



Multiple environmental factors influence the spatial distribution and structure of reef communities in the northeastern Arabian Peninsula

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ABSTRACT

Multivariate analysis revealed distinct sub-regional coral communities among the southern Persian Gulf, Strait of Hormuz, and Gulf of Oman. Differences in community structure among locations were associated with considerable spatial heterogeneity in oceanic conditions, and strong directional environmental gradients. Despite clear community differences, considerable changes to coral community structure have occurred throughout the northeastern Arabian Peninsula as compared with previous studies. The most dramatic of these are the apparent changes from *Acropora* dominated to poritid and faviid dominated communities, particularly in the southern Persian Gulf and Strait of Hormuz. Although temperature and salinity have previously been cited as the major environmental factors structuring coral communities around the region, additional environmental parameters, including chlorophyll-*a*, surface currents and winds are shown to be important in structuring reef communities throughout the northeastern Arabian Peninsula.

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1. Introduction

Irrespective of location, coral reef communities must respond to substantial variations in environmental conditions in order to successfully recruit, grow, reproduce and survive (Kleypas et al., 1999; Done, 1999). On local and geographic scales, the structure and development of coral reef communities are subject to diverse and often interacting environmental variables (e.g., temperature, light, salinity, solar radiation, sedimentation, hydrodynamic factors) (Brown, 1997; Kleypas et al., 1999; Done, 2011). Collectively, these factors can affect the growth rate, growth form, reproduction, and the overall abundance, composition and diversity of communities (Brown, 1997; Kleypas et al., 1999; Done, 2011). However, fluctuations in a range of environmental variables (i.e., physical and chemical), mediated by changes in global climate, are predicted to directly affect the abundance, diversity, and composition of coral reef communities (Done, 1999; Purkis and Riegl, 2005; Baker et al., 2008), and may lead to further degradation of these reef systems globally (Hughes et al., 2003). Therefore, determining how different coral reef communities vary over their present range of environmental conditions, particularly reefs already surviving in

extreme conditions, will be vital in understanding how these communities may respond to increasing changes in global climate (Kleypas et al., 1999).

The northeastern Arabian Peninsula is bounded by the Persian Gulf and the Gulf of Oman, two marginal seas distinguished by substantially different environmental and oceanographic conditions (Sheppard et al., 1992; Reynolds, 2002). Due to its high-latitude position, shallow nature and restricted water exchange, the marine environment of the Persian Gulf is characterized by extremes in salinity and sea surface temperature (SST) (Sheppard et al., 1992; Coles, 2003), with high levels of sedimentation and turbidity (Riegl, 1999) and low levels of primary production (Nezlin et al., 2007). In contrast, the adjacent Gulf of Oman is well mixed by strong seasonal upwelling from the Arabian Sea (Reynolds, 1993; Böhm et al., 1999), resulting in comparatively mild seasonal changes in SST (range 22–32 °C) and salinity (35–37 psu) (Coles, 1997; Schils and Wilson, 2006), with relatively high primary production in the upper ocean as a response to seasonal winter monsoons (Piontkovski et al., 2011). Amid the Persian Gulf and Gulf of Oman, the Strait of Hormuz approximates a boundary between the two systems (Reynolds, 1993). Water exchange and circulation patterns result in strong seasonal stratification (Thoppil and Hogan, 2010), with SST and salinity comparatively lower in range than the Persian Gulf but higher than in the Gulf of Oman (Thoppil and Hogan, 2009).

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Several studies have shown that coral reef communities along the northeastern Arabian Peninsula are a distinct biogeographical subset, separated from communities in the wider Indo-Pacific and the Red Sea (Sheppard, 1987, 1998; Sheppard and Sheppard, 1991; Sheppard et al., 1992). Coral communities in this region support about 10% of the species that occur throughout the Indo-Pacific (Sheppard et al., 1992; Coles, 2003). Compared to most Indo-Pacific reefs, coral reef communities in the Arabian region exhibit relatively low coral diversity, with few species in the family Acroporidae and a high representation of the families Siderasteridae and Faviidae (Veron, 2000; Coles, 2003). Such dissimilarities between Arabian and Indo-Pacific reef communities have traditionally been related to extreme temperature and salinity regimes throughout the Arabian region. However, the majority of these studies only considered these variables in relative isolation (Sheppard, 1987; Sheppard and Sheppard, 1991; Sheppard et al., 1992; Coles, 2003), with little consideration of other oceanic variables important in structuring reef communities (Brown, 1997; Done, 1999).

