



ELSEVIER

Contents lists available at SciVerse ScienceDirect

Continental Shelf Research

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

Research papers

Phytoplankton along the coastal shelf of an oligotrophic hypersaline environment in a semi-enclosed marginal sea: Qatar (Arabian Gulf)



Antonietta Quigg^{a,b,*}, Mohsin Al-Ansi^c, Nehad Nour Al Din^d, Chih-Lin Wei^{b,1}, Clifton C. Nunnally^{b,2}, Ibrahim S. Al-Ansari^e, Gilbert T. Rowe^{a,b}, Yousria Soliman^e, Ibrahim Al-Maslamani^e, Ismail Mahmoud^c, Nabihia Youssef^c, Mohamed A. Abdel-Moati^d

^a Department of Marine Biology, Texas A&M University at Galveston, Galveston, TX 77553, USA

^b Department of Oceanography, Texas A&M University, College Station, TX 77843, USA

^c Environmental Studies Center, Qatar University, P.O. Box 2713, Doha, Qatar

^d Ministry of Environment, P.O. Box 39320, Doha, Qatar

^e Department of Biological and Environmental Science, Qatar University, Doha, Qatar

ARTICLE INFO

Article history:

Received 30 October 2012

Received in revised form

9 February 2013

Accepted 3 April 2013

Available online 17 April 2013

Keywords:

Qatar

Arabian (Persian) Gulf

Phytoplankton biomass

Primary production

Community composition

Nutrient enrichment bioassay

ABSTRACT

Phytoplankton biomass (chlorophyll *a* concentration), primary production, abundance, species diversity and species groupings were measured in the coastal waters surrounding Qatar (Arabian Gulf) at 13 stations in February 2010, July 2010, February 2011 and May 2011. In addition, a broad suite of physico-chemical characteristics were measured: temperature, salinity, pH, dissolved oxygen, turbidity, and nutrients (dissolved and particulate). Waters surrounding the Qatari peninsula were found to be highly diverse (125 species of diatoms, dinoflagellates and cyanobacteria were identified) but were low in both biomass (0.18–2.19 $\mu\text{g Chl } a \text{ l}^{-1}$) and productivity (0.14–0.97 $\text{mg C m}^{-2} \text{ day}^{-1}$). Phytoplankton physiology (F_v/F_m , σ_{PSII} , τ_{QA} , p) revealed acclimation strategies consistent with phytoplankton populations receiving ample light but insufficient nutrients. The finding of low primary production is consistent with water column nutrient ratios (DIN:P and DIN:Si ratios < 1) and nutrient enrichment experiments in which the addition of nitrate or the addition of near-bottom waters stimulated biomass production of phytoplankton. This study in an oligotrophic, hypersaline semi-enclosed marginal sea is intended to contribute to the growing body of ecological information on this ecosystem functions.

© 2013 Elsevier Ltd. All rights reserved.

1. Introduction

The performance of an ecosystem depends on its ecological integrity or 'health', defined as the ability to support and maintain a balanced, integrated composition of physico-chemical habitat characteristics, as well as biotic components on temporal and spatial scales (Roux, 1999). Globally, many coastal and estuarine ecosystems are under increased pressure from eutrophication associated with urbanization and industrialization (Howarth and Marino, 2006), shipping and ballast discharge (Steichen et al., 2012), and development from the petroleum and other offshore industries (Sheppard et al., 2010). Concurrently, the demands for ecosystem services (e.g., fisheries, tourism) are increasing,

arguably nowhere more than in the Arabian (Persian) Gulf (hereafter Gulf) in recent years. Understanding phytoplankton dynamics (abundances, biomass, productivity and species diversity and composition), is key to determining the current health of an ecosystem. Increased frequency, magnitude and duration of harmful algal blooms are indicative of decreased water quality (Anderson et al., 2012); consequences of which include, but are not limited to, fish kills (Thronson and Quigg, 2008), inability to use water for desalinization (Richlen et al., 2010; Sheppard et al., 2010), alterations to higher trophic levels as a result of a change in food source and supply (Granéli and Turner 2006; Anderson et al., 2012; Dorado et al., 2012).

Phytoplankton community structure in the Gulf (Fig. 1a and b) was reviewed by Subba Rao and Al-Yamani (1998). These authors found a north to south gradient in the distribution of phytoplankton. The Shatt Al-Arab estuarine waters in the north have low species diversity (< 116), high biomass ($\sim 94 \mu\text{g Chl } a \text{ l}^{-1}$) and high production ($\sim 3181 \mu\text{g C l}^{-1} \text{ h}^{-1}$). Nearby in Kuwait, species diversity is higher (148) but biomass ($\sim 14 \mu\text{g Chl } a \text{ l}^{-1}$) and production ($\sim 867 \mu\text{g C l}^{-1} \text{ h}^{-1}$) is lower. To the south, in the Gulf of Oman and Strait of Hormuz, were the gulf opens to the ocean, the

* Corresponding author at: Department of Marine Biology, Texas A&M University at Galveston, Galveston, TX 77553, USA. Tel.: +1 409 740 4990; fax: +1 409 740 5001.

E-mail address: quigga@tamug.edu (A. Quigg).

¹ Present address: Ocean Science Centre, Memorial University of Newfoundland, St. John's, NL, Canada A1C 5S7.

² Present address: Department of Oceanography, University of Hawaii, Honolulu, HI 96822, USA.

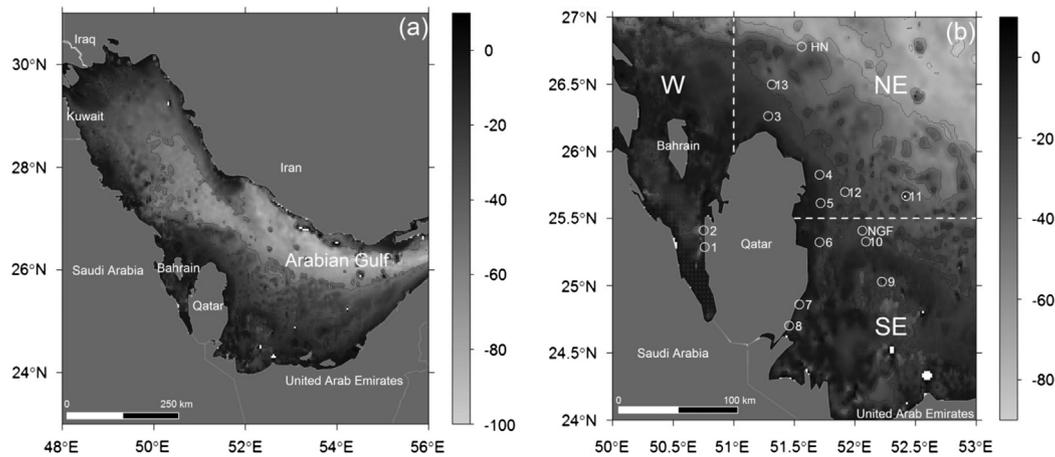


Fig. 1. (A) The Gulf, Shatt Al-Arab to Gulf of Oman region and (B) sampling locations around Qatar. St. 1 through St. 13 were sampled in February 2010, July 2010, February 2011, and May 2011. The sampling area was divided into west (stations 1 and 2), northeast (stations 3–5, 11–13), and southeast (stations 6–10) of the Qatar Peninsula with the delineations shown in B.

species diversity is greatest (527) and biomass the lowest ($\sim 1.18 \mu\text{g Chl } a \text{ l}^{-1}$; production not reported). While there is a paucity of published data (that is, not in reports) on primary productivity and diversity of phytoplankton in this region, existing information reveals north to south trends and those driven by particular environmental features (e.g., coastal versus open gulf).

Perhaps then it is not surprising that the first documented toxic algal bloom in the region was reported just over a decade ago (Subba-Rao et al., 1999) with a second shortly thereafter (Heil et al., 2001). In the latter, the authors describe a *Gymnodinium* sp. (dinoflagellate) bloom in Kuwait Bay associated with eutrophication and fish kills. The study highlighted the need for monitoring and research programs in the region that focus on nutrient enrichment, in addition to oil related pollution issues. More recently, from 2008 to 2009, the marine ichthyotoxic dinoflagellate *Cochlodinium polykrikoides* was found responsible for killing thousands of tons of fish and limiting traditional fishery operations in the United Arab Emirates and the Gulf of Oman (Richlen et al., 2010). Indirect consequences of this harmful algal bloom included damage to coral reefs and a reduction in ecosystem services (e.g. lowered coastal tourism). Perhaps, the most important consequence of this bloom was the closure of desalination plants, the primary source of freshwater to the large populations in the countries surrounding the Gulf (Richlen et al., 2010). Recurring significant harmful (toxic) algal blooms will pose a serious threat to the drinking water supply in West Asia (Sheppard et al., 2010).

The coastal marine ecosystem of Qatar's peninsula is a valuable resource for fisheries, tourism, and recreation, but it must coexist with human population growth and investments in expanding natural gas and petroleum industry. Discharges from coastal dredging operations, effluents from power and desalination plants, petrochemical industries, expansion of harbor and port facilities, increased shipping and associated ballast water, farming operations (e.g., dairy, slaughter houses) and sewage treatment plants multiply the stress on this unique ecosystem (Ibrahim and El Samra, 1987; Jacob and Al-Muzaini, 1995; QMEMP, 2005; Nour El-Din and Al-Khayat, 2005; Al-Yamani et al., 2006; Sheppard et al., 2010). Relative to other Gulf countries, coral decline (species, abundance, health) around Qatar is more intense with those corals remaining covered in algal turf; a phenomenon symptomatic of eutrophication in this and other regions of the world (Sheppard et al., 2010; Anderson et al., 2012).

Conservation, sustainable use and development programs ultimately depend on a comprehensive scientific understanding of

species and how they relate to their environment (Brook et al., 2006; Sheppard et al., 2010). The purpose of the 'Carbon Cycle' project (2010–2011) was to determine the present state of Qatar's coastal waters. Phytoplankton biomass (chlorophyll *a* concentration), primary production, abundance, species diversity and species groupings along with water quality parameters were measured at thirteen stations surrounding the peninsula in February 2010, July 2010, February 2011 and May 2011. The biodiversity component of the study is restricted to those species $> 5 \mu\text{m}$; the lower boundary of resolution for microscopic studies. Nonetheless, herein we provide essential new information on the structure and functioning on phytoplankton communities and how they are driven by natural gradients of environmental conditions.

2. Materials and methods

2.1. Study area

Qatar ($25^{\circ}30\text{N}$, $51^{\circ}15\text{E}$) is a peninsula (land mass $\sim 11,500 \text{ km}^2$) connected to Saudi Arabia in the southern section of the Gulf (Fig. 1b). The $> 700 \text{ km}$ coast line comprises approximately 23% of the entire Gulf; its shallow nature ($< 35 \text{ m}$ average) means almost all parts lie within the photic zone (Sheppard, 1993). The temperature in this arid climate varies seasonally ($11\text{--}15^{\circ}\text{C}$ in winter and $34\text{--}40^{\circ}\text{C}$ in summer) (Rezai et al., 2004). The high evaporation and low precipitation ($\sim 70 \text{ mm year}^{-1}$) result in salinities (presented throughout using the unit-less practical salinity scale) ranging from 40 along the northern and eastern coast up to 70 along the southwestern coast (Jacob and Al-Muzaini, 1995; ROPME, 1999).

The Gulf is an inland sea ($239,000 \text{ km}^2$; $\sim 1000 \text{ km}$ long, $200\text{--}300 \text{ km}$ wide) connected to the Gulf of Oman (Middle East). In the northern section, the Shatt Al-Arab estuary introduces the majority of freshwater to the Gulf with the Euphrates and Tigris Rivers in Iraq discharging $35\text{--}133 \text{ km}^3$ annually (Sheppard et al., 2010). The Gulf also receives fresh water from numerous small seasonal streams in the Zagros Mountains of Iran. Currents in the Arabian Sea result from the removal of surface water during the summer monsoon and its replacement by cooler upwelling water (Sheppard et al., 1992). To the south, the Gulf is connected to the Gulf of Oman through the narrow Straits of Hormuz that lead to the Arabian Sea (Fig. 1a and b).

2.2. Sampling strategy

Four cruises (February 2010, July 2010, February 2011 and May 2011) on the R/V Mukhtabar Al-Bihar sampled 13 stations around the Qatar peninsula (Fig. 1b). Stations were chosen to represent several environmental conditions important in establishing biological patterns (salinity, temperature, water depth, surface patterns of primary productivity, sources of inorganic nutrients, and proximity to anthropogenic contaminants). Vertical profiles of temperature, salinity, dissolved oxygen (DO), pH, and turbidity were obtained with a YSI model 650 MDS Water Quality Data Logger attached to 6920 V2 Multiparameter Water Quality Sonde; these parameters were found to be homogenous with depth at most stations and most cruises (not shown).

Discrete samples were collected using Niskin bottles deployed at the surface (top 1 m) and bottom (< 1 m) for chlorophyll (Chl) *a*, total dissolved solids (TDS), total and suspended solids (TSS), and nutrients (inorganic and organic, dissolved and particulate) analyzed using a Skalar San++ Spectrophotometer with DA-3500 Discrete Analyzer according to Parsons et al., (1984). Dissolved nutrient samples were immediately filtered onto precombusted GF/F filters and frozen in acid washed bottles. The filters were retained frozen for later Chl *a* analysis. Total nitrogen (TN) and phosphorous (TP) were collected and stored frozen at -20°C . Concentrations of dissolved organic nitrogen (DON) were calculated by subtracting all inorganic nitrogen concentrations from the total dissolved nitrogen (TDN) concentrations. Dissolved organic phosphorus (DOP) concentrations were calculated as the difference between total dissolved phosphate (TDP) and inorganic phosphate (DIP). The precision obtained for the different analyzes at full scale was better than 0.1% for nitrite, 0.2% for nitrate, 1.1% for phosphate and 0.2% for silicate. Water samples and filters were frozen immediately upon collection.

