In other countries bordering the red sea such as Eritrea, no information is available on phytoplankton communities.

3. Cysts of potentially toxic dinoflagellate species in the Red Sea

Several species of dinoflagellates (200 out of 2300) produce resistant resting cysts that can be preserved in sediments as a part of their life cycle to ensure the survival through unfavorable conditions (Head, 1996; Matsuoka and Fukuyo, 2003.). About 10% of these cyst-producing species are known to produce toxins and cause harmful algal blooms (Nehring, 1993). Cysts in sediments can germinate under suitable conditions forming motile dinoflagellate cells, and thus initiate algal blooms in the water column (Orlova et al., 2004; Mohamed and Al-Shehri, 2011). Therefore, cysts may indicate the presence of species in the water column, and provide an early warning signal for HABs caused by dinoflagellates (Aydın et al., 2015). Distribution of dinoflagellate cysts has been largely investigated in many coastal areas around the world (Ho et al., 2013). Nevertheless, studies on dinoflagellate cysts in the Red Sea coastal areas remain limited. Mohamed and Al-Shehri (2011) investigated the abundance of dinoflagellate cyst assemblages in surface sediments from south-western Red sea coasts of Saudi Arabia. The authors stated that cyst abundance in south-western Red sea coasts of Saudi Arabia was strongly correlated with sediment characteristics, the highest numbers being recorded in sediments with large contents of organic carbon, silt and clay. Cyst assemblages in this region were dominated by potentially toxic species, including *Cochlodinium polykrikos*, *Prorocentrum minimum*, *Dinophysis acuminata*, *Alexandrium catenella* and *Scrippsiella trochoidea* (Table 2). Recently, Elshanawany et al. (2016) identified 35 taxa of dinoflagellate cysts in sediments of the northern Red Sea and Gulf of Aqaba. Noticeably, most of these cysts are related to potentially harmful and toxic dinoflagellate species including *Gonyaulax spinifera, Gymnodinium nolleri, Lingulodinium polyedrum, Protoceratium reticulatum, Protoperidinium spp.* and *Pyrodinium bahamense,* (Table 2). Those authors recorded a high cyst abundance of mixtrophic dinoflagellates (e.g. *Lingulodinium polyedrum* and *Gonyaulax spinifera*) in the northern Red Sea and Gulf of Aqaba, when their prey of the cyanobacterium *Synechococcus* spp. was found with high cell densities. More research on the distribution of dinoflagellate cysts in the Red Sea coasts is needed to improve understanding of environmental conditions and changes.

Table 2
Occurrence of cysts of potentially harmful dinoflagellates in the Red Sea sediments.

Country	Region/Coordinates	Algal species	Temp (°C)	Salinity	References
Saudi Arabia	Southern Red Sea, Al-Shuqaiq coast 19°65′-19°80′N, 42°18′E	*Alexandrium catenella Alexandrium minutum* *Cochlodinium polykrikoides* *Scrippsiella trochoidea Prorocentrum minimum Dinophysis acuminata* *Cochlodinium spp. Protoperidnium* spp.	17–19	37–39	Mohamed and Al-Shehri 2011
Egypt	Northern Red Sea& Gulf of Aqaba 29°24′ −29°31′N, 34°54′-34°58′E	*Gonyaulax spinifera*	24	40.8	Elshanawany et al., 2016
		Lingulodinium polyedrum	24.5	40.8	
		Protoceratium reticulatum	26	40.1	
		Protoperidinium spp.	24	40.8	
		Pyrodinium bahamense	26	40.1	
		Gymnodinium nolleri	24	40.8	