This paper provides a comprehensive regional examination of coral communities within the northeastern Arabian Peninsula, and the first in over two decades (Sheppard, 1987; Sheppard and Sheppard, 1991). Here we examined and compared the abundance, composition, diversity and richness of coral reef communities throughout the northeastern Arabian Peninsula. Moreover, we investigated and quantitatively compared the range of environmental variables considered important in structuring these communities between locations.

2. Materials and methods

2.1. Benthic community surveys

Benthic reef communities were surveyed at 18 sites within the southern Persian Gulf, Arabian Peninsula side of Strait of Hormuz and Gulf of Oman from October to November 2008 (Fig. 1, see Appendix A for site details). At each site, surveys were conducted on eight 30 × 1 m belt transects at a depth of 6–8 m (Bauman et al., 2010). Along each transect benthic communities were

surveyed within a 0.25 m² quadrat photographed at 3 m intervals (Bauman et al., 2010). Composition and percent cover of benthic taxa were quantified within each quadrat using 50 randomly distributed points within CPCE image analysis software, version 5 (Kohler and Gill, 2006). Benthic cover were categorized into eight major groups: (i) hard coral, (ii) soft coral, (iii) sponge, (iv) filamentous/fleshy algae (FFA), (v) coralline crustose algae (CCA), (vi) other live, (vii) recently dead coral (RDC), and (viii) sand, pavement and rubble (SPR). Hard coral were further identified to species level where possible (Veron, 2000; Claereboudt, 2006). Samples were standardized as percent of total cover.

2.2. Environmental variables

Physical parameters of temperature, salinity and ocean currents (east and north components) for each location were obtained from a numerical ocean model: the 1/12° Global Hybrid Coordinate Ocean Model (HYCOM), maintained by the Naval Research Laboratory (NRL), Stennis Space Center (Metzger et al., 2010). The non-assimilative version (18.2) of the model was selected due to its extended time span (2004–2009) as compared with the assimilative version (90.8, 2009–2010) and because comparisons during the 1-year overlap indicated similar results at the study locations. At each site monthly temperature and salinity data were extracted and long-term mean, variability and annual range were calculated. Monthly ocean currents were binned into octants (45°), and the mean current and percentage of time within each octant was determined. Using shoreline direction, the mean current and percentage of time were also calculated for along-shore and cross-shore quadrants at each survey site.

To provide a comparison of primary productivity between the locations, 8-day composites of chlorophyll-*a* (chl-*a*) data at 0.05° resolution from MODIS Aqua were acquired for the period 4 July, 2002–20 July, 2010. Data were examined within a 5 × 5-pixel box centered at each survey location and the median value (of up to ~100 values) for each month calculated. This was undertaken to exclude data with contamination due to bottom-reflectance in shallow waters (see Cannizzaro and Carder, 2006) in evaluating variation across the three locations.