Phytoplankton tows were collected using a 0.5 m diameter 67 μm phytoplankton net fitted with a digital flow meter. Samples were preserved in 4% buffered formalin for quantitative and taxonomic studies. Community composition was determined to species level, when possible. The lower boundary of resolution was species > 5 μm . Preserved samples were fixed and kept in the dark at room temperature until analysis.

2.3. Fluorescence induction and relaxation (FIRE) system (February 2010 only)

A FIRE fluorometer was used to measure photo-physiological responses of phytoplankton in water samples (3 ml) from each station and depth. Fluorescence transients were fit with the biophysical model of Kolber et al., (1998) to obtain the minimal and maximal fluorescence yields (F_0 and F_m respectively) on dark acclimated (30 min) samples. The efficiency of photosystem II (PSII) is defined as the maximum change in the quantum yield of photochemistry (F_v/F_m) in which variable fluorescence is calculated as the difference between F_m and F_0 . The functional absorption cross-section for PSII (σ_{PSII} ; $\text{\AA}^2 \text{quanta}^{-1}$), the minimum turnover time of electron transfer between reaction centers (τ_{Qa} ; μs) and the connectivity factor (p) were also derived.

Given the low biomass in the water column, we found the light-dark bottle method was not sufficiently sensitive to measure primary production (data not shown). Further, it was not possible to use ^{14}C on the R/V Mukhtabar Al-Bihar. Hence, we used the FIRE to calculate the electron transport rate (ETR_{PSII}) as $\sigma_{\text{PSII}}(F'_q/F'_v)/(F_v/F_m)E$, where F'_q is $(F_m - F)$ and E (light intensity) as a proxy for rates of primary productivity (Suggett et al., 2010; Quigg et al., 2012). A series of single turnover (1 μs) saturating flashes for sequential PSII closure was applied for ten light intensities (0–1050 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$). The specific absorption of PSII ($a_{\text{PSII}}^{\text{chl}}$) was calculated

as $[\sigma_{\text{PSII}}(\text{RC}_{\text{PSII}}/\text{chl}a)]/[F_v/F'_m]$, where $\text{RC}_{\text{PSII}}/\text{chl}a$ is equal to 0.002 given the diatom dominated community. We assumed a photosynthetic quotient of 1.0 to convert from oxygen to carbon units and a Chl:C ratio of 50 to convert from Chl *a* to C units (Jacob et al., 1982).

2.4. Nutrient enrichment bioassays (February and May 2011 only)

Bioassays were performed using water collected at four randomly selected stations during each cruise in 2011. Triplicate treatments of (i) surface water samples (top 1 m), (ii) surface waters plus nitrate (20 μM final concentration) and (iii) surface waters combined with bottom waters (9:1 ratio), were prepared. These represent control (C), plus nitrogen (N) and plus deep (D) treatments respectively. Short-term bioassays (24–30 h) were performed at in situ temperatures in flow-through containers covered with 50% shade cloth. At the beginning and the end of the assays, Chl *a* biomass was measured as described above. The phytoplankton response index (PRI) was calculated according to Fisher et al. (1999) to normalize the data and to allow direct comparisons between treatments and cruises.

2.5. Statistical analysis

Multivariate analyses and mapping were performed using PRIMER 6 (Clarke and Gorley, 2006) and a variety of software packages in R 2.15 (R Development Core Team, 2012) including “vegan” (Oksanen et al., 2011), “sp” (Bivand et al., 2008) and “raster” (Hijmans and van Etten, 2012). A total of 18 surface and 22 bottom environmental parameters, as well as 125 phytoplankton species (or taxa) were recorded from the 13 stations (Fig. 1, Supplemental Tables 1 and 2) which were repeatedly sampled during the four cruises. All errors were calculated as standard deviations.

The environmental data were logarithm (base of 10) transformed, centered (subtracted by sample mean) and normalized (divided by standard deviation) to reduce data skewness. Environmental ordination used Principal Component Analysis (PCA), which projects the multivariate data in reduced dimensions. In the PCA algorithm, PC1 is the axis explaining most of the variance in multivariate space (environmental properties). PC2 axis is perpendicular to PC1 but also maximizes the variance explained. The first two PC axes define a “best fitting” plane, with the placement of samples (on the ordination map) representing the dissimilarity of environmental properties. A PC axis is a linear combination of the values for each environmental variable; hence, the coefficients for each variable (positive or negative loading) for PC1 and PC2 axes represent the importance of a variable on the “best fitting” plane. These coefficients were used as coordinates to plot vectors on the ordination map, with the length indicating the variable importance and direction (away from the center) representing the increasing environmental values.

The transformed environmental data and presence and absence of phytoplankton species were converted to inter-sample Euclidean distance and Bray–Curtis dissimilarities (Bray and Curtis, 1957), respectively. The shortest geographic distances between sampling stations (Supplemental Fig. 1a and b) were calculated using R package “gdistance” (van Etten, 2011) to avoid the land-mass between the western and eastern sampling sites. The inter-sample distances (environmental or geographic) were used as a proxy to characterize habitats and correlated with the inter-sample biotic dissimilarities using Mantel test with Spearman's rank correlations (Legendre and Legendre, 1998). The multivariate spatial autocorrelation of phytoplankton composition was examined using Mantel Correlogram based on the incremental increase of geographic distance classes (Legendre and Legendre, 1998; Borcard and Legendre, 2012). The best subset of environmental variables (highest correlations with floral resemblances) was

selected from all possible variable combinations. The individual variables with significant correlations ($P < 0.05$) were overlaid on the ordination maps of biotic resemblances to visualize the bio-environmental relationships. This was done in a similar way to the PCA vector overlays. First, the inter-sample biotic resemblances were subjected to non-metric multi-dimensional scaling (nMDS). The MDS is similar to PCA and yet more widely used in the field of community ecology because it accommodates all types of similarity indices. It only preserves the “ranks” of inter-sample similarities; hence, the placement of samples (distances on the ordination map) only reflects the “relative values” of inter-sample dissimilarities. Second, correlation coefficients were calculated between the best environmental variables to the first (x) and second (y) axes of MDS ordination map. Third, these correlations were again used as coordinates to plot vectors on the MDS map, with the lengths indicating the strength of the bio-environmental

relationships and the directions illustrating increasing environmental values on the biotic ordination plane.

The same flora resemblance was subjected to agglomerative hierarchical cluster analysis based on Ward’s minimum variance method to minimize the within-group sum of squares (Ward, 1963). The natural groupings of samples were based on a standard cut-off height on the dendrogram. Similarity profile test (SIMPROF) was also performed using R package “clustsig” (Whitaker and Christman, 2010) to define significant cluster structure ($P < 0.05$), which was then used as a prerequisite for defining the natural grouping.

In order to examine the temporal (time of sampling) and spatial effects (geographic area), two-way cross Analysis of Similarity (ANOSIM) was applied to the surface and bottom environmental distance, as well as the phytoplankton resemblance matrices. The effect of the sampling time was examined across all levels of geographic locations (west, northeast, and southeast off the coast

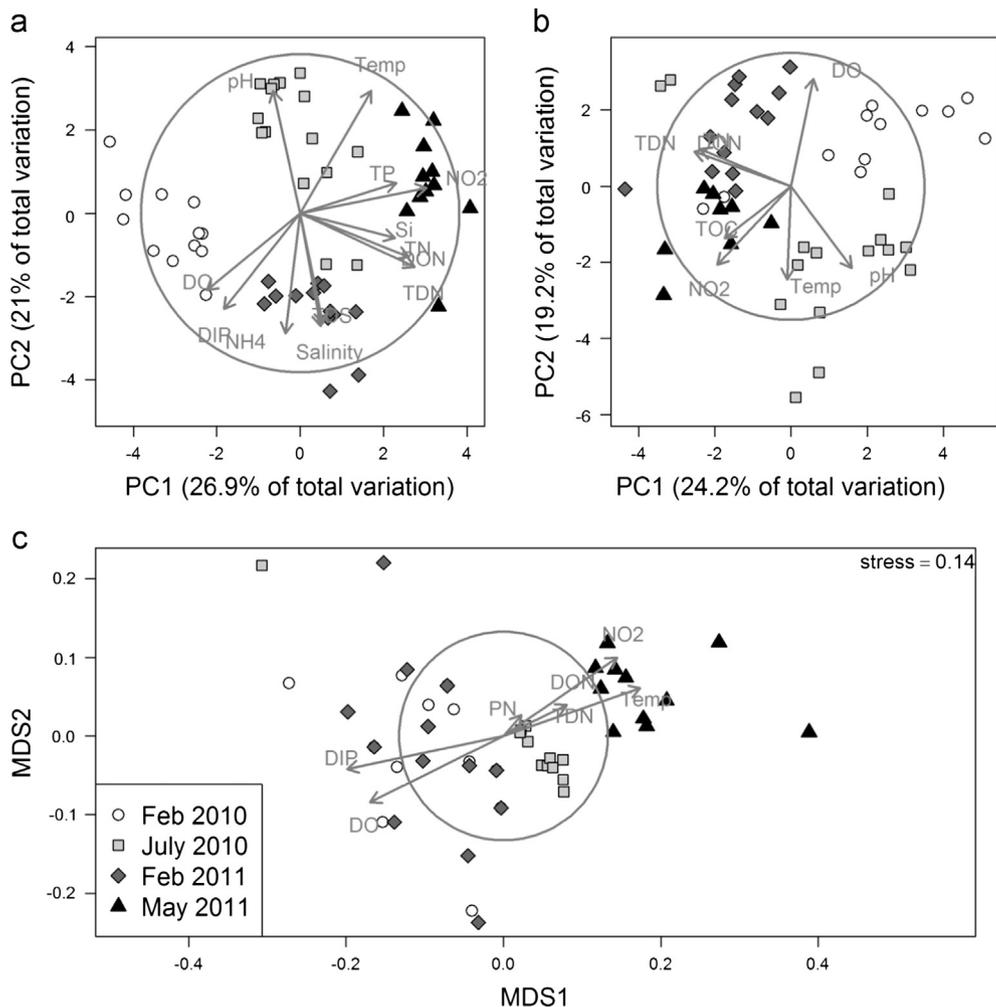


Fig. 2. Principal component analysis (PCA) on the (A) 18 surface and (B) 22 bottom environmental variables during the Qatar cruises. Symbols indicate the times of sampling. The environmental data were \log_{10} transformed, centered (subtracted by sample mean) and normalized (divided by standard deviation) before the PCA. PC1 is the axis explaining most of the variance in the multivariate space (environmental properties). The first two PC axes define a “best fitting” plane and the placement of samples (distances between the symbols) representing the dissimilarity of environmental properties. The PC axis is linear combinations of the values for each environmental variable; hence, the coefficients of each variable (positive or negative loading) for PC1 and PC2 axes can be plot as a vector on the “best fitting” plane, with the length indicating the variable importance and direction (away from the center) representing the increasing environmental values. Here, only the vectors with the longest lengths (> 0.3) are shown. The vector lengths were calculated as the square root of the sum of square variable coefficients for the PC1 and PC2 axes. Circle shows vector length equal 0.5. (C) Non-metric multi-dimensional scaling (nMDS) on presence and absence of phytoplankton species based on inter-sample Bray–Curtis dissimilarities. Symbols indicate the times of sampling. Similar to PCA (Fig. 4a and b), nMDS is an ordination method; however, the placement of the samples (distances between symbols) only represent the “relative” values of flora dissimilarities, because nMDS only preserves the ranks of the inter-sample dissimilarities. The vector overlays show the correlation coefficients (Spearman’s rank correlation) of surface environmental variables with the MDS1 (x -axis) and MDS2 axis (y -axis). The length of the vector is the square root of the sum of the square coefficients with MDS1 and MDS2. The longer the vector the stronger the correlation of that environmental variable with the 2-D MDS plane. The vector direction away from the center indicates the increasing environmental value on the 2-dimensional MDS plane. Circle shows that the vector length equal 0.5. Here, the vectors only show the environmental variables with significant correlations to the phytoplankton flora resemblance matrices ($P < 0.05$, Mantel test).

of the Qatar peninsula, Fig. 1b) and the effect of the locations was examined across all levels of sampling times (February 2010, July 2010, February 2011, and May 2011 cruises). Moreover, the community characteristics across the different time of sampling and geographic area were also examined, including the following parameters:

- (1) Number of phytoplankton species,
- (2) Species richness: Species accumulation curve was estimated by randomly accumulating samples (without replacement). The randomization was repeated form 100 times and the mean and 95% confidence interval of the curves were reported, and
- (3) Similarity percent contribution (SIMPER): Average similarities were broken down to similarity percent contribution of each species. The species that contributed the most within the areas or sampling times were examined as characteristics species.

3. Results

The water quality characteristics of the Qatari coastal waters measured during the cruises are summarized in Supplemental Table 1. Seawater temperature in February (19.8 ± 0.7 °C—2010;

18.7 ± 1 °C—2011) was much cooler than that measured in May (29.4 ± 0.9 °C) and July (31 ± 0.2 °C). Salinity did not fluctuate significantly between the cruises (43 ± 4), with high values due to high evaporation rates. Dissolved oxygen concentrations were homogenous throughout the water column, ranging from ~ 7 mg l⁻¹ in February down to ~ 5 mg l⁻¹ in May and July. Turbidity (in nephelometric turbidity units) is low year round, ranging from 0.9 to 1.6 NTU. We found the waters around the Qatar coast at these 13 stations to be homogeneously mixed from surface to bottom (examples given in Supplemental Fig. 2).