4. Conclusions, current research gaps and future directions

The available data indicate that many potentially harmful and toxic species of microalgae have spread along the Red Sea coasts. Among these, certain species (e.g. *H. akashiwo, N. scintillans, P. bahamense*, *P. bahamense* var. *bahamense* and *Trichodesmium* sp.*)* were associated with the occurrence of HAB events and have been confirmed to be toxic in the Red Sea region and elsewhere in the world. These data could be the catalyst for the establishment of a monitoring and management program for harmful algal blooms in the Red Sea coastal waters. However, there remain some gaps that require additional and collaborative efforts from researchers and authorities. The majority of studies presented in this review are sporadic describing the seasonal abundance and bloom dynamics of algal species only, ignoring toxins produced by these blooms. It is therefore important to establish collaborative research and monitoring programs on HABs and their toxins at a national governmental level with systematic sampling along the Red Sea coasts at regular time intervals. Indeed, remotely sensed HABs in the Red Sea has never been attempted yet. Therefore, it is also essential to use satellite remote sensing to monitor HABs and coordinate satellite data with *in situ* measurements of marine environmental parameters in the Red Sea (Brewin et al., 2013, 2015; Racault et al., 2015; Dreano et al., 2017). The Red Sea is indeed a highly dynamic environment and its circulation features (eddies, surface currents) can move water masses between the two continents of the Red Sea (> 250 km away) within two weeks (Raitsos et al., 2017). Perhaps the strength of these currents can redistribute HABs in the Red Sea, and future studies are therefore needed to address this issue. Studying the cysts in the sediments of the Red Sea should be broadened to include the coasts of all bordering countries. This assists in mapping the distribution of cysts of harmful dinoflagellate species and provides information about the mechanism of recurrence and spreading of HAB species in the Red Sea. HABs are well known to have public health, fisheries, ecological and societal impacts worldwide (Anderson et al., 2012). Unfortunately, these impacts have not been well quantified and documented in the countries bordering the Red Sea. For example, many die-off fish incidents have frequently occurred in the Red Sea coastal regions, but only one study linked die-off fish to HABs in the Red Sea region (Alkawri et al., 2016a, Table 1). Furthermore, although all microalgae responsible for various types of fish and shellfish poisoning of humans such as PSP, DSP and ASP are present in Red Sea coastal waters, no linked cases of phycotoxin poisoning have yet been verified from eating fish or shellfish collected from the Red Sea. This is probably the result of a lack of knowledge of the general public, vets and physicians about phycotoxins in the Red Sea countries. Misdiagnosis of some phycotoxin poisoning cases may reflect the large gap between environmental toxicologists and the medical community in these countries. Therefore, an effective monitoring and risk management program for the presence of phycotoxins in fish and shellfish collected from the Red Sea waters should be undertaken by experts in multiple fields, such as biology, chemistry, toxicology, medicine and public health. HABs can cause reduction in desalination plants production because of HABs toxin remains in the produced water (Berktay, 2011); and damage to desalination plants by clogging the intake filters and damaging sensitive membrane (Caron et al., 2010); . In extreme cases, HAB events have caused sealing off of the desalination plants held on the Arabian seas, particularly in UAE and Oman (Al Shehhi et al., 2014). Unfortunately, such negative impacts on desalination facilities have not been addressed yet in the Red Sea countries, and a dedicated program is needed to assess the potential impact of HABs on operations of desalination plants along the Red Sea. The presence of harmful dinoflagellates and their cysts in ballast water and sediments of ships has been documented worldwide and has been suggested as one of the dominant vectors responsible for the distribution of invasive species and the global increase of harmful algal blooms in the marine environments (Choi, 2009; Fahnenstiel et al., 2009). This issue has received little attention and is poorly known in the Red Sea region. Therefore, the presence of potentially harmful dinoflagellates in ballast water and sediments should be examined in commercial ships from the Red Sea coasts.

References

Abel Rahman, N.S., Nassar, M.Z., 2005. Preliminary studies on plankton communities associated with the mangrove forest habitats at Halayib-Shalatin Sector, Red Sea, Egypt. Pakistan J. Mar. Sci. 14, 133–144.

Abd-Elhaleem, Z.A., Abd-Elkarim, M.A., 2011. Pattern of food poisoning in Egypt, a retrospective study. J. Pharmacol. Toxicol. 6, 505–515.