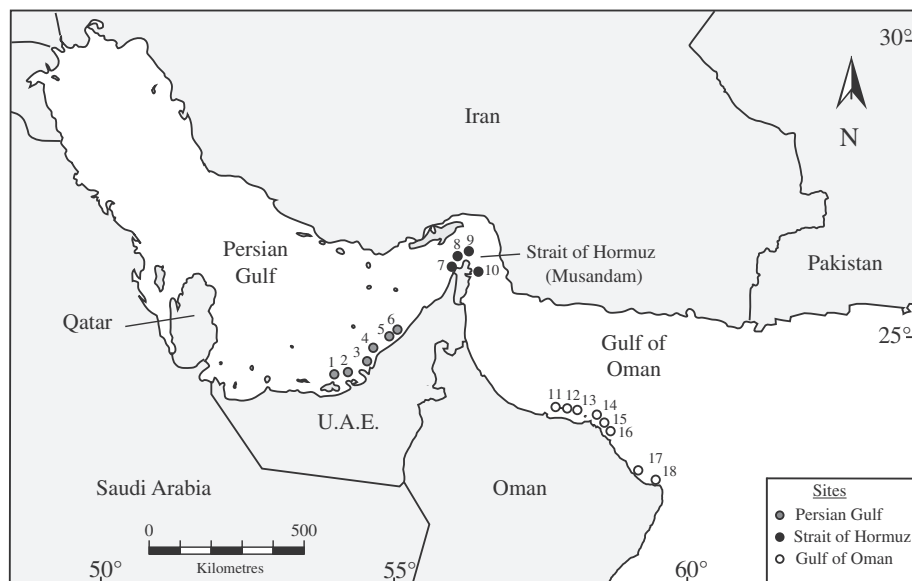


Fig. 1. Map of study sites around the northeastern Arabian Peninsula, with numbers indicating sampling sites. Southern Persian Gulf (1. Bu Tinah, 2. Al Hiel, 3. Saadiyat, 4. Ras Ghanada, 5. Saih Al Shaib, 6. Ras Hasyan); Strait of Hormuz (7. Khasab Reef, 8. Coral Garden, 9. Rashid Island West, 10. E. Musandam); and Gulf of Oman (11. Al Ghattan, 12. Al Jazeera, 13. Fort Island, 14. Qantab, 15. Jussa West, 16. Jussa Point, 17. Al Heddl, 18. Turtle Beach).

Wind data for each site were acquired from 2002 to 2011 from the Blended Sea Winds product (<http://www.ncdc.noaa.gov/oarsad/air-sea/seawinds.html>). Monthly means of the east- and north-directed components were calculated. Mean wind speed and percentage of time in each 45° octant and for along- and cross-shore quadrants were determined at each survey site.

2.3. Data analysis

Non-metric multidimensional scaling (MDS) was used to examine benthic group patterns across locations (Clarke and Warwick, 2001). Prior to analysis, mean benthic cover was obtained by pooling transect data across each site, and then categorizing sites within each location. All data were then arcsine square-root transformed. Analysis of similarity (ANOSIM) was then used to test the significance of differences between *a priori* defined 'benthic groups' and 'locations'. ANOSIM is a multivariate randomization test used to compare individual sites within locations based upon ranked benthic abundance data using Bray–Curtis dissimilarity matrices. The tests yield *R* statistics ranging between –1 and 1 that infer a degree of location separation. *R*-values close to zero suggest there are no differences among locations (i.e., the null hypothesis is true), while *R*-values of magnitude > 0.5 indicate a strong difference among locations (i.e. the null hypothesis is false) (Clarke and Warwick, 2001). *P* values were then calculated for each *R* statistic using a permutation test of random rearrangement. Where there were significant differences in benthic cover between locations, a similarity percentage analysis (SIMPER) was performed to identify and quantify the contribution of benthic groups to community dissimilarity. SIMPER is a method for assessing which groups are primarily responsible for an observed difference between samples (Clarke and Ainsworth, 1993). One-way ANOVA with post hoc Tukey's unequal-N HSD tests were then used to identify significant differences in benthic groups among locations.

Coral species composition and diversity patterns were compared between locations. ANOSIM analysis was used to test for differences in coral community composition between locations (Clarke and Warwick, 2001). ANOSIM results were graphically interpreted using MDS, and SIMPER analysis was then used to determine which coral species contributed to community differences (Clarke and Warwick, 2001). Only coral species found in more than 5% of sites were included in multivariate analyses to preclude the confounding effects of outliers (McCune and Grace, 2002). Patterns of coral species diversity among location were then calculated using three diversity metrics, species richness (*S*), Shannon–Wiener diversity index (*H'*) and Pielou's evenness (*J'*) and analyzed using one-way ANOVA and post hoc unequal-N HSD tests.

Temperature, salinity and chl-*a* data were compared among locations using one-way ANOVA. Prior to analysis the data were square-root transformed. Where there were significant differences in each environmental variable between locations, unequal-N HSD Tukey's tests were used to identify differences. The BEST analyses (using the BIO-ENV procedure, PRIMER v6, Clarke and Gorley, 2006) were used to assess the influence of environmental variables on patterns of benthic groups, and separately on coral community distribution patterns (Clarke and Ainsworth, 1993; Clarke et al., 2008). The null hypothesis tested was that there was no relationship between environmental variables and benthic groups or coral community patterns among locations. Prior to analyses untransformed and \log_e transformed environmental variables were normalized to account for different scales and units. Where possible, the range, mean maximum and mean minimum values of each environmental variable were used in the analysis. Environmental variables were pre-screened for multi-collinearity using draftsman plots (Clarke and Ainsworth, 1993), and any subsets of variables strongly collinear (i.e., >0.95) were reduced to a single representa-

tive variable. The BIO-ENV was run using Spearman rank correlations (ρ) and the significance of correlations was tested with the global BEST permutation tests (Clarke and Ainsworth, 1993).