Nutrient concentrations were variable between locations and sampling times (Supplemental Table 1; Fig. 2a and b). Notably, we found that nitrate and nitrite were rarely > 0.2 μ M with exceptions in May 2011. Nitrate, nitrite, ammonium and DIN concentrations were 1000-times greater than DON, PN and TP. For example, DIN concentrations (mean of 0.50 μ M, range 0.02 – 7.4 μ M) relative to DON concentrations (mean 0.46 nM, 0.14 – 1.05 nM). The mean DIP (0.48 μ M) and silicate (1.39 μ M) concentrations were an order of magnitude greater than inorganic nitrogen concentrations in most cases. As a result, DIN:P and DIN:Si ratios were on average 1.31 (range 0.05 – 4.12) and 0.43 (range 0.08 – 0.60) respectively. Nutrients were frequently present in higher concentrations at the bottom of the water column relative to the surface (Supplemental

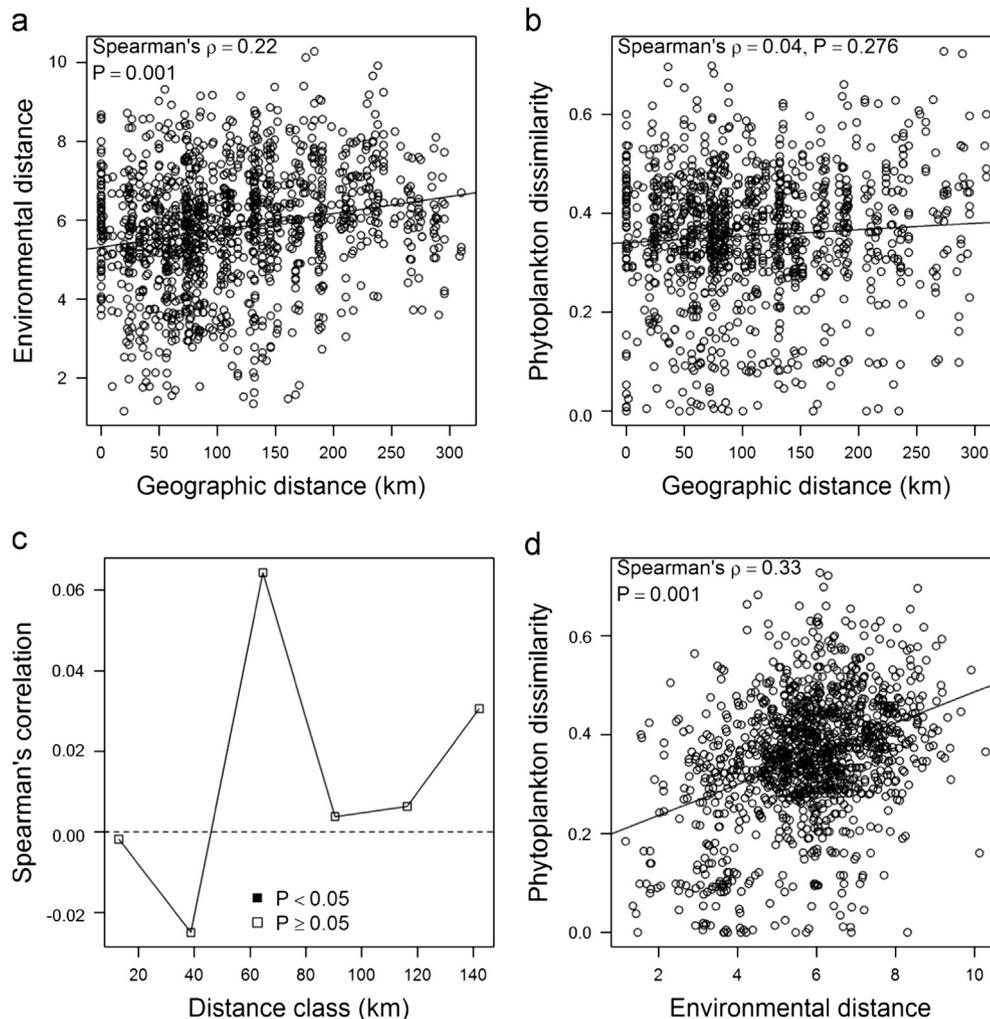


Fig. 3. Correlation among inter-sample shortest geographic distances, surface environmental distances, and phytoplankton flora dissimilarities. (A) Spearman's correlation between the geographic distances and environmental distances. (B) Spearman's correlation between the geographic distances and phytoplankton flora dissimilarities. (C) Mantel correlogram for phytoplankton flora dissimilarities. Solid symbol indicates significant correlation within geographic distance class. (D) Spearman's correlation between the environmental distances and phytoplankton flora dissimilarities.

Table 1; Fig. 2). This included nitrate, DOP and TDP (July 2010 and February 2011), nitrite and DIP (February 2010 and May 2011), NH_4^+ and DIN (two cruises in 2011), TP (all except May 2011) and Si (all except July 2010).

3.1. Surface and bottom environmental conditions

The first two principal component axes explained 48% of the total variation in the surface environmental data (Fig. 2a). Temperature had the highest contribution (0.44, longest vector length) to the “best fitting” plane defined by PC1 and PC2 axes. Nitrite had the second longest vector (0.40), followed by TDN (0.4), DON (0.4), pH (0.39), DIP (0.39), NH_4^+ (0.38), DO (0.38), TN (0.37), salinity (0.36), TDS (0.35), TP (0.32) and Si (0.31). Nevertheless, the vectors of DON, TDN and TN, as well as salinity and TDS, almost overlap (Fig. 2a), indicating high correlations (Pearson's $\rho > 0.87$) within these two sets of variables. On the PCA ordination map (Fig. 2a), the placement of samples (symbols) was clearly separated by the different sampling times. The July 2010 and May 2011 cruises were separated from February (2010 and 2011) samplings toward the direction of increasing temperature, pH, TP and nitrite or decreasing dissolving oxygen, DIP, NH_4^+ and TDS/salinity. In contrast with the 2010 samples (February and July), the surface water of the February and May 2011 cruises had higher DON/TDN/TN and silicate.

The first two principal component axes explained 43.3% of the total variation in the bottom environmental properties (Fig. 2b). The DO had the highest contribution (0.41, longest vector length) to the “best fitting” plane, followed by nitrite (0.4), TDN (0.38), DON (0.38), pH (0.38), TN (0.37), temperature (0.35) and TOC (0.32). Again, among these important variables, the vectors of DON, TDN and TN were almost overlapped and highly correlated (Pearson's $\rho > 0.94$). Generally, the PCA ordination (Fig. 2b) shows that the placement of samples was also separated by the different time of sampling; however, the separation was not as clear as the surface environmental data (Fig. 2a). Some mixing of sample placements occurred between the February 2010 and 2011 and May 2011 cruises. The bottom environmental properties for the February and July 2010 cruises were characterized by lower DON/TDN/TN and higher pH, and vice versa for the February and May 2011 cruises. Within the same sampling year, the February samplings had higher DO while the May or July samplings had higher nitrite, TOC and temperature.

3.2. Biological patterns and bio-environmental relationships

Inter-sample surface environmental distances were significantly correlated with the minimum geographic distances between sampling sites (Mantel test, $\rho=0.22$, $P=0.001$, Fig. 3a). The inter-sample phytoplankton Bray–Curtis dissimilarities, however, were not significantly correlated with the geographic distances (Mantel test, $\rho=0.04$, $P=0.276$, Fig. 3b). Moreover, the phytoplankton species composition showed no evidence of spatial autocorrelation in any of the geographic distance classes (Mantel test, $P < 0.05$, Fig. 3c). The combined surface environmental distances (18 variables) were significantly correlated to the phytoplankton resemblances (Mantel test, $\rho=0.33$, $P=0.001$, Fig. 3d). Individually, DIP had the highest correlation to phytoplankton resemblance, followed by temperature, DO, nitrite, PN, TDN, and DON (Mantel test, $\rho=0.11$ – 0.4 , $P < 0.05$, Fig. 4a). The combination of DIP, PN and temperature was the best subset of environmental variables giving the highest correlation to flora resemblances (Mantel test, $\rho=0.53$, $P < 0.001$, Fig. 4b). MDS ordination of phytoplankton resemblance (Fig. 2c) showed that the samples can be separated by the time of sampling except for the two February cruises (2010 and 2011) that overlapped, indicating similar phytoplankton composition. The clear separation of July 2010 and

May 2011 from the February 2010 and 2011 sampling was correlated with higher temperature, nitrite, DON, and TDN, as well as lower DIP and DO.

Except for the Stations 3, 4 and 13 reoccurring in the same groups during the two February cruises (cluster b, Fig. 5a and c), the geographic grouping (by W, NE, and SE off Qatar Peninsula) was not evident on the dendrograms (Fig. 5a–d). Many clusters comprised of samples from different geographic regions. These dendrograms also agreed with the previous results, suggesting that phytoplankton composition surrounding the Qatari water showed strong temporal (Fig. 2c) but weak spatial patterns (Fig. 3b and c).

3.3. Statistical comparisons across temporal and spatial scales

Two-way cross ANOSIM suggested that both “cruise” and “location” effects were significant across all environmental distance or biotic dissimilarity matrices (global tests, $P < 0.05$, Table 1). In other words, the environmental properties (surface and bottom) and species composition (phytoplankton) were significantly different among the four cruises and three geographic locations surrounding the Qatar Peninsula. The R-statistic in ANOSIM test can be used to measure the degree of group separations. Among all three ANOSIM tests, the “cruise” groups (higher R, Table 1) consistently have better separation (larger R) than the “location” groups (smaller R), suggesting that the effects of “cruise” was stronger than the effects of “location”. Pairwise ANOSIM suggested significant differences between most of the factor levels, except for the phytoplankton resemblance between February 2010 and 2011 cruises (pairwise test, $R=-0.154$, $P=0.98$, Table 1), as well as phytoplankton resemblances between the NE and SE off the coast of the Qatar Peninsula (pairwise test, $R < 0.095$, $P=0.091$). Hence, we found that the diversity and species composition in February 2010 were similar to that of the February 2011. The July and May samples, however, were all quite different from the two February cruises (see Figs. 2c, 6a and 7a–d).

3.4. Phytoplankton community composition

Of the 125 species identified, 66% were diatoms, 33% were dinoflagellates and the remaining 1% cyanobacteria (Supplemental Table 2). There were many more species present, but only those which were clearly identifiable are included in this analysis. Among the diatoms, species of *Chaetoceros* made up $> 50\%$ of the phytoplankton present examined in February 2010, 30% in July 2010 but only 8–10% of the population in 2011 (not shown). Annual changes were observed with some but not all species. For example, *Climacodium frauenfeldianum*, *Lauderia annulata*, *Melosira moniliformis*, *Pleurosigma* sp., *Rhizosolenia imbricata* and *Thalassionema nitzschioides*, all diatoms, were dominant during both cruises in 2010 but not in 2011 (Table 2; Supplemental Table 2). Other species were important during one but not all cruises. This includes *Dactyliosolen mediterraneus* and *Ceratium furca* during July 2010 and *Peridinium* and *Prorocentrum* species which were frequently observed during February 2011. The cyanobacteria *Trichodesmium thiebautii* was more abundant in 2011 than 2010 (Supplemental Table 2).

3.5. Characteristics of the geographic communities

The July 2010 sampling had the highest mean number of species (Fig. 6a) of which Stations 10, 11, 12, 13 had the highest mean number of species (102–106 spp.). Except for the May 2011 sampling, the NE region had the highest mean number of species. The mean species accumulation curve approached 125 species when a total of 61 plankton samples were combined (Fig. 6b). Species richness does not increase when the additional 33 samples

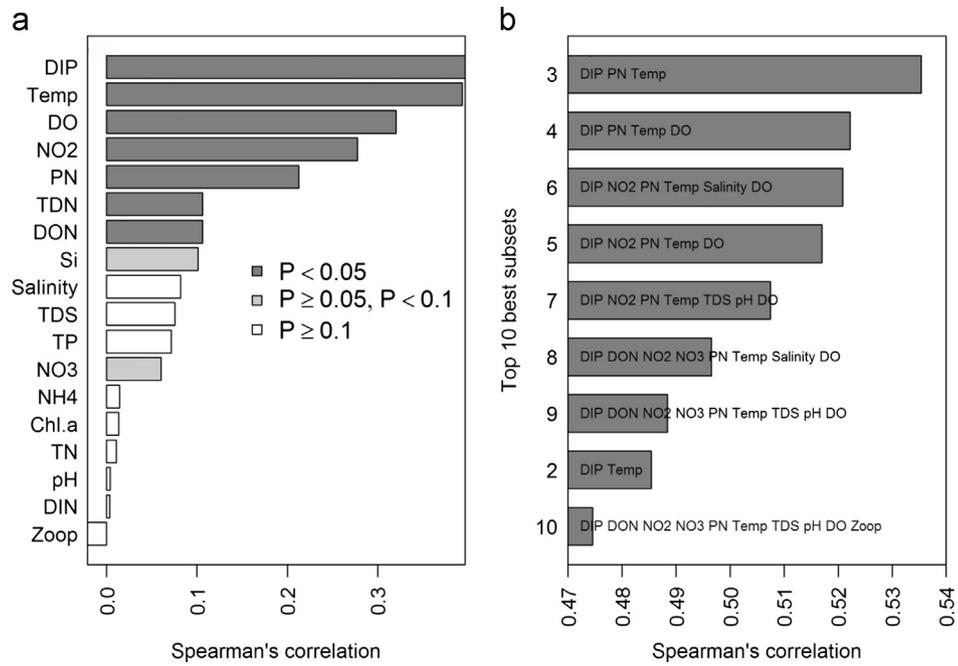


Fig. 4. Mantel tests between (A) individual surface environmental variables and flora resemblance matrix and for (B) the best subsets of surface environmental variables giving the highest correlation to the flora resemblance matrix. The environmental variable was \log_{10} transformed, centered, normalized, and converted to inter-sample Euclidean distances. The presence/absence of flora species-by-sample matrices was converted to inter-sample Bray–Curtis dissimilarities. Both the distances and dissimilarities were ranked from high to low to calculate the Spearman's rank correlation coefficient.