Acker, J., Leptoukh, G., Shen, S., Zhu, T., Kempler, S., 2008. Remotely-sensed chlorophyll a observations of the northern Red Sea indicate seasonal variability and influence of coastal reefs. J. Mar. Syst. 69, 191–204.

Ali, E.B., Churchill, J.H., Barthel, K., Skjelvan, I., Omar, A.M., de Lange, T.E., Eltaib, E.B.A., 2018. Seasonal variations of hydrographic parameters off the Sudanese coast of the Red Sea, 2009–2015. Reg. Stud. Mar. Sci. 18, 1–10.

Ali, M.H.M., 2015. Ecological Study on the Phytoplankton in the Sudanese Red Sea Coast (Port Sudan Area). M.Sc. thesis. university of Khartoum.

Alkawri, A., 2016. Seasonal variation in composition and abundance of harmful dinoflagellates in Yemeni waters, southern Red Sea. Mar. Pollut. Bull. 112, 225–234.

Alkawri, A., Morad, Al, Areeki, M.A., Kaid Alsharaby, K., 2016a. The first recorded bloom of *Protoperidinium quinquecorne* and its link to a massive fish kill in Yemeni coastal waters, Southern Red Sea. Plankton Benthos Res. 11, 75–78.

Alkawri, A., Abker, M., Qutaei, E., Alhag, M., Qutaei, N., Mahdy, S., 2016b. The first recorded bloom of *Pyrodinium bahamense* var *bahamense* plate in Yemeni coastal waters off Red Sea, near Al Hodeida City. Turk. J. Fish. Aquat. Sci. 16, 275–282.

Alkershi, A., Nandini Menon, N., 2011. Phytoplankton in polluted waters of the Red Sea coast of Yemen. J. Mar. Biol. Assoc. India 53, 1–6.

Al-Najjar, D., Badran, M.I., Richter, C., Meyerhoefer, M., Sommer, U., 2007. Seasonal dynamics of phytoplankton in the Gulf of Aqaba, red sea. Hydrobiologia 579, 69–83.

Al-Shehhi, M.R., Gherboudj, I., Ghedira, H., 2014. An overview of historical harmful algae blooms outbreaks in the Arabian Seas. Mar. Pollut. Bull. 86, 314–324.

Al-Shehri, A.M., Mohamed, Z.A., 2007. Mass occurrence and toxicity of the cyanobacterium *Lyngbya majuscula* under phosphorus-limited conditions in the Red Sea. Ecohydrol. Hydrobiol. 7, 51–57.

Anderson, D.M., Cembella, A.D., Hallegraeff, G.M., 2012. Progress in understanding harmful algal blooms: paradigm shifts and new technologies for research, monitoring, and management. Annual Review of Marine Science 4, 143–176.

Aydın, H., Yürür, E.E., Uzar, S., Küçüksezgin, F., 2015. Modern dinoflagellate cyst assemblages of Aliağa and Nemrut Bay: influence of industrial pollution. Turk. J. Fish. Aquat. Sci. 15, 543–554.

Banguera-Hinestroza, E., Eikrem, W., Mansour, H., Solberg, I., Cúrdia, J., Holtermann, K., Edvardsen, B., Kaartvedt, S., 2016. Seasonality and toxin production of *Pyrodinium bahamense* in a Red Sea lagoon. Harmful Algae 55, 163–171.

Bazzoni, A.M., Caddeo, T., Pulina, S., Padedda, B.M., Satta, C.T., Sechi, N., Lugliè, A., 2015. Spatial distribution andmultiannual trends of potentially toxicmicroalgae in shellfish farms along the Sardinian coast (NW Mediterranean Sea). Environ. Monit. Assess. 86.

Berktay, A., 2011. Environmental approach and influence of red tide to desalination process in the Middle East region. Int. J. Chem. Environ. Eng. 2, 183–188.