Environmental variables identified by BEST procedure were subsequently included as explicative variables in a linkage tree using LINKTREE (PRIMER v6 Clarke and Gorley, 2006). This technique constructs a hierarchical tree that reflects how biotic samples from an underlying resemblance matrix are most naturally split into successively smaller groups for a set of observations (Clarke et al., 2008). The position of divisions on the vertical axis of the dendrogram indicates the absolute measure of group differences (*B*%) at that level. Quantitative thresholds for each division are provided for each relevant variable from the explanatory data. A similarity profile permutation test using $p > 0.05$ as the significance criterion (SIMPROF; Clarke et al., 2008) was used in conjunction with the LINKTREE for stopping unwarranted subdivisions at those links in which no significant multivariate structure was considered present among remaining biological samples.

3. Results

3.1. Benthic groups

MDS ordination indicated strong differences in benthic groups between the three locations (Fig. 2a). ANOSIM confirmed significant differences between locations ($R = 0.66$, $P < 0.001$) and for all three pair-wise comparisons (Persian Gulf \times Gulf of Oman: $R = 0.63$, $p < 0.001$; Persian Gulf \times Strait of Hormuz: $R = 0.67$, $p < 0.01$; Gulf of Oman \times Strait of Hormuz: $R = 0.74$, $p < 0.001$). SIMPER showed that dissimilarity in benthic groups among

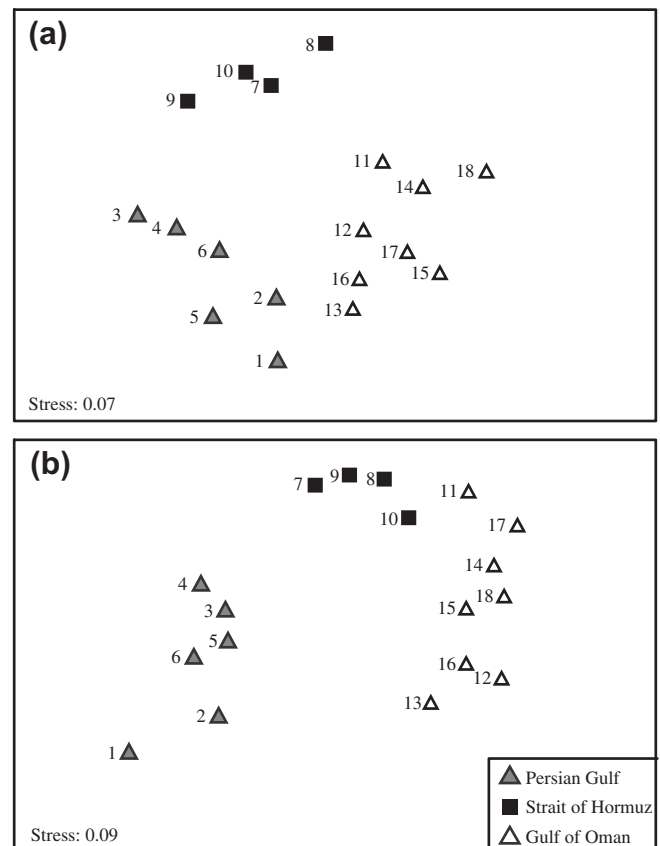


Fig. 2. MDS ordination plots of (a) benthic groups and (b) coral communities in the southern Persian Gulf, Strait of Hormuz and the Gulf of Oman. Each point represents the mean community at each of the 18 sites.

Table 1

Results of comparisons among benthic groups in the Persian Gulf, Strait of Hormuz and the Gulf of Oman, pooled for each location. The *R*-statistic and its *p*-value for comparisons among locations are shown, along with average percent dissimilarity (Mean δ %), individual and cumulative contribution (δ %) to dissimilarity from SIMPER. Where significantly different, percent cover of benthos that contributed >10% to dissimilarity are listed. CCA = crustose coralline algae; SPR = sand, pavement and rubble; FFA = filamentous/fleshy algae.