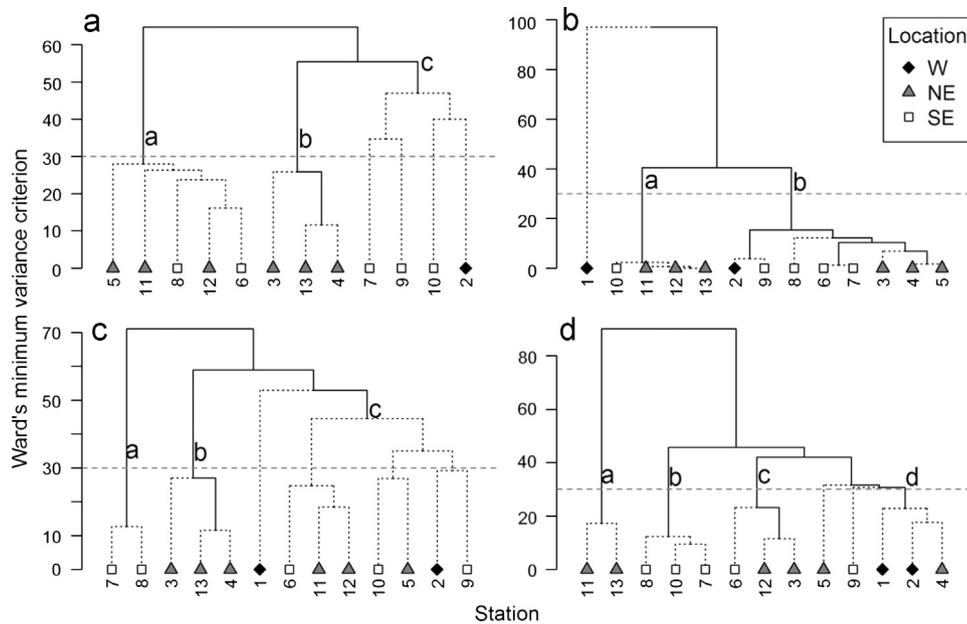


Fig. 5. Agglomerative hierarchical cluster analysis based on inter-sample Bray–Curtis dissimilarities of phytoplankton communities during the (A) February 2010, (B) July 2010, (C) February 2011, and (D) May 2011 cruises. Solid black line indicates significant dendrogram structure (SIMPROF test, $P < 0.05$) while the dotted line shows non-significant structure. The dashed line indicates the standard cut-off height. Alphabetical label shows the natural grouping based on the prerequisite of significant dendrogram structure.

were added, suggesting that our sampling has properly estimated the total phytoplankton species richness in the Qatar peninsula. The phytoplankton communities along the western coast appeared to have the lowest species richness (Fig. 6c); however, the 95% confidence interval of the mean species accumulation curve still overlapped with the NE and SE communities (Fig. 6d and e). Interestingly, despite that the July 2010 sampling had the highest mean number of species (Fig. 6a), the February 2011 recorded the highest total species richness (Fig. 6f–i).

Characteristic species in each sampling time and geographic area were identified based on the species contribution to the average faunal similarity for the specific community. Table 2 lists the characteristic species cumulatively contributing to at least 20% of the average similarity. Generally, the species with highest contribution were those occurring ubiquitously in all stations (see also Supplemental Table 2). Except for the May 2011 sampling, dinoflagellate species comprised more than half of the most contributed species list (Table 2). In fact, the dinoflagellates

Table 1
Two-Way Cross Analysis of Similarity (ANOSIM). Pairwise test only lists non-significant pairs ($P > 0.05$).

Variables	Test	Factor/level	R-statistic	Sig. Level
Environment (surface)	Global	CRUISE	0.867	0.001
	Global	LOCATION	0.378	0.001
Environment (Bottom)	Global	CRUISE	0.68	0.001
	Global	LOCATION	0.413	0.001
Phytoplankton	Global	CRUISE	0.561	0.001
	Pairwise	Feb 2010, Feb 2011	-0.154	0.974
	Global	LOCATION	0.208	0.005
		NE, SE	0.095	0.091

accounted for over 60% of the prevalent species (occurring in all stations) in February 2010, 2011 and July 2010 samplings. The list of the most contributed species was almost identical between February 2010 and 2011 samplings. Moreover, when all the species contributions were aggregated across cruises (Fig. 7a–d), the density distributions of diatom and dinoflagellate contributions appear to be similar between the February 2010 (Fig. 7a) and 2011 cruises (Fig. 7c). These evidences supports the MDS ordination (Fig. 2c) and ANOSIM results (Table 1) suggesting the species composition were similar between these two sampling periods. Except for diatom *Thalassionema nitzschioides* and dinoflagellates *Ceratium furca*, *Ceratium massiliense* and *Dinophysis caudata*, as well as dinoflagellate *Ceratium breve* and *Peridinium divergens* and cyanophyta *Trichodesmium thiebautii*, the most contributed species were largely different between the February (2010 and 2011) and July 2010 and May 2011 samplings, respectively. Similarly, the most contributed species in geographic areas were those almost occurring at every station and throughout the four different sampling times (Table 2). Three of the most contributed species in the western area (Diatom *Thalassiothrix frauenfeldii* and Dinoflagellate *Prorocentrum gracile* and *Prorocentrum micans*) also contributed greatly in the NE area. Many of the most contributed species were identical between the NE and SE areas (e.g. diatom *Rhizosolenia imbricate*, dinoflagellates *Ceratium breve*, *Dinophysis caudata*, *Peridinium divergens* and cyanophyta *Trichodesmium thiebautii*). The density distributions of the diatom and dinoflagellate species contribution were also more similar between the NE and SE areas (Fig. 7e–f), supporting that the phytoplankton composition were not significantly different in these two areas ($R=0.095$, $P=0.091$, pairwise ANOSIM, Table 1); however, the most contributed species list were entirely different between the W and SE area (Table 2).

3.6. Phytoplankton biomass, physiology and productivity

Phytoplankton biomass in the waters surrounding Qatar was generally low ($0.18\text{--}2.19 \mu\text{g l}^{-1}$) (Supplemental Table 1), with most values $< 1 \mu\text{g l}^{-1}$. There was no clear seasonal variation in Chl *a* based on the available data but generally higher biomass in July 2010 and February 2011 relative to February 2010 and May 2011 (Fig. 2; Supplemental Table 1). At the western stations (1 and 2), phytoplankton biomass was generally lower (mean = $0.55 \mu\text{g l}^{-1}$) than those in the NE stations (3, 4, 5, 11, 12 and 13) and those in the SE stations (6–10) which had mean Chl *a* of $1.33 \mu\text{g l}^{-1}$ and $0.95 \mu\text{g l}^{-1}$ respectively (Fig. 8a). These differences were not statistically significant.

Due to technical issues, we only have F_{IR}e data from the first cruise (February 2010). Nonetheless this provides useful information for understanding some phytoplankton physiology in this environment. For example, the pattern for F_o (Fig. 8b) was similar to that of Chl *a* (Fig. 8a). The quantum yield of photochemistry (F_v/F_m) was $0.30 (\pm 0.03)$ in the W, increasing to $0.38 (\pm 0.10)$ and

$0.36 (\pm 0.07)$ in the NE and SE respectively (Fig. 8c). F_v/F_m was not significantly different between surface and bottom waters (not shown), but was frequently found to be higher in bottom waters relative to surface waters.

We observed a gradient of decreasing σ_{PSII} values from stations on the W ($704 \text{ \AA}^2 \text{ quanta}^{-1} \pm 47$), NE ($313 \text{ \AA}^2 \text{ quanta}^{-1} \pm 81$) to SE ($300 \text{ \AA}^2 \text{ quanta}^{-1} \pm 95$) (Fig. 8d) which followed patterns of increasing light availability (Secchi depths; not shown) but not nutrient patterns (see Supplemental Table 1). The opposite pattern to σ_{PSII} was observed for τ_{Qa} (Fig. 7d and e respectively). τ_{Qa} was increased from the western stations ($547 \mu\text{s} \pm 17$), around the coast to $595 \mu\text{s} (\pm 274)$ and $673 \mu\text{s} (\pm 332)$ in the eastern stations (Fig. 8e). Faster τ_{Qa} time constants reflect more effective photosynthetic electron transfer on the acceptor side of PSII. Energy transfer between PSII reaction centers is a function of the connectivity (p); low values were measured at all stations in this system (Fig. 8f; mean = 0.11).

In order to use the F_{IR}e to estimate primary productivity, the Chl *a* specific light absorption by PSII, $a_{\text{PSII}}^{\text{chl}}$, was determined first. These values exhibited a gradient from stations in the W ($0.031 \text{ m}^2 \text{ mg Chl a}^{-1} \pm 0.001$) to those in the NE ($0.013 \text{ m}^2 \text{ mg Chl a}^{-1} \pm 0.007$) and to those in the SE ($0.012 \text{ m}^2 \text{ mg Chl a}^{-1} \pm 0.005$) (Fig. 8g). The electron transport rate (ETR_{PSII}) was not measurable at the western stations, that is, fluorescence was below detection limits even for the F_{IR}e. At the northeastern and southeastern stations, ETR_{PSII} was similar, that is, $214 \pm 70 \mu\text{mol C mg Chl a}^{-1} \text{ min}^{-1}$ and $186 \pm 23 \mu\text{mol C mg Chl a}^{-1} \text{ min}^{-1}$ respectively, which is equivalent to $1.10 \pm 0.25 \text{ mg C m}^{-2} \text{ day}^{-1}$ and $0.84 \pm 0.32 \text{ mg C m}^{-2} \text{ day}^{-1}$ (Fig. 8h).

3.7. Bioassays

Nutrient enrichment bioassays were performed at four stations around the Qatari peninsula during the February and May 2011 cruises (Fig. 9). While none of the treatments were statistically different ($P > 0.05$), the strongest response (that is, the highest PRI) was measured at station 2 in February (Fig. 9a). In all cases, during the May cruise, the addition of nitrate as a nitrogen source stimulated phytoplankton biomass (Chl *a*) above that in the control treatments (Fig. 9e–h). Whilst not statistically different, there was a 25% increase at station 13 (Fig. 9h); the smallest increase was observed at station 5 (10%; Fig. 9f). In February, the addition of nitrogen stimulated productivity at stations 2 and 11 (Fig. 8a and d but not at stations 7 and 8 (Fig. 8b and c)). We also found that mixing deep water with surface waters (1:9) only stimulated phytoplankton growth at two of the eight stations: we observed an 11% and 27% increase respectively at stations 13 and 11 in these mixed treatments during the May cruise (Fig. 9g and h).

4. Discussion

Qatar's seemingly pristine environment is threatened by potential concomitant impacts that development may have on this ecosystem. Among these threats are loss of critical habitat to development, contamination with toxic chemicals by industry (particular that associated with oil exploration) and farming operations, invasive species from ballast waters and eutrophication (e.g., Ibrahim and El Samra, 1987; Jacob and Al-Muzaini, 1995; Subba-Rao et al., 1999; Nour El-Din and Al-Khayat, 2005; QMEMP, 2005; Sheppard et al., 2010). Further, "brine" discharged from desalination plants with salinities > 75 psu will increase salinity in one of the world's hypersaline water bodies (Abdul Aziz et al., 2003; Hashim and Hajjaj, 2005; Lattemann and Hopner, 2008; Sheppard et al., 2010). Here we describe spatial and temporal variation among the phytoplankton community and show that

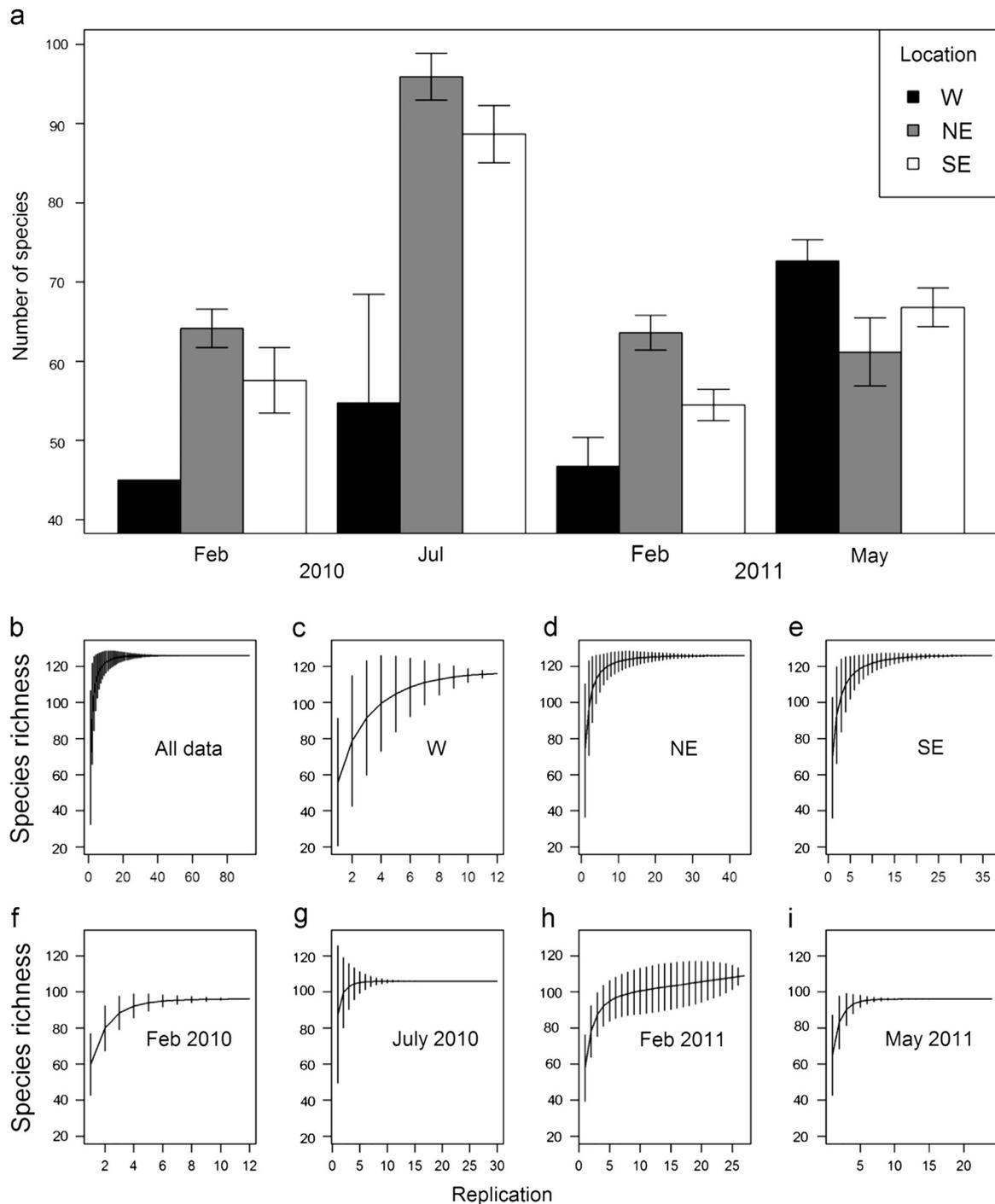


Fig. 6. Phytoplankton community structure including (A) mean species numbers and (B) overall mean species accumulation curve as a function of plankton tows. The remaining panels show the species accumulation curves for (C) west area, (D) northeast area, (E) southeast area, (F) February 2010 sampling, (G) July 2010 sampling, (H) February 2011 sampling and (I) May 2011 sampling. The error bars (A) show the standard error of the mean. In panel (B)–(D), the vertical lines indicate 95% confidence interval of the mean accumulation curves based on 100 resampling.

nitrogen limitation plays a role in the functioning of this seemingly stressed ecosystem.