Beyer, J., Staalstrøm, A., Wathne, B.M., Omer, R.K., Ahmed, S.E., 2015. Marine Ecological Baselines and Environmental Impact Assessment Studies in the Sudanese Coastal Zone: a Review. NIVA - The Norwegian Institute for Water Research, The Norwegian Oil for Development Programme.

Brewin, R.J.W., Raitsos, D.E., Dall'Olmo, G., Zarokanellos, N., Jackson, T., Racault, M.-F., Boss, E.S., Sathyendranath, S., Jones, B.H., Hoteit, I., 2015. Regional ocean-colour chlorophyll algorithms for the Red Sea. Rem. Sens. Environ. 165, 64–85.

Brewin, R.J.W., Raitsos, D.E., Pradhan, Y., Hoteit, I., 2013. Comparison of chlorophyll in the red sea derived from MODIS-Aqua and in vivo fluorescence. Rem. Sens. Environ. 136, 218–224.

Brindley, H., Osipov, S., Bantges, R., Smirnov, A., Banks, J., Levy, R., et al., 2015. An assessment of the quality of aerosol retrievals over the Red Sea and evaluation of the climatological cloud-free dust direct radiative effect in the region. J. Geophys. Res. 120, 10862–10878.

Carmichael, W.W., Li, R.H., 2006. Cyanobacteria toxins in the Salton Sea. Saline Syst. 2, 1–13.

Caron, D.A., Garneau, M.E., Seubert, E., Howard, M.D.A., Darjany, L., Schnetzer, A., Cetinic, I., Filtea, G., Lauri, P., Jones, B., Trussell, S., 2010. Harmful algae and their potential impacts on desalination operations of southern California. Water Res. 44, 385–416.

Catania, D., Richlen, M.L., Mak, Y.L., Morton, S.L., Laban, E.H., Xu, Y., Anderson, D.M., Chan, L.L., Berumen, M.L., 2017. The prevalence of benthic dinoflagellates associated with ciguatera fish poisoning in the central Red Sea. Harmful Algae 68, 206–216.

Chaidez, V., Dreano, D., Augusti, S., Duarte, C., Hoteit, I., 2017. Decadal trends in Red Sea maximum surface temperature. Sci. Rep. 7, 8144.

Choi, K., 2009. Risk assessment of ballast water-mediated invasions of phytoplankton: a modeling study. Ocean Sci. J. 44, 221–226.

Churchill, J.H., Bower, A.S., McCorkle, D.C., Abualnaja, Y., 2014. The transport of nutrient-rich Indian Ocean water through the Red Sea and into coastal reef systems. J. Mar. Res. 72, 165–181.

Cox, P.A., Banack, S.A., Murch, S.J., Rasmussen, U., Tien, G., Bidigare, R.R., Metcalf, J.S., Morrison, L.F., Codd, G.A., Bergman, B., 2005. Diverse taxa of cyanobacteria produce _-N-methylamino-L-alanine, a neurotoxic amino acid. Proc. Natl. Acad. Sci. U.S.A.