Benthic variable	Locations compared (% cover)		Contribution δ (%)	Cumulative δ (%)	<i>R</i>	<i>p</i>	Mean δ (%)
Soft coral	Persian Gulf	Gulf of Oman			0.63	<0.001	26.9
	0	14.3	25.98	25.98			
	20.4	14.9	14.88	40.87			
	6.8	0.86	12.53	53.40			
CCA	Persian Gulf	Gulf of Oman			0.67	<0.001	34.3
	54.1	19.9	25.83	25.83			
	20.4	43.2	18.89	44.72			
	0	13.4	15.92	60.64			
SPR	Persian Gulf	Strait of Hormuz			0.74	<0.001	35.1
	54.1	19.9	25.83	25.83			
	20.4	43.2	18.89	44.72			
	0	13.4	15.92	60.64			
FFA	Persian Gulf	Strait of Hormuz			0.74	<0.001	35.1
	54.1	19.9	25.83	25.83			
	20.4	43.2	18.89	44.72			
	0	13.4	15.92	60.64			
CCA	Gulf of Oman	Strait of Hormuz			0.74	<0.001	35.1
	14.9	43.2	26.84	26.84			
	49.1	19.9	20.31	47.16			
	10.6	3.9	17.29	64.44			
CCA	Gulf of Oman	Strait of Hormuz			0.74	<0.001	35.1
	14.9	43.2	26.84	26.84			
	49.1	19.9	20.31	47.16			
	10.6	3.9	17.29	64.44			

locations was driven mainly by differences in hard and soft coral, and sand, pavement and rubble (SPR) (Table 1). Benthic groups in the Persian Gulf and Gulf of Oman were the most similar (26.9% dissimilar) (Table 1). SPR was the most common benthic group throughout locations, ([average cover \pm SE], $41.3 \pm 10.8\%$), while hard coral ($26.2 \pm 8.6\%$) and soft coral ($9.25 \pm 0.69\%$) were the next most abundant benthic groups. All other benthic groups made up a relatively minor component of the reef communities (Fig. 3).

All benthic groups identified in the SIMPER analysis as driving regional community differences showed significant differences among locations in one-way ANOVAs (with the exception of sponge [ANOVA $F_{(2,141)} = 13.9$, $p = 0.68$], and soft corals [ANOVA $F_{(2,141)} = 21.3$, $p = 0.37$]) (Fig. 3). Post hoc comparisons showed that hard coral and coralline algae cover were significantly higher in the Strait of Hormuz than the other locations ($p < 0.05$ for each comparison), while the Persian Gulf had significantly more recently dead coral (RDC; $p < 0.05$), and the Gulf of Oman had significantly higher percent of other live ($p < 0.05$; Fig. 3). The Persian Gulf and Gulf of Oman both had significantly higher cover of filamentous/fleshy algae and SPR than the Strait of Hormuz (Fig. 3, $p < 0.05$ for each comparison, respectively).

3.2. Coral communities

A total of 76 coral species from 30 genera were identified among the three locations (see Appendix B for complete species list). Species richness (*S*), Shannon–Wiener diversity (*H'*) and Pie-

lou's evenness (*J'*) all showed significant differences among locations (ANOVA $F_{(2,15)} = 12.63$, $F_{(2,15)} = 8.04$, and $F_{(2,15)} = 4.17$, respectively, $p < 0.05$ for each). Post hoc unequal-N HSD tests showed that the Persian Gulf had significantly lower total species richness and diversity than the Strait of Hormuz and Gulf of Oman ($p < 0.001$ each), while Gulf of Oman had significantly higher total species evenness than Persian Gulf and Strait of Hormuz ($p < 0.001$ each; Table 2). ANOSIM indicated significant differences in species composition between locations ($R = 0.58$, $p < 0.001$; Fig. 2b), although pair-wise comparisons showed no differences in species composition between Strait of Hormuz and the Gulf of Oman ($R = 0.11$, $p = 0.25$). In contrast, coral communities in the Strait of Hormuz and the Gulf of Oman were both significantly different from Persian Gulf (Persian Gulf \times Gulf of Oman: $R = 0.81$, $p < 0.001$; Persian Gulf \times Strait of Hormuz: $R = 0.71$; $p < 0.001$; Fig. 2b). SIMPER analysis indicated the highest dissimilarity in species composition between Persian Gulf and Gulf of Oman (76.6% dissimilar), and relatively high dissimilarity between Persian Gulf and Strait of Hormuz (67.3% dissimilar; Table 3). Of the coral species that predominantly contributed to dissimilarity in community structure between locations, 69% were more abundant in Strait of Hormuz and the Gulf of Oman; five of these species were absent from the Persian Gulf (Table 3).