4.1. Species diversity and groups

Bohm (1931) presented the first account of phytoplankton from the Gulf, listing 34 dinoflagellates. Since then, more than 1480 eukaryotic and prokaryotic primary producers have been described for this region (Jacob and Al-Muzaini, 1995). More recent publications have found a dominance of epiphytic, tycho-pelagic diatoms to the north and a mix of diatoms and

dinoflagellates to the south (see review by Subba Rao and Al-Yamani (1998)). In addition, diatoms and dinoflagellates, cyanobacteria dominate the communities in the Gulf and Qatar (e.g., Abdul Azis et al., 2003; Al-Harbi, 2005; QMEMP, 2005; Nour El-Din and Al-Khayat, 2005).

While Dorgham and Muftah (1986) identified 390 species from preserved water samples collected along the Qatar coastline (225 diatoms, 152 dinoflagellates, 2 silicoflagellates and 11 cyanobacteria), we only identified one-third (125 total) as many species similarly to Nour El-Din and Al-Khayat (2005) and QMEMP (2005) who identified ~100 species around Qatar. In the present study,

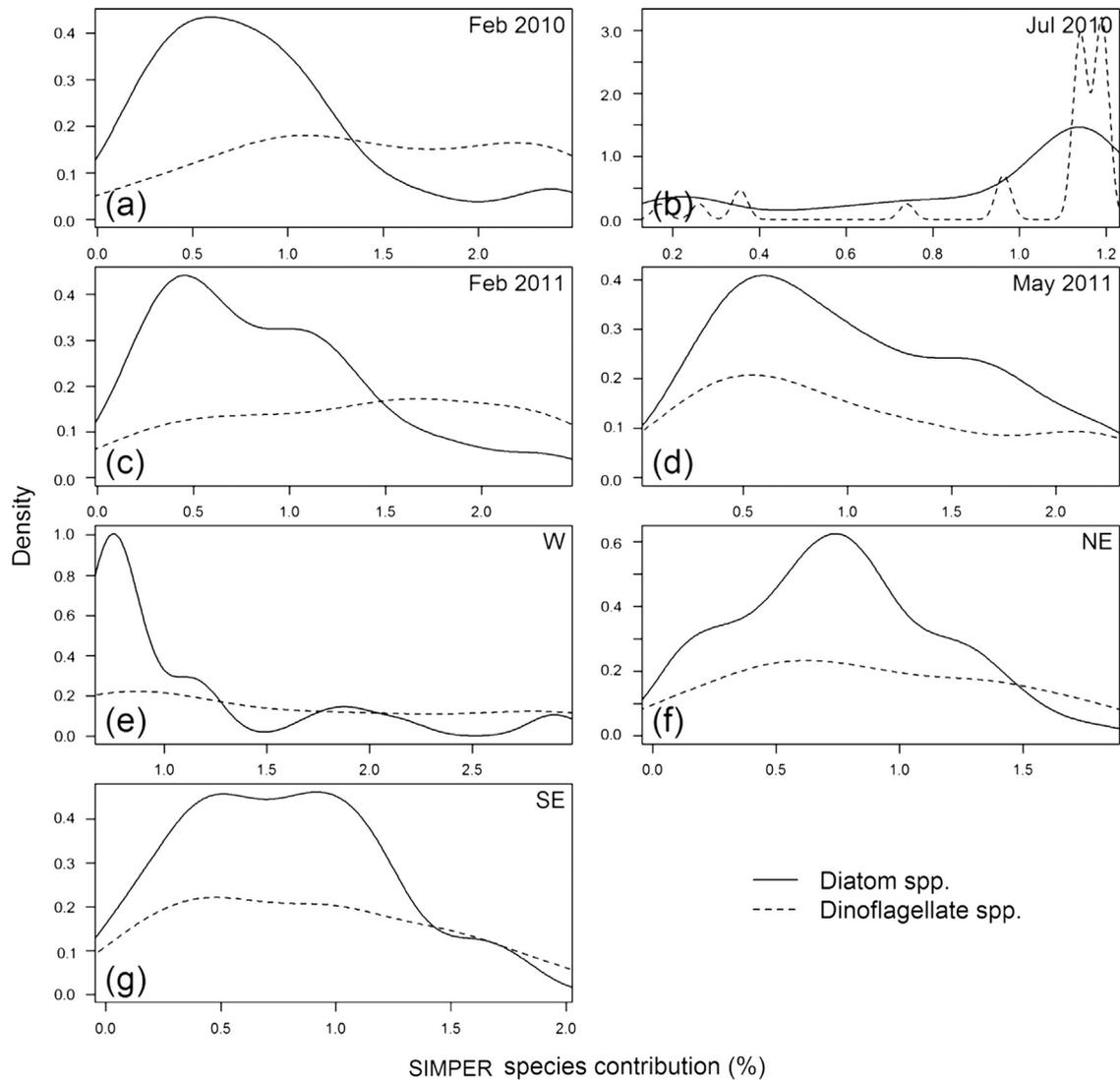


Fig. 7. Density distribution of SIMPER species contributions for (A) February 2010 sampling, (B) July 2010 sampling, (C) February 2011 sampling, (D) May 2011 sampling, (E) west area, (F) northeast area and (G) southeast area. The average similarity for specific sampling time and geographic area were broken down to percent similarity contribution (2 way cross SIMPER). The density was calculated using Kernel density estimation with Gaussian smoothing. Solid line indicates the contribution for diatom species and dashed line for dinoflagellate species. The area under the density curve estimates the overall percent contribution.

the majority of phytoplankton identified were diatoms (82), with 41 dinoflagellates and 2 cyanobacteria (Table 2; Supplemental Table 2); in ratios similar to those reported in Jacob and Al-Muzaini (1995). We were not able to identify members of the chlorophyceae, euglenophytes, silicoflagellates, coccolithophores or cryptomonads in our samples although species from these groups have been reported previously in the Gulf (Subba Rao and Al-Yamani, 1998; QMEMP, 2005; and references therein). Further, we were not able to identify prokaryotic and eukaryotic ultraplankton which are known to be numerically dominant in oligotrophic waters such as the Gulf of Aqaba (Al-Najjar et al., 2007) and other regions. This does not reflect an absence of these species in Qatar during our study but rather the difficulty in identifying many groups of phytoplankton, particularly the smaller and cell wall-less species.

In many cases, we observed previously reported genera but not always the same species; it is difficult to know if this is a function of changes in nomenclature or due to a change in members of the phytoplankton community between studies. Given the shallow nature of the sampling locations, it was not surprising that we found a number of tychopelagic diatom genera including *Amphora*, *Campylodiscus*, *Diploneis*, *Fragilaria*, *Grammatophora* and *Licmophora*.

Of the species we observed, known oceanic species in this region include *Bacteriastrium* sp., *Chaetoceros peruvianum*, *Climacodium frauenfeldianum*, *Rhizosolenia alata*, *Thalassiosira subtilis* *Thalassiothrix frauenfeldii*, *Gonyaulax spinifera*, *Prorocentrum gracile* and *Pyrodinium bahamense*. Examples of coastal phytoplankton species include *Bellerochea malleus*, *Leptocylindrus danicus*, and *Skeletonema costatum* (see Subba Rao and Al-Yamani, 1998; Al-Harbi, 2005). As with Dorgham et al., (1987), Abdul Azis et al. (2003) and Nour El-Din and Al-Khayat (2005) we found that *Trichodesmium* spp. was the most abundant filamentous cyanobacteria in Qatari coastal waters. This species is also important in the Gulf of Aqaba (Al-Najjar et al., 2007), the Gulf of Mexico (Dorado et al., 2012), and other oligotrophic regions.

In the review by Jacob and Al-Muzaini (1995), the three diatoms found to dominate phytoplankton communities in the Gulf were *Thalassionema nitzschioides*, *Thalassiothrix frauenfeldii*, *Climacodium frauenfeldianum*. While we also found these to be important (dominant) species, *Chaetoceros* spp. were far more important as a fraction of the entire community (Table 2 and Supplemental Table 2). This earlier study also identified the following dinoflagellates: *Ornithocercus thumii*, *Dinophysis caudate*, *Ceratium massiliense* and *C. furca* to dominate the community;

Table 2

Similarity percentage (SIMPER) contribution for phytoplankton species. Percent contributions (Contib%) were examined for the "LOCATION" groups across all "CRUISE" groups using the same 2-Way layout in the ANOSIM tests (Table 3). Only the most contributed species (highest Contib%) with at least 20% of cumulative contribution (Cum.%) of the average similarity (Av.Sim) are shown. When the contributions were tied, all species with the same "Contrib%" are listed. "DIA" denotes diatoms. "DIN" denotes dinoflagellates. "CYA" denotes cyanophyta.

Cat	Species	Occur	Contrib%	Cum.%	Cat	Species	Occur	Contrib%	Cum.%
Cruise					July 2010 continue (Avg similarity: 90.71)				
Feb 2010 (Avg similarity: 68.25)					Feb 2011 (Avg similarity: 69.75)				
DIA	<i>Navicula</i> sp.	12	2.4	2.4	DIN	<i>Peridinium</i> sp.	15	1.19	19.04
DIA	<i>Pleurosigma</i> sp.	11	2.4	4.8	DIN	<i>Prorocentrum gracile</i>	15	1.19	20.23
DIA	<i>Rhizosolenia imbricata</i>	11	2.4	7.2	DIN	<i>Prorocentrum micans</i>	15	1.19	21.42
DIA	<i>Thalassionema nitzschioides</i>	12	2.4	9.6	DIN	<i>Prorocentrum sigmoides</i>	15	1.19	22.61
DIN	<i>Ceratium breve</i>	12	2.4	12	May 2011 (Avg similarity: 71.23)				
DIN	<i>Ceratium furca</i>	12	2.4	14.4	DIA	<i>Navicula membranacea</i>	13	2.22	2.22
DIN	<i>Ceratium fusus</i>	11	2.4	16.8	DIA	<i>Pleurosigma itium</i>	13	2.22	4.45
DIN	<i>Ceratium massiliense</i>	12	2.4	19.19	DIA	<i>Rhizosolenia calcar avis</i>	13	2.22	6.67
DIN	<i>Dinophysis caudata</i>	12	2.4	21.59	DIA	<i>Thalassiosira subtilis</i>	13	2.22	8.89
DIN	<i>Peridinium divergens</i>	11	2.4	23.99	DIN	<i>Ceratium breve</i>	13	2.22	11.11
DIN	<i>Prorocentrum sigmoides</i>	12	2.4	26.39	DIN	<i>Peridinium divergens</i>	13	2.22	13.34
CYA	<i>Trichodesmium thiebautii</i>	12	2.4	28.79	DIN	<i>Ceratium dens</i>	13	2.22	15.56
July 2010 (Avg similarity: 90.71)					DIN	<i>Peridinium ovum</i>	12	2.15	17.71
DIA	<i>Diploneis splendida</i>	15	1.19	1.19	CYA	<i>Trichodesmium thiebautii</i>	12	2.15	19.86
DIA	<i>Rhizosolenia calcar avis</i>	15	1.19	2.38	DIA	<i>Triceratium</i> sp.	12	2.15	22.01
DIA	<i>Rhizosolenia setigera</i>	15	1.19	3.57	NE continue (Avg similarity: 77.62)				
DIA	<i>Skelotenema costatum</i>	15	1.19	4.76	DIA	<i>Dactyliosolen mediterraneus</i>	23	1.5	15.49
DIA	<i>Thalassionema nitzschioides</i>	15	1.19	5.95	DIA	<i>Pleurosigma</i> sp.	23	1.5	16.99
DIA	<i>Thalassiothrix frauenfeldii</i>	15	1.19	7.14	DIN	<i>Ceratium fusus</i>	23	1.5	18.49
DIN	<i>Ceratium furca</i>	15	1.19	8.33	DIN	<i>Prorocentrum gracile</i>	22	1.42	19.91
DIN	<i>Ceratium massiliense</i>	15	1.19	9.52	DIA	<i>Thalassiothrix frauenfeldii</i>	22	1.41	21.32
DIN	<i>Ceratium trichoceros</i>	15	1.19	10.71	SE (Avg similarity: 76.10)				
DIN	<i>Ceratium tropis</i>	15	1.19	11.9	DIN	<i>Ceratium breve</i>	21	1.95	1.95
DIN	<i>Dinophysis caudata</i>	15	1.19	13.09	DIN	<i>Ceratium fusus</i>	21	1.95	3.9
DIN	<i>Gonyaulax diegensis</i>	15	1.19	14.28	DIN	<i>Peridinium divergens</i>	21	1.95	5.85
DIN	<i>Gonyaulax kofoidii</i>	15	1.19	15.47	CYA	<i>Trichodesmium thiebautii</i>	20	1.79	7.64
DIN	<i>Peridinium islandicum</i>	15	1.19	16.66	DIA	<i>Coscinodiscus</i> sp.	20	1.76	9.4
DIN	<i>Peridinium mita</i>	15	1.19	17.85	DIA	<i>Navicula</i> sp.	20	1.76	11.16
Geographic area					DIA	<i>Thalassionema nitzschioides</i>	20	1.72	12.88
W (Avg similarity: 60.27)					DIA	<i>Rhizosolenia imbricata</i>	19	1.65	14.54
DIA	<i>Diploneis splendida</i>	7	2.9	2.9	DIN	<i>Dinophysis caudata</i>	19	1.65	16.19
DIA	<i>Rhizosolenia calcar avis</i>	7	2.9	5.8	DIA	<i>Skelotenema costatum</i>	19	1.59	17.78
DIA	<i>Thalassiothrix frauenfeldii</i>	7	2.9	8.7	DIN	<i>Ceratium tropis</i>	19	1.57	19.35
DIN	<i>Ceratium furca</i>	7	2.9	11.6	DIA	<i>Pleurosigma</i> sp.	18	1.56	20.91
DIN	<i>Ceratium massiliense</i>	7	2.9	14.5	NE (Avg similarity: 77.62)				
DIN	<i>Gonyaulax diegensis</i>	7	2.9	17.39	DIA	<i>Rhizosolenia imbricata</i>	25	1.82	1.82
DIN	<i>Gonyaulax kofoidii</i>	7	2.9	20.29	DIN	<i>Ceratium breve</i>	25	1.82	3.64
DIN	<i>Peridinium</i> sp.	6	2.9	23.19	DIN	<i>Dinophysis caudata</i>	25	1.82	5.46
DIN	<i>Prorocentrum gracile</i>	7	2.9	26.09	DIN	<i>Peridinium ovum</i>	25	1.82	7.28
DIN	<i>Prorocentrum micans</i>	7	2.9	28.99	DIN	<i>Peridinium divergens</i>	25	1.82	9.09
NE (Avg similarity: 77.62)					DIN	<i>Prorocentrum micans</i>	24	1.67	10.77
DIA	<i>Rhizosolenia imbricata</i>	25	1.82	1.82	DIA	<i>Thalassionema nitzschioides</i>	24	1.63	12.4
DIN	<i>Ceratium breve</i>	25	1.82	3.64	CYA	<i>Trichodesmium thiebautii</i>	23	1.59	13.99
DIN	<i>Dinophysis caudata</i>	25	1.82	5.46					
DIN	<i>Peridinium ovum</i>	25	1.82	7.28					
DIN	<i>Peridinium divergens</i>	25	1.82	9.09					
DIN	<i>Prorocentrum micans</i>	24	1.67	10.77					
DIA	<i>Thalassionema nitzschioides</i>	24	1.63	12.4					
CYA	<i>Trichodesmium thiebautii</i>	23	1.59	13.99					