102, 5074–5078.
Dreano, D., Raitsos, D., Gittings, J., Krokos, G., Hoteit, I., 2016. Southern Red Sea summer phytoplankton blooms regulated by the Gulf of Aden intermediate water intrusion. PLoS One 11, e0168440.
Dreano, D., Triantafyllou, G., Tsiaras, K., Hoteit, I., 2017. Forecasting the ecology of the Red Sea using a cluster of regional 1D marine ecosystem assimilative models. Ocean Dynam. 67, 935–947.
El Hag, A.G.D., Nasr, D.H., 1989. Studies in planktonic populations in Port Sudan coastal area. Sudan J. Sci. 4, 12–26.
El Semary, N., 2016. Benthic dinoflagellates from Red Sea, Egypt: early records. Egypt. J. Aquat. Res. 42, 177–184.
Elshanawany, R., Karin, A.F., Zonneveld, K.A.F., 2016. Dinoflagellate cyst distribution in the oligotrophic environments of the Gulf of Aqaba and northern Red Sea. Mar. Micropaleontol. 124, 29–44.
El-Tahera, A., Madkour, H.A., 2014. Environmental and radio-ecological studies on shallow marine sediments from harbor areas along the Red Sea coast of Egypt for identification of anthropogenic impacts. Isot. Environ. Health Stud. 50, 120–133.
Fahnenstiel, G., Hong, Y., Millie, D., Doblin, M., Johengen, T., Reid, D., 2009. Marine dinoflagellate cysts in the ballast tank sediments of ships entering the Laurentian Great Lakes. Verh Internat Verein Limnol 30, 1035–1038.
Faimali, M., Giussani, V., Piazza, V., Garaventa, F., Corrà, C., Asnaghi, V., Privitera, D., Gallus, L., Cattaneo-Vietti, R., Mangialajo, L., Chiantore, M., 2012. Toxic effects of harmful benthic dinoflagellate *Ostreopsis ovata* on invertebrate and vertebrate marine organisms. Mar. Environ. Res. 76, 97–107.
Fleming, L.E., Baden, D.G., Bean, J.A., Weisman, R., Blythe, D.G., 1998. Seafood toxin diseases: issues in epidemiology and community outreach. In: Reguera, B., Blanco, J., Fernandez, M.L., Wyatt, T. (Eds.), Harmful Algae. Xunta de Galicia and Intergovernmental Oceanographic Commission of UNESCO, Paris, pp. 245–248.
Gittings, J.A., Raitsos, D.E., Krokos, G., Hoteit, I., 2018. Impacts of warming on phytoplankton abundance and phenology in a typical tropical marine ecosystem. Sci. Rep. 8, 2240.
Head, M.J., 1996. Modern dinofalgelate cysts and their biological affinities. In: In: Jansonius, J., McGregory, D.C. (Eds.), Palynology: Principles and Applications 3. American Association of Stratigraphic Palynologists Foundation, pp. 1197–1248.
Ho, S.H., Dhongil1, L., Soung-Yun, P., Seung, H., So-Young, K., 2013. Distribution of dinoflagellate cysts in Yellow Sea sediments. Acta Oceanol. Sin. 32, 91–98.
Hoyt, S.F., 1912. The name of the red sea. J. Am. Orient. Soc. 32, 115–119.
Hussain, M.I., Khoja, T.M., 1993. Intertidal and subtidal blue-green algal mats of open and mangrove areas in the Farasan Archipelago (Saudi Arabia), Red Sea. Bot. Mar. 36, 377–388.
Ismael, A.A., 2015. Phytoplankton of the RedSea. Chapter in Book: The Red Sea. pp. 567–583.
Kürten, B., Khomayis, H.S., Devassy, R., Audritz, S., Sommer, U., Struck, U., El-Sherbiny, M.M., Al-Aidaroos, A.M., 2015. Ecohydrographic constraints on biodiversity and distribution of phytoplankton and zooplankton in coral reefs of the Red Sea, Saudi Arabia. Mar. Ecol. 36, 1195–1214.
Lefebvre, K.A., Frame, E.R., Kendrick, P.S., 2012. Domoic acid and fish behavior: a review. Harmful Algae 13, 126–130.