The Persian Gulf and Strait of Hormuz were dominated by a relatively small number of coral genera, reflected by relatively low evenness values for both locations (Persian Gulf *E*: 0.42; Strait of Hormuz *E*: 0.47) (Fig. 4). In the Persian Gulf and Strait of Hormuz

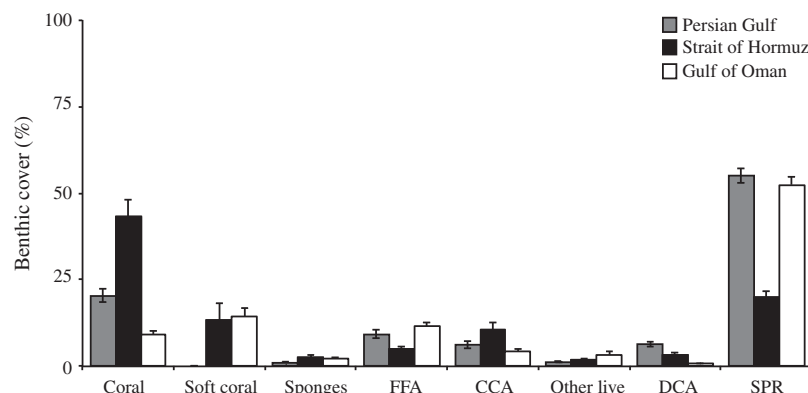


Fig. 3. Benthic community patterns: percent cover of the major benthic categories at each location. FFA = filamentous/fleshy algae; CCA = crustose coralline algae; RDC = recently dead coral; SPR = sand, pavement and rubble.

Table 2

Coral richness (*S*), diversity (*H'*) and evenness (*J'*) from the southern Persian Gulf, Strait of Hormuz and the Gulf of Oman. *Indicates significant difference at $p < 0.05$.

Location	Richness (<i>S</i>)	Diversity (<i>H'</i>)	Evenness (<i>J'</i>)
Persian Gulf	29*	$1.9 \pm 0.19^*$	0.42 ± 0.03
Straits of Hormuz	49	3.1 ± 0.11	0.47 ± 0.02
Gulf of Oman	55	3.4 ± 0.09	$0.83 \pm 0.04^*$

the genus *Porites* accounted for >50% of total coral cover (Persian Gulf: $61.3 \pm 1.41\%$; Strait of Hormuz: $51.2 \pm 3.65\%$), while faviids represented >25% total coral cover in both locations. In contrast, Gulf of Oman coral communities held a relatively high number of coral genera, reflected in a high evenness value for this location (Gulf of Oman *E*: 0.83) (Fig. 4). Within the Gulf of Oman four genera: *Platygyra* ($19.2 \pm 1.41\%$), *Porites* ($15.8 \pm 1.01\%$), *Hydnophora* ($13.1 \pm 0.78\%$) and *Acropora* ($12.2 \pm 0.24\%$) accounted for approximately 60% of total coral cover.

3.3. Environmental variables

Although mean annual SST showed negligible differences among locations ($p = 0.412$), the mean annual range of SST varied considerably among locations (Table 4). Mean annual range of SST within the southern Persian Gulf was 4.6°C and 6.3°C greater than within the Strait of Hormuz and Gulf of Oman, respectively. Mean annual salinity differed significantly among locations ($F_{(2,15)} = 4.98$, $p < 0.05$), with significantly higher salinity in the southern Persian Gulf ($p < 0.05$; Table 4). The mean annual range in salinity also differed among locations, with the largest annual

range in salinity apparent in the southern Persian Gulf (Table 4). Mean annual chl-*a* concentrations differed significantly among locations ($F_{(2,24)} = 4.51$, $p < 0.05$), with significantly higher chl-*a* concentrations in the Gulf of Oman ($p < 0.05$; Table 4). The annual range in mean chl-*a* also differed among locations, with the largest range in chl-*a* concentration apparent within the Gulf of Oman (Table 4). The months of mean highest and lowest chl-*a* concentrations were identical for the Strait of Hormuz and Gulf of Oman (February = highest, May = lowest), in contrast to the southern Persian Gulf (September = highest, March = lowest). Importantly, these results are consistent with recent reports of seasonal chl-*a* from the region (see Nezlin et al., 2010; Piontkowski et al., 2011).