Gonyaulax spp. and *Peridinium* spp. were numerical more common in the present study. Al-Harbi (2005) reported that the greatest contribution to phytoplankton populations in their study were multiple species of *Ceratium* (especially *massiliense* which we also found) and *Peridinium depressum*, and the diatoms, *Coscinodiscus* genera, *Leptocylindrus minimus* and *Rhizosolenia alata*. The questions to be addressed in future studies: what are the location specific patterns? Are shifts in the dominant species/genera observed in different studies associated with permanent changes resulting from development and alterations to the natural system? Are changes associated with eutrophication? What are the consequences to higher trophic levels?

4.2. Biomass and primary production

Chl *a*, a measure of the phytoplankton biomass, ranged from 0.31 to 1.14 $\mu\text{g Chl } a \text{ l}^{-1}$ in the western, from 0.65 to 2.07 $\mu\text{g Chl } a \text{ l}^{-1}$ in the northeastern and from 0.49 to 1.90 $\mu\text{g Chl } a \text{ l}^{-1}$ in the southeastern areas (Figs. 2 and 7; Supplemental Table 1). These values are similar to those previously reported in the Gulf. For the Shatt Al-Arab estuary to the north, Huq et al. (1981) and Al-Saadi et al. (1989) measured values between 0.22 and 3.25 $\mu\text{g Chl } a \text{ l}^{-1}$, with highs to 9.07 $\mu\text{g Chl } a \text{ l}^{-1}$ during the autumn (Huq et al., 1978). In Kuwait waters, algal biomass varied between 0.2 and 13.9 $\mu\text{g Chl } a \text{ l}^{-1}$ from January to

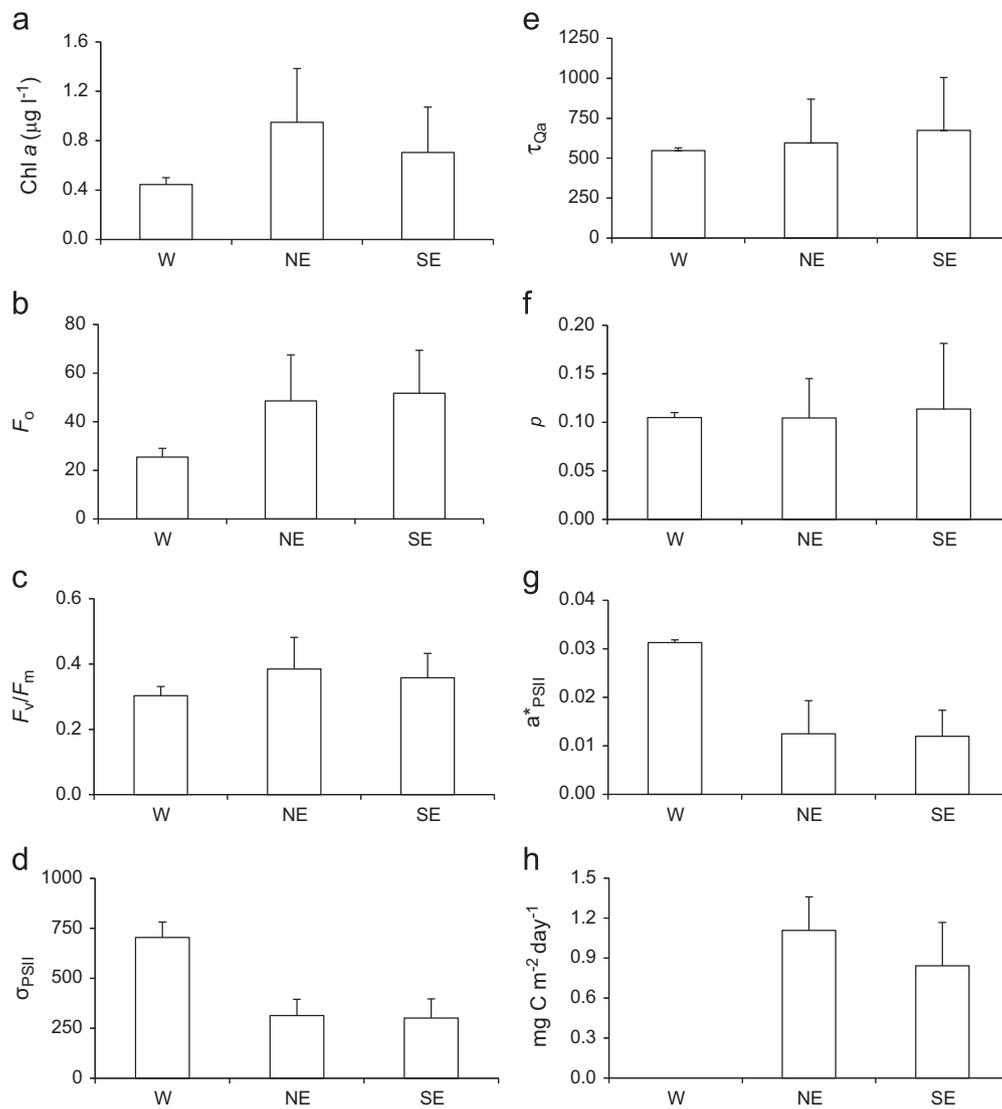


Fig. 8. Phytoplankton biomass and physiological characteristics measured in February 2010. (A) Chl *a*; $\mu\text{g l}^{-1}$, (B) F_0 , (C) F_v/F_m , (D) σ_{PSII} ; $\text{A}^2 \text{ quanta}^{-1}$, (E) τ_{O_2} ; μs , (F) ρ , (G) a^*_{PSII} ; $\text{m}^2 \text{ mg Chl } a^{-1}$ and (H) primary productivity; $\text{mg C m}^{-2} \text{ day}^{-1}$.

May (Jacob et al., 1979, 1980). In a more recent study, Al-Yamani et al. (2006) found Chl *a* concentrations were higher in the northern waters off Kuwait ($4.4 \mu\text{g Chl } a \text{ l}^{-1}$) adjacent to a river runoff area relative to those further south ($1.5 \mu\text{g Chl } a \text{ l}^{-1}$). Consistent with our findings, Nour El-Din and Al-Khayat (2005) previously reported Chl *a* was low ($< 2.5 \mu\text{g Chl } a \text{ l}^{-1}$), even undetectable concentrations, in several of the inland seas of Qatar characterized by elevated salinities. In the southern waters of the Gulf region, chlorophyll levels varied from 0.96 to $1.18 \mu\text{g Chl } a \text{ l}^{-1}$ while in the Gulf of Oman they were 0.55 – $0.87 \mu\text{g Chl } a \text{ l}^{-1}$, respectively (El-Gindy and Dorgham, 1992). Also characterized as oligotrophic, the nearby Gulf of Aqaba phytoplankton biomass rarely exceeds $1 \mu\text{g Chl } a \text{ l}^{-1}$ (Al-Najjar et al., 2007; Suggett et al., 2009).

Jacob et al. (1982) estimated primary productivity to vary 10-fold from 60 to 600 mg C m^{-3} on the coast of Kuwait. We measured generally lower values, from 8.9 to 365 mg C m^{-3} around Qatar during the study period. There are few studies on primary production in the Gulf (Hadi et al., 1989; Sheppard et al., 1992; Subba Rao and Al-Yamani, 1998; Al-Yamani et al., 2006), fewer near Qatar (Ibrahim and El Samra, 1987). In the Shatt Al-Arab estuary, primary production values ranged from 5.44 to $52.9 \mu\text{g C l}^{-1} \text{ h}^{-1}$ (Al-Saadi et al., 1989; Hadi et al., 1989) and in the

northwest, 10.7 and $31.6 \mu\text{g C l}^{-1} \text{ h}^{-1}$ (Huq et al., 1978). In Kuwait, Al-Muzaini et al. (1991) found primary production varied from 1.32 to $27.2 \mu\text{g C l}^{-1} \text{ h}^{-1}$ with lower values in southern waters and higher values nearest to river runoff, respectively. Ibrahim and El Samra (1987) measured gross primary production rates of 59 – $82 \mu\text{g C l}^{-1} \text{ h}^{-1}$ in the spring of 1986 south of Doha, the capital of Qatar.

We estimated integrated primary production using average water column Chl *a* values, the assumption of a Chl:C ratio of 50 (Jacob et al., 1982), and the known water depth. For the latter assumption, we found the photic zone depth (measured with a Secchi disk) was equivalent to water column depth in 85% of cases. This is also consistent with the very high water transparency measured (NTU < 2 ; Supplemental Table 1). We found productivity at the western stations were decreased ($5.8 \pm 3.8 \mu\text{g C l}^{-1} \text{ h}^{-1}$), with highest values measured at the northeastern stations ($40.3 \pm 31 \mu\text{g C l}^{-1} \text{ h}^{-1}$) and relative high values at the southeastern stations of $30.7 \pm 15.6 \mu\text{g C l}^{-1} \text{ h}^{-1}$ (not shown). This pattern is consistent with observations for Chl *a* (Fig. 7a) and the fluorescence based estimates (Fig. 10h). The large standard deviations reflect seasonal variability. Our estimates are also similar to the values reported in the Shatt Al-Arab estuary (Al-Saadi et al., 1989; Hadi et al., 1989), Kuwait in the northwest, 10.7 and