López-Cortés, D.J., Núñez-Vázquez, E.J., Band-Schmidt, C.J., Gárate-Lizárraga, I., Hernández-Sandoval, F.E., Bustillos-Guzmán, J.J., 2015. Mass fish die-off during a diatom bloom in the Bahía de La Paz, Gulf of California. HIDROBIOLOGICA 25, 39–48.
Madkour, F.F., El-Sherbiny, M.M., Aamer, M.A.A., 2010. Phytoplankton population along certain Egyptian coastal regions of the Red Sea. Egypt Journal of Aquatic Biology and Fisheries 14, 95–109.
Matsuoka, K., Fukuyo, Y., 2003. Taxonomy of cysts. In: Hallegraeff, G.M., Anderson, D.M., Cembella, A.D. (Eds.), Manual on Harmful marine Microalgae Manual and Guides. International Oceanographic Commission of UNESCO, Paris, France, pp. 563–592.
Mohamed, Z.A., Al-Shehri, A.M., 2012. The link between shrimp farm runoff and blooms of toxic *Heterosigma akashiwo* in Red Sea coastal waters. Oceanologia 54, 287–309.
Mohamed, Z.A., Al-Shehri, A.M., 2015. Biodiversity and toxin production of cyanobacteria in mangrove swamps in the Red Sea off the southern coast of Saudi Arabia. Bot. Mar. 58, 23–34.
Mohamed, Z.A., Mesaad, I., 2007. First report on *Noctiluca scintillans* blooms in the Red Sea off the coasts of Saudi Arabia: consequences of eutrophication. Oceanologia 49, 337–351.
Mohamed, Z.A., Al-Shehri, A.M., 2011. Occurrence and germination of dinoflagellate cysts in surface sediments from the Red Sea off the coasts of Saudi Arabia. Oceanologia 53, 121–136.
Mustafa, G.A., Abd-Elgawad, A., Ouf, A., Siam, R., 2016. The Egyptian Red Sea coastal microbiome: a study revealing differential microbial responses to diverse anthropogenic pollutants. Environ. Pollut. 214, 892–902.
Nassar, M.Z., Hamdy, R.M., Khiray, H.M., Rashedy, S.H., 2014. Seasonal fluctuations of phytoplankton community and physico-chemical parameters of the north western part of the Red Sea, Egypt. Egypt. J. Aquat. Res. 40, 395–403.
Nassar, M.Z., Mohamed, L.I., El Sawy, A., 2016. Seasonal variations of phytoplankton and nutrients in the Egyptian harbors of the northern red sea. Int. J. Mar. Sci. 6, 1–17.
Nassar, M.Z., Shams El-Din, N.G., Gharib, S.M., 2015. Phytoplankton variability in relation to some environmental factors in the eastern coast of Suez Gulf, Egypt. Environ. Monit. Assess. 187, 1–18.
Nassar, M.Z., 2007. Species composition and distribution of phytoplankton in the western coast of Suez Gulf. Egypt. Egypt. J. Aquat. Res. 33, 113–132.
Nehring, S., 1993. Mechanisms for recurrent nuisance algal blooms in coastal zones: resting cyst formation as life-strategy of dinoflagellates. In: Sterr, H., Hofstade, J., Plag, H.P. (Eds.), Interdisciplinary Discussion of Coastal Research and Coastal Management Issues and Problems. Lang, Frankfurt, Germany, pp. 454–467.
Orlova, T.Y., Morozova, T.V., Gribble, K.E., Kulis, D.M., Anderson, D.M., 2004. Dinoflagellate cysts in recent marine sediments from the east coast of Russia. Bot. Mar. 47, 184–201.
Post, A.F., Dedej, Z., Gottlieb, R., Li, H., Thomas, D.N., El-Absawi, M., El- Naggar, A., El-Gharabawi, M., Sommer, U., 2002. Spatial and temporal distribution of Trichodesmium spp in the stratified Gulf of Aqaba, red sea. Mar. Ecol. Prog. Ser. 239, 241–250.
Racault, F., Raitsos, D.E., Berumen, M.L., Brewi, R.J.W., Platt, T., Sathyendranath, S., Hoteit, I., 2015. Phytoplankton phenology indices incoral reef ecosystems: application to ocean-color observations in the Red Sea. Rem. Sens. Environ. 160, 222–234.
Raitsos, D.E., Hoteit, I., Prihartato, P.K., Chronis, T., Triantafyllou, G., Abualnaja, Y., 2011. Abrupt warming of the Red Sea. Geophys. Res. Lett. 38, L14601.
Raitsos, D.E., Pradhan, Y., Brewin, R.J.W., Stenchikov, G., Hoteit, I., 2013. Remote sensing the phytoplankton seasonal succession of the Red Sea. PLoS One 8, e64909.
Raitsos, D.E., Yi, X., Platt, T., Racault, M.-F., Brewin, R.J.W., Pradhan, Y., Papadopoulos, V.P., Sathyendranath, S., Hoteit, I., 2015. Monsoon oscillations regulate fertility of the Red Sea. Geophys. Res. Lett. 42, 855–862.
Raitsos, D.E., Brewin, R.J.W., Zhan, P., Dreano, D., Pradhan, Y., Nanninga, G.B., Hoteit, I., 2017. Sensing coral reef connectivity pathways from space. Sci. Rep. 7, 9338.
Rigosi, A., Carey, C.C., Ibelings, B.W., Brookes, J.D., 2014. The interaction between climate warming and eutrophication to promote cyanobacteria is dependent on trophic state and varies among taxa. Limnol. Oceanogr. 59, 99–114.
Sahraoui, I., Bouchouicha, D., Mabrouk, H.H., Hlaili, A.S., 2013. Driving factors of the potentially toxic and harmful species of Prorocentrum Ehrenberg in a semi-enclosed Mediterranean lagoon (Tunisia, SW Mediterranean). Mediterr. Mar. Sci. 14, 353–362.
Smayda, T., 2006. Harmful Algal Bloom Communities in Scottish Coastal Waters: Relationship to Fish Farming and Regional Comparisons – a Review. Diatom Blooms and Fish Mortality. Natural Scotland, Scottish Executive Environment Group, Scotland. pp. 97–99. Available online at. http://www.scotland.gov.uk/Publications/2006/02/03095327/0.
Shaikh, E.A., Roff, J.C., Dowidar, N.M., 1986. Phytoplankton ecology and production in the red sea off Jeddah, Saudi Arabia. Mar. Biol. (Berl.) 92, 405–416.
Stambler, N., 2005. Bio-optical properties of the northern red sea and the Gulf of Eilat (Aqaba) during winter 1999. J. Sea Res. 54, 186–203.
Tester, P.A., Kibler, S., Holland, W., Usup, G., Vandersea, M., Leaw, C.P., Teen, L.P., Larsen, J., Mohammad-Noor, N., Faust, M.A., Litaker, R.W., 2014. Sampling harmful benthic dinoflagellates: comparison of artificial and natural substrate methods. Harmful Algae 39, 8–25.
Touliabah, H.E., Abu El-Kheir, W.S., Kuchari, M.G., Abdulwass, N.I.H., 2010. Phytoplankton composition at Jeddah coast—red Sea, Saudi Arabia in relation to some ecological factors. J. King Abdulaziz Univ. - Sci. 22, 115–131.
Triantafyllou, G., Yao, F., Petihakis, G., Tsiaras, K.P., Raitsos, D.E., Hoteit, I., 2014. Exploring the Red Sea seasonal ecosystem functioning using a three-dimensional biophysical model. Journal of Geophysical Research:Oceans 119, 1791–1811.
Villacorte, L.O., Tabatabai, S.A.A., Anderson, D.M., Amy, G.L., Schippers, J.C., Kennedy, M.D., 2015. Seawater reverse osmosis desalination and (harmful) algal blooms. Desalination 360, 61–80.
Wafar, M., Qurban, M.A., Ashraf, M., Manikandan, K.P., Flandez, A.V., Balala, A.C., 2016. Patterns of distribution of inorganic nutrients in Red Sea and their implications to primary production. J. Mar. Syst. 156, 86–98.
Zhai, L., Platt, T., Tang, C., Sathyendranath, S., Walls, R., 2011. Phytoplankton phenology on the Scotian Shelf. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 68, 781–791.
Zhan, P., Subramanian, A., Yao, F., Hoteit, I., 2014. Eddies in the Red Sea: a statistical and dynamical study. J. Geophys. Res. 119, 3909–3925.