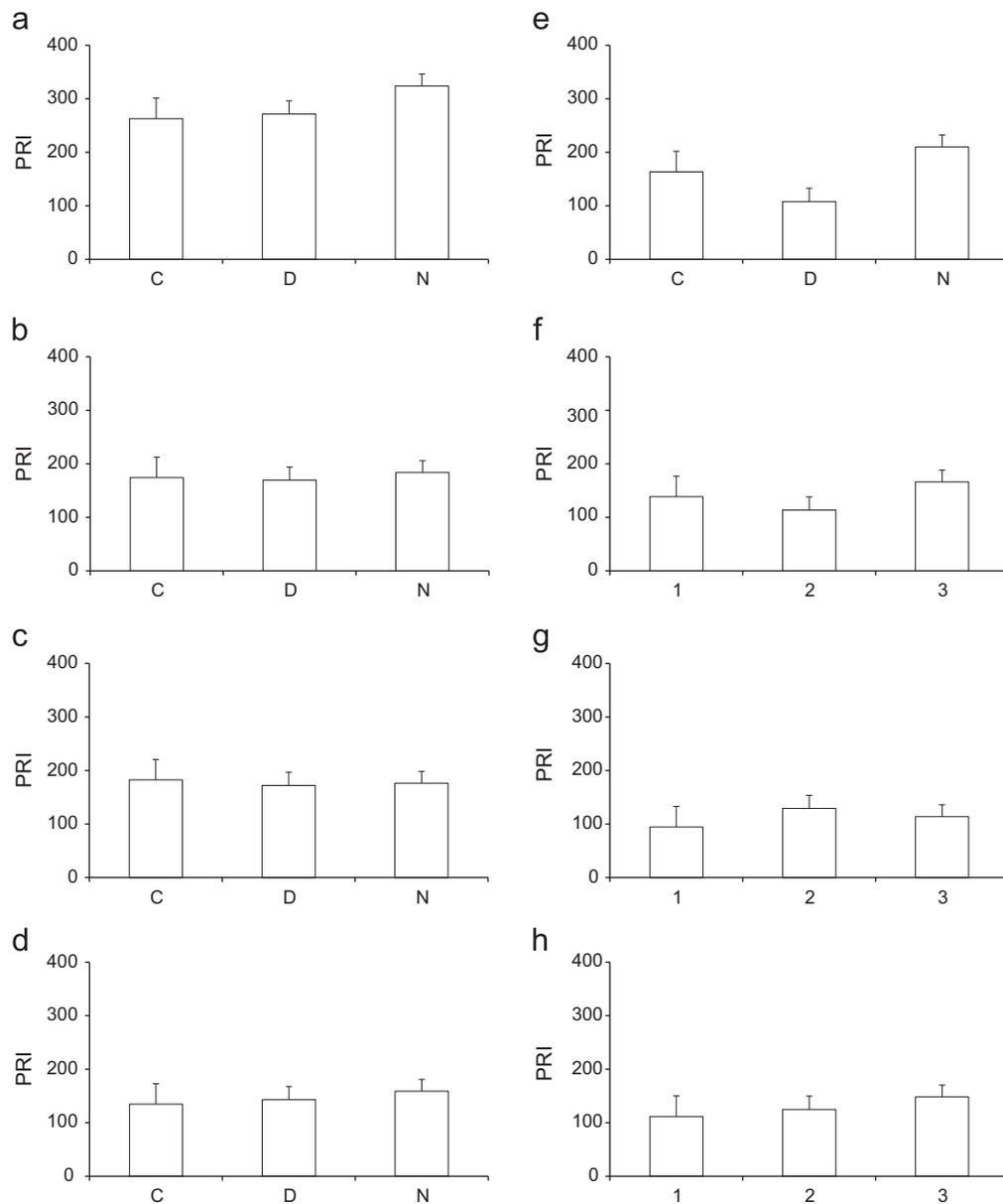


Fig. 9. Bioassays performed at select stations in February and May 2011 reveal nitrogen (as nitrate) limitation. The phytoplankton response index (PRI) was calculated from the change in Chl *a* ($\mu\text{g l}^{-1}$) concentration in the treatments: control (C), deep plus surface waters (D) and nitrogen addition (N). Bioassays were performed at (A) station 2, (B) station 7, (C) station 8 and (D) station 11 in February 2011 and at (E) station 5, (F) station 7, (G) station 11 and (H) station 13 in May 2011.

$31.6 \mu\text{g C l}^{-1} \text{h}^{-1}$ (Huq et al., 1978) and Qatar (Ibrahim and El Samra, 1987). The low productivity despite high species diversity has been reported for other subtropical and tropical seas (e.g., Venrick, 1993; DuRand et al., 2001).

4.3. Importance of nitrogen in driving primary production

For comparison to the literature in other parts of the world, we converted our primary production rates to more commonly used units: $0.14 \text{ gC m}^{-2} \text{ day}^{-1}$, $0.97 \text{ gC m}^{-2} \text{ day}^{-1}$ and $0.74 \text{ gC m}^{-2} \text{ day}^{-1}$ (averages of all four cruises) for the western, northeastern and southeastern stations, respectively. These values are consistent with the oligotrophic nature of this ecosystem, its low nutrient concentrations (see Supplemental Table 1) and ratios (DIN:P and DIN:Si ratios < 1). These low rates are likely the result of nutrient (as nitrogen) limitation, a contention supported by the nutrient enrichment assays performed (Fig. 10) and with earlier studies performed in the Gulf (e.g., Dorgham et al., 1987; Dorgham and Muftah, 1989; Al-Saadi et al., 1989; El-Gindy and Dorgham, 1992;

Jacob and Al-Muzaini, 1995) that hypothesized nitrogen limitation as the dominant factor controlling phytoplankton primary production. Interestingly, when we added nutrients collected from close to the sediment-water interface (bottom waters) to surface waters, phytoplankton growth was stimulated in two of the eight assays. Al-Qutob et al. (2002) and Suggett et al. (2009) showed stimulation of productivity in surface waters could be triggered by the addition of bottom waters. We have observed similar such responses in assays performed in the Gulf of Mexico and the Pacific Ocean (off the west coast of the US) (unpublished data). This suggests that benthic regeneration of nutrients may be an important source of nutrients to phytoplankton in this region.

An alternative source of 'natural' new nitrogen in the Gulf is *Trichodesmium* spp. which is abundant in the oligotrophic warm waters of the region (Table 2, Supplemental Table 2). It was estimated by El Samra et al. (1986) that $0.4\text{--}6.3 \text{ kg N km}^{-2} \text{ day}^{-1}$ of the total nitrogen budget from the Gulf comes from diazotrophy. Gruber and Sarmiento (1997) defined a quasi-conservative tracer, N^* , to investigate the distribution of N_2 fixation and denitrification

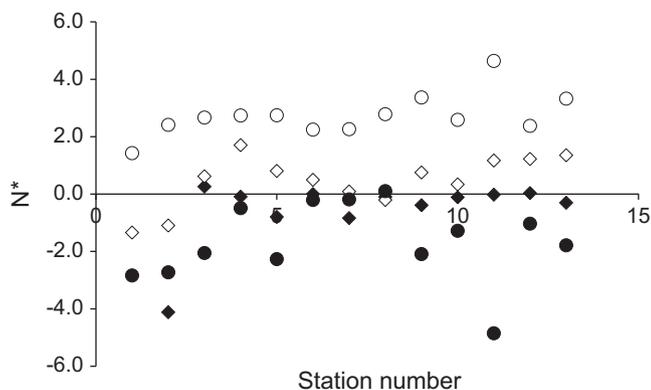


Fig. 10. Potential biological N_2 fixation measured using N^* values calculated for each station for the February 2010 (◆), July 2010 (◇), February 2011 (●) and May 2011 (○) cruises. Positive N^* values indicate products of N_2 fixation are utilized by primary producers in this system.

in the ocean. Using the principal described, we calculated an average N^* from all four cruises of $-4.10 \mu\text{mol kg}^{-1}$ for the Qatar peninsula, similar to their $< -3 \mu\text{mol kg}^{-1}$ for the Arabian Sea. By calculating the difference between the average N^* and the measured N^* for each station on each cruise we found an interesting pattern: in general, we had $-N^*$ values during the February cruises (2010 and 2011) and $+N^*$ values during the May 2011 and July 2010 cruises (Fig. 10). These patterns suggest the source of N for water column photosynthesis is variable between cooler and warmer months. Negative N^* values measured in February indicate the use of a nitrified source by primary producers while positive N^* values measured during warmer months suggests a denitrified source (explained by biological N_2 fixation) drives production. Examination of the changing patterns of abundance in *Trichodesmium* spp. observed in the present study support these switches (Table 2, Supplemental Table 2) as well as its known distribution in other world gyres. Measuring the natural abundance of stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopes may help to further elucidate spatial and temporal trends in the use of differential nitrogen sources within this system; this strategy providing interesting findings in the Gulf of Mexico (Dorado et al., 2012).

4.4. Potential response to development

Historically, nitrates, phosphates and silicates are generally more abundant in the Northwest region of the Gulf than those off Qatar and the United Arab Emirates to the south (Al-Saadi and Hadi, 1987; Hulburt et al., 1981; Halim, 1984). This is because the major source of riverine water (and with it nutrients) to the Gulf are the Euphrates and Tigris Rivers which discharge into the Shatt Al-Arab estuary in the north. However, with the current level of development in Gulf countries, this trend may no longer be valid. The consequence of increased nutrient inputs in some instances has resulted in harmful algal blooms with devastating impacts on the fishery (e.g., Subba-Rao et al., 1999; Heil et al., 2001; Richlen et al., 2010). Also of concern with alterations to nutrient inputs from the major rivers versus other sources, is a potential depletion of silicates, and with that a possible shift from a diatom dominated community to one dominated by dinoflagellates (which do not require silica). This has been observed in other areas such as in the Baltic Sea (Suikkanen et al., 2007; Wasmund and Uhlig, 2003). Aside from the potential for more harmful algal blooms associated with dinoflagellates, there is likely to be a negative impact on the

fishery (Sheppard et al., 2010). This kind of alteration to the food web has been observed in the Black Sea (Humborg et al., 1997).

Dorgham et al. (1987) and others have reported that there has been an increase in the number of diatoms and dinoflagellates appearing in the Gulf. The study suggested that the organic enrichment maybe the main reason but allochthonous transfer of species into the Gulf from the Arabian Sea and the Gulf of Oman was also postulated to play a role. Based on studies conducted in other locations (e.g., Galveston Bay; Steichen et al., 2012), the introduction of exotic algae into the area may also be related to ballast water associated with the thousands of cargo ships and oil tankers moving in and out of the region. There are serious concerns that these introductions could trigger ecological changes in the phytoplankton community structure, leading to potential economic loss to commercial fisheries (Subba Rao et al., 1994).

With population growth and development in Qatar, concerns have been raised concerning regarding the observations of algal blooms, some of which are associated with harmful or toxin producing species. Natural and aquaculture fish deaths observed nearby in Kuwait Bay (1999) and the United Arab Emirates and the Gulf of Oman (2008–2009) were associated with dinoflagellate blooms (*Gymnodinium* sp. and *Cochlodinium polykrikoides* respectively); these were linked to elevated nutrient concentrations (Subba-Rao et al., 1999; Heil et al., 2001; Richlen et al., 2010). Several decades earlier Dorgham et al. (1987) was first to predict and observe the abundant growth of the dinoflagellates in the Gulf associated with eutrophication, specifically the three harmful dinoflagellates *Pyrodinium bahamense*, *Gonyaulax polyedra* and *Prorocentrum micans*, species known to reside in the waters off Qatar and United Arab Emirates. Other toxic phytoplankton species have been reported to form blooms in the northwestern Arabian Sea (Dorgham and Muftah, 1989; Al-Yamani et al., 1997; Subba Rao and Al-Yamani, 1998; Subba-Rao et al., 1999). Whilst we observed these and other dinoflagellates in our samples, we did not observe any blooms during the four sampling campaigns on the coastline of Qatar. Blooms typically appear during March/April and October when water temperatures are cooler ($\sim 20^\circ\text{C}$). The lack of any pronounced seasonal blooms was recently examined for Kuwait by Al-Yamani et al., (2006) which agrees with our findings. These authors suggested a lack of stratification and turnover associated with seasons, losses due to lateral advection, grazing by zooplankton and/or bacterial activity as possible explanations. We did not find any stratification but did find the system to be heterotrophic (pers. obs). Lastly, the increasing number of dinoflagellate species in Qatari waters is of concern not only because they are able capable of forming harmful algal blooms but also because they are effective competitors for scarce resources (Al-Qutob et al., 2002).

Of the other species we observed, *Chaetoceros* spp., *Rhizosolenia* spp., *Dinophysis* spp., *Prorocentrum* spp., and the two *Trichodesmium* spp. are known to form blooms in this (Al-Hasan et al., 1990) and other regions. In many cases (except for the cyanobacteria), blooms of these species are often cited as symptomatic of increasing inorganic nutrient enrichment associated with eutrophication, pollution and increases in aquaculture. Greater sampling frequency is required to determine if and when these species may be blooming in the region, however our nutrient addition assays highlight the potential for eutrophication in this system.

5. Conclusion

The waters surrounding Qatar are comparable to the shallow littoral areas characterized by moderate to strong currents, sea-floor within the euphotic zone, and oxygenated water column. For the latter, circulation and wind (the 'Shamal') patterns ensure

waters are well mixed. We found these among other environmental parameters play a role in the relatively low phytoplankton biomass and gross production rates but high species diversity measured in this study. Furthermore, nutrient addition assays suggest future pressures related to development are likely to have a profound impact on primary production and the primary producers in the Qatari peninsula, a phenomenon already observed in the neighboring countries of Kuwait, the United Arab Emirates, the nearby Gulf of Oman and worldwide. As part of the 'Carbon Cycle' project (2010–2011) we have determined the present state of Qatar's coastal waters, creating an extensive database against which future conditions in Qatar's coastal habitats can be compared. These findings are intended to contribute to the growing body of ecological information on the unique conditions of the Gulf in comparison with regions elsewhere in the world where similar studies have been conducted.

Acknowledgments

Researchers at Qatar University (Environmental Studies Center), Texas A&M University at Galveston and Ministry of Environment would like to thank the Qatar National Research Fund (QNRF) for the support of Grant NPRP 08-497-1-086. The captain and crew of the research vessel "*Mukhtabar Al Bihar*" who made the work at sea possible, and the Qatar University ESC laboratory staff and technicians where all chemical and biological analyses of the samples were accomplished in Doha, are thanked. The ideas and content of this paper do not reflect the views of QNRF but rather those of the manuscript authors. We thank the two anonymous reviewers and the editor for comments which enhanced the quality of the manuscript.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.csr.2013.04.015>.

References

- Abdul Aziz, P.K., Al-Tisan, I.A., Daili, M.A., Green, T.N., Dalvi, A.G.I., Javeed, M.A., 2003. Chlorophyll and plankton of the Gulf coastal waters of Saudi Arabia bordering a desalination plant. *Desalination* 154, 291–302.
- Al-Harbi, S.M., 2005. Phytoplankton Composition of ROPME Sea Area (Arabian Gulf). *Journal of King Abdulaziz University, Marine Science* 16, 105–114.
- Al-Hasan, R.H., Ali, A.M., Radwan, S.S., 1990. Lipids, and their constituent fatty acids, of *Phaeocystis* sp. from the Arabian Gulf. *Marine Biology* 105, 9–14.
- Al-Muzaini, S., Samhanand, O., Hamoda, M.F., 1991. Sewage related impact on Kuwait's marine environment—a case study. *Water Science and Technology* 23, 203–210.
- Al-Najjar, T., 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-Qutob, M., Häse, C., Tilzer, M.M., Lazar, B., 2002. Phytoplankton drives nitrite dynamics in the Gulf of Aqaba, Red Sea. *Marine Ecology Progress Series* 239, 233–239.
- Al-Saadi, H.A., Hadi, R.A.M., Schiewer, U., Al-Mousawi, A.H., 1989. On the influence of the sewage drainage from Basrah City on the phytoplankton and related nutrients in the Shatt al-Arab estuary, Iraq. *Archives of Hydrobiology* 114 (443), 152.
- Al-Saadi, H.A., Hadi, R.A.M., 1987. Ecology and taxonomical studies on phytoplankton in Arab Gulf. *Journal of Biological Sciences* 18, 7–31.
- Al-Yamani, F.D., Subba Rao, A.M., Ismail, W., Al-Rifaie, K., 2006. Primary production off Kuwait, an arid zone environment, Arabian Gulf. *International Journal of Oceans and Oceanography* 1, 67–85.
- Al-Yamani, F.Y., Bishop, J., Al-Rifaie, K., Ismail, W., Al-Yaqout, A., Al-Omran, L., Kwarteng, A., Al-Ghadban, A., Sheppard, C., 1997. Assessment of the Effects of the Shatt al-Arab's Altered Discharge Regimes on the Ecology of the Northern Arabian Gulf. Final Report. Kuwait Institute for Scientific Research, Report No. KISR 5174, Kuwait.
- 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.
- Bivand, R.S., Pebesma, E.J., Gomez-Rubio, V., 2008. *Applied Spatial Data Analysis* with R. Springer, NY.
- Bohm, A., 1931. Peridinen aus dem Perisischen Golf und dem Golf von Oman. *Archiv fuer Protistenkunde* 74, 188–197.
- Borcard, D., Legendre, P., 2012. Is the Mantel correlogram powerful enough to be useful in ecological analysis? A simulation study. *Ecology* 93, 1473–1481.
- Bray, J.R., Curtis, J.T., 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs* 27, 326–349.
- Brook, M.C., Al Houqani, H., Al Mugrin, A., 2006. The current status and future requirements of water resources management in the Arabian Peninsula. In: Amer, K.M., Boer, B., Brook, M.C., Adeel, Z., Clusener-Godt, M., Saleh, W., Hamilton, (eds.). *Policy Perspectives for Ecosystem and Water Management in the Arabian Peninsula*. United Nations University International Network on Water, Environment and Health and UNESCO, Canada. United Nations University, UNU-INWEH.
- Clarke, K.R., Gorley, R.N., 2006. *PRIMER v6: User Manual/tutorial*. PRIMER-E, Plymouth, UK.
- Dorado, S., Rooker, J.R., Wissel, B., Quigg, A., 2012. Isotope baseline shifts in pelagic food webs of the Gulf of Mexico. *Marine Ecology Progress Series* 464, 37–49.
- Dorgham, M.M., Muftah, A., 1989. Environmental condition and phytoplankton distribution in the Arabian Gulf and Gulf of Oman, September 1986. *Journal of Marine Biological Association of India* 31, 36–53.
- Dorgham, M.M., Muftah, A., El-Deeb, I., 1987. Plankton Studies in the Arabian Gulf II. Autumn phytoplankton in the northwestern area. *Agricultural and Biological Sciences* 85, 215–235.
- Dorgham, M.M., Muftah, A., 1986. Plankton studies in the Arabian Gulf. I. Preliminary list of phytoplankton species in Qatari waters. *Arab Gulf Journal of Scientific Research* 4, 421–436.
- DuRand, M.D., Olson, R.J., Chisholm, S.W., 2001. Phytoplankton population dynamics at the Bermuda Atlantic time-series station in the Sargasso Sea. *Deep Sea Research* 48, 8–9.
- El-Gindy, A.A., Dorgham, M.M., 1992. Interrelations of phytoplankton, chlorophyll and physico-chemical factors in the Arabian Gulf and Gulf of Oman during summer. *Indian Journal of Marine Sciences* 21, 257–261.
- El Samra, M.I., Emara, H.I., Shunbo, F., 1986. Dissolved petroleum hydrocarbons in the Northwestern Arabian Gulf. *Marine Pollution Bulletin* 17, 65–68.
- Fisher, T.R., Gustafson, A.B., Sellner, K., Lacutere, R., Haas, L.W., Magnien, R., Karrh, R., Michael, B., 1999. Spatial and temporal variation in resource limitation in Chesapeake Bay. *Marine Biology* 133, 763–778.
- Granéli, E., Turner, J.T., 2006. *Ecology of harmful algae*. Series: Ecological Studies, vol. 189. Springer Verlag, Heidelberg 413 pp.
- Gruber, N., Sarmiento, J.L., 1997. Global patterns of marine nitrogen fixation and denitrification. *Global Biogeochemical Cycles* 11, 235–266.
- Hadi, R.A.M., Al-Mousawi, A.H., Al-Zubaidy, A.J.M., 1989. A study on the primary productivity in the Shatt Al-Arab estuary at Basrah, Iraq. *Journal of Biological Sciences Research* 20, 593–606.
- Halim, Y., 1984. Plankton of the Red Sea and the Arabian Gulf. *Deep-Sea Research* 34, 969–982.
- Hashim, A., Hajjaj, M., 2005. Impact of desalination plants fluid effluents on the integrity of seawater, with the Arabian Gulf in perspective. *Desalination* 182, 373–393.
- Heil, C.A., Glibert, P.M., Al-Sarawi, M.A., Faraj, M., Behbehani, M., Husain, M., 2001. First record of a fish-killing *Gymnodinium* sp. bloom in Kuwait Bay, Arabian Sea: chronology and potential causes. *Marine Ecology Progress Series* 214, 15–23.
- Hijmans, R.J., van Etten, J., 2012. *Raster: Geographic Analysis and Modeling with Raster Data*. R Package Version 1.9-82. (<http://CRAN.R-project.org/package=raster>).
- Howarth, R.W., Marino, R., 2006. Nitrogen as the limiting nutrient for eutrophication in coastal marine ecosystems: Evolving views over 3 decades. *Limnology and Oceanography* 51, 364–376.
- Hulburt, E.M., Mohmoodian, F., Russell, M., Stalcup, F., Lalezary, S., Amirhor, P., 1981. Attributes of the plankton flora at Bushehr, Iran. *Hydrobiologia* 79, 51–63.
- Humborg, C., Ittekkot, V., Cociasu, A., Bodungen, B.V., 1997. Effect of Danube River dam on Black Sea biogeochemistry and ecosystem structure. *Nature* 386, 385–388.
- Huq, M.F., Al-Saadi, A., Hameed, H.A., 1981. Studies on the primary production of the river Shatt Al-Arab at Basrah, Iraq. *Hydrobiologia* 77, 25–29.
- Huq, M.F., Al-Saadi, H.A., Hadi, R.A., 1978. Preliminary studies on the primary production of north-west Arabian Gulf during post monsoon period. *Journal of Oceanographical Society of Japan* 34, 78–80.
- Ibrahim, M.A., El Samra, M.I., 1987. Inhibition effect of four oil dispersants on primary productivity in Qatar water (Arabian Gulf). *Qatar University Science Bulletin* 7, 379–391.
- Jacob, P.G., Al-Muzaini, S., 1995. Marine plants of the Arabian Gulf and effects of oil pollution. *Mahasagar* 28, 83–101.
- Jacob, P.G., Zarba, M.A., Mohammad, O.S., 1982. Water quality characteristics of selected beaches of Kuwait. *Indian Journal of Marine Sciences* 11, 233–238.
- Jacob, P.G., Zarba, M.A., Anderlini, V., 1980. Observations on the plankton and hydrography of the Kuwaiti waters. *Mahasagar* 13, 325–334.
- Jacob, P.G., Zarba, M.A., Anderlini, V., 1979. Hydrography, chlorophyll and plankton of the Kuwaiti coastal waters. *Indian Journal of Marine Sciences* 8, 150–154.

- Kolber, Z.S., Prasil, O., Falkowski, P.G., 1998. Measurements of variable chlorophyll fluorescence using fast repetition rate techniques: defining methodology and experimental protocols. *Biochimica et Biophysica Acta* 1367, 88–106.
- Lattemann, S., Hopner, T., 2008. Environmental impact and impact assessment of seawater desalination. *Desalination* 220, 1–15.
- Legendre, P., Legendre, L., 1998. *Numerical Ecology*, 2nd edition. Elsevier Science, BV, Amsterdam 853 pp.
- Nour El-Din, N.M., Al-Khayat, J.A., 2005. Phytoplankton-zooplankton relations in three inland seas along the Qatari coast (Arabian Gulf). *International Journal of Environmental Studies* 62, 375–390.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2011. *Vegan: Community Ecology Package*. R Package Version 2.0-2. (<http://CRAN.R-project.org/package=vegan>).
- Parsons, T.R., Maita, Y., Lalli, C.M., 1984. *A Manual of Chemical and Biological Methods for Seawater Analysis*. Pergamon Press, New York.
- QMEMP, 2005. Qatar Marine Environment Monitoring Program, Prepared by Technical Affairs Department, Supreme Council for the Environment and Natural Reserves (Currently Ministry of Environment), State of Qatar, 54 pp.
- Quigg, A., Kotabová, E., Jarešová, J., Kaňá, R., Šetlík, J., Šedivá, B., Komárek, O., Prášil, O., 2012. Photosynthesis in *Chromera velia* represents a simple system with high efficiency. *PLOS One* 7 (10), e47036.
- R Development Core Team, 2012. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rezai, H., Wilson, S., Claerebolid, M., Riegl, B., 2004. Coral reef status in the ROPME Sea area: Arabian/Persian Gulf, Gulf of Oman and Arabian Sea. In: Wilkinson, C. (ed.), *Status of the Coral Reefs of the World*. pp. 155–170. Status of Coral Reefs of the World: 2004, vol. 1. Australian Institute of Marine Science, Townsville, Queensland, Australia. 301 pp.
- Richlen, M.L., Morton, S.L., Jamali, E.A., Rajan, A., Anderson, D.M., 2010. The catastrophic 2008–2009 red tide in the Arabian gulf region, with observations on the identification and phylogeny of the fish-killing dinoflagellate *Cochlodinium polykrikoides*. *Harmful Algae* 9, 163–172.
- ROPME (Regional Organization for the Protection of the Marine Environment), 1999. *Regional Report of the State of the Marine Environment*, Regional Organization for the Protection of the Marine Environment, State of Kuwait, March 1999.
- Roux, D.J., 1999. Design of a national programme for monitoring and assessing the health of aquatic ecosystems, with specific reference to the South African river health programme. *Environmental Science Forum* 96, 13–32.
- Sheppard, C.R.C., Al-Husiani, M., Al-Jamali, F., Al-Yamani, F., Baldwin, R., Bishop, J., Benzoni, F., Dutrieux, E., Dulvy, N.K., Subba-Rao, D.V., Jones, D.A., Loughland, R., Medio, B., Nithyanandan, M., Pillingm, G.M., Polikarpov, I., Price, A.R.G., Purkis, S., Riegl, B., Saburova, M., Namin, K.S., Taylor, O., Wilson, S., Zainal, K., 2010. The Gulf: a young sea in decline. *Marine Pollution Bulletin* 60, 13–38.
- Sheppard, C.R.C., 1993. Physical environment of the Gulf relevant to marine pollution: an overview. *Marine Pollution Bulletin* 27, 3–8.
- Sheppard, C.R.C., Price, A.R.G., Roberts, C.M., 1992. *Marine Ecology of the Arabian Region: Patterns and Processes in Extreme Tropical Environments*. Academic Press, London.
- Steichen, J., Windham, R., Brinkmeyer, R., Quigg, A., 2012. Ballast water impacts on Galveston Bay, Texas. *Marine Pollution Bulletin* 64, 779–789.
- Subba-Rao, D.V., Al-Yamani, F., Lennox, A., Pan, Y., As-Said, T.F.O., 1999. Biomass and production characteristics of the first red tide noticed in Kuwait Bay, Arabian Gulf. *Journal of Plankton Research* 21, 805–810.
- Subba-Rao, D.V., Al-Yamani, F., 1998. Phytoplankton ecology in the water between Shatt Al-Arab and the Straits of Hormuz, Arabian Gulf: a review. *Plankton Biology and Ecology* 45, 101–116.
- Subba Rao, D.V., Sprules, W.G., Locke, A., Carlton, J.T., 1994. Exotic phytoplankton from ship's ballast waters: risk of potential spread to mariculture sites on Canada's East Coast. *Canadian Data Report of Fisheries and Aquatic Sciences* 937, 1–51.
- Suggett, D.J., Prasil, O., Borowitzka, M.A., 2010. Chlorophyll a Fluorescence in Aquatic Sciences: Methods and Applications. Springer, Dordrecht 103–127.
- Suggett, D.J., Stambler, N., Prášil, O., Kolber, Z., Quigg, A., Vázquez-Domínguez, E., Zohary, T., Berman, T., Iluz, D., Levitan, O., Lawson, T., Meeder, E., Lazar, B., Bar-Zeev, E., Medova, H., Berman-Frank, I., 2009. Nutrient control of oceanic microbial growth during spring in the Gulf of Aqaba. *Aquatic Microbial Ecology* 56, 227–239.
- Suikkanen, S., Laamanen, M., Huttunen, M., 2007. Long-term changes in summer phytoplankton communities of the open northern Baltic Sea. *Estuarine, Coastal and Shelf Science* 71, 580–592.
- Thronson, A., Quigg, A., 2008. Fifty five years of fish kills in Coastal Texas. *Estuaries and Coasts* 31, 802–813.
- van Etten, J., 2011. *Gdistance: Distances and Routes on Geographical Grids*. R Package Version 1.1-2. (<http://CRAN.R-project.org/package=gdistance>).
- Venrick, E.L., 1993. Phytoplankton seasonality in the Central North Pacific: the endless summer reconsidered. *Limnology and Oceanography* 38, 1135–1149.
- Ward, J.H., 1963. Hierarchical grouping to optimize an objective function. *Journal of American Statistical Association* 48, 236–244.
- Wasmund, N., Uhlig, S., 2003. Phytoplankton. Trends in the Baltic Sea. *ICES Journal of Marine Science* 60, 177–186.
- Whitaker, D., Christman, M., 2010. *Clustsig: Significant Cluster Analysis*. R Package Version 1.0. (<http://CRAN.R-project.org/package=clustsig>).