Summaries of the currents and wind data are provided as rose plots for each location (Fig. 5), where direction indicates the motion for both parameters (i.e., oceanographic, not meteorological, convention). For most cases the most frequent directions of currents/wind also recorded the highest mean speeds; the exceptions to this were currents in the Gulf of Oman and the Strait of Hormuz, which is most likely related to variations in the orientation of the coast at sites in these locations. Currents in the southern Persian Gulf were predominantly southward, and winds were primarily offshore (Fig. 5). Within the Strait of Hormuz, surface currents were predominantly to the north and east but with a significant component to the west. Examination of individual sites in the Strait of Hormuz indicated that the dominant current pattern was along-shore and into the Persian Gulf. Additionally, winds within the Strait of Hormuz were predominantly to the north and east (Fig. 5). Gulf of Oman currents were the strongest across the three locations (Table 4) and were predominantly directed along-shore to the east and southeast (i.e., away from the Persian

Table 3

Percentage dissimilarity (δ) of coral communities identified by SIMPER, with the contribution of the 10 most important species driving differences listed.

Species	Locations		Contribution of δ (%)	Cumulative δ (%)
	Persian Gulf	Gulf of Oman		
	76.6% dissimilarity			
<i>Porites harrisoni</i>	37.3	0.0	18.20	18.20
<i>Porites lutea</i>	15.7	2.5	9.38	27.59
<i>Platygyra daedalea</i>	10.7	19.1	6.81	34.40
<i>Favia pallida</i>	10.0	0.62	6.52	40.92
<i>Cyphastrea microphthalma</i>	8.6	1.4	5.93	46.85
<i>Porites lobata</i>	4.2	0.26	4.88	51.72
<i>Porites</i> sp.	3.4	13.7	4.12	55.84
<i>Goniopora</i> sp.	0.0	6.3	3.44	59.28
<i>Hydnophora pilosa</i>	0.0	13.4	3.29	62.58
	Persian Gulf	Straits of Hormuz		
	67.6% dissimilarity			
<i>Porites</i> sp.	3.4	26.9	13.25	13.25
<i>Platygyra daedalea</i>	10.7	22.7	10.23	23.48
<i>Porites harrisoni</i>	37.3	3.6	9.84	33.32
<i>Porites cumulates</i>	0.0	8.2	4.15	37.47
<i>Favia pallida</i>	10.0	0.14	4.03	41.50
<i>Stylophora pistillata</i>	0.0	4.5	3.89	45.39
<i>Acropora valida</i>	0.0	1.6	3.87	49.26
<i>Symphyllia recta</i>	0.0	1.9	3.69	52.95
<i>Goniopora</i> sp.	0.0	1.6	3.45	56.40
<i>Montipora</i> sp.	0.0	1.4	3.40	59.80
	Strait of Hormuz	Gulf of Oman		
	55.6% dissimilarity			
<i>Hydnophora pilosa</i>	13.4	0.0	12.23	12.23
<i>Porites</i> sp.	13.7	26.9	7.68	19.91
<i>Porites lutea</i>	2.5	8.2	6.34	26.25
<i>Stylophora pistillata</i>	0.2	4.3	4.24	30.49
<i>Acropora khayranensis</i>	4.8	0.8	4.03	34.52
<i>Favites pentagona</i>	4.2	0.8	3.87	38.39
<i>Porites harrisoni</i>	1.1	3.6	3.53	41.92
<i>Acropora valida</i>	3.5	1.6	3.22	45.14
<i>Goniopora</i> sp.	0.0	6.3	3.17	48.31
<i>Montipora aequituberculata</i> cf.	1.4	0.3	3.11	51.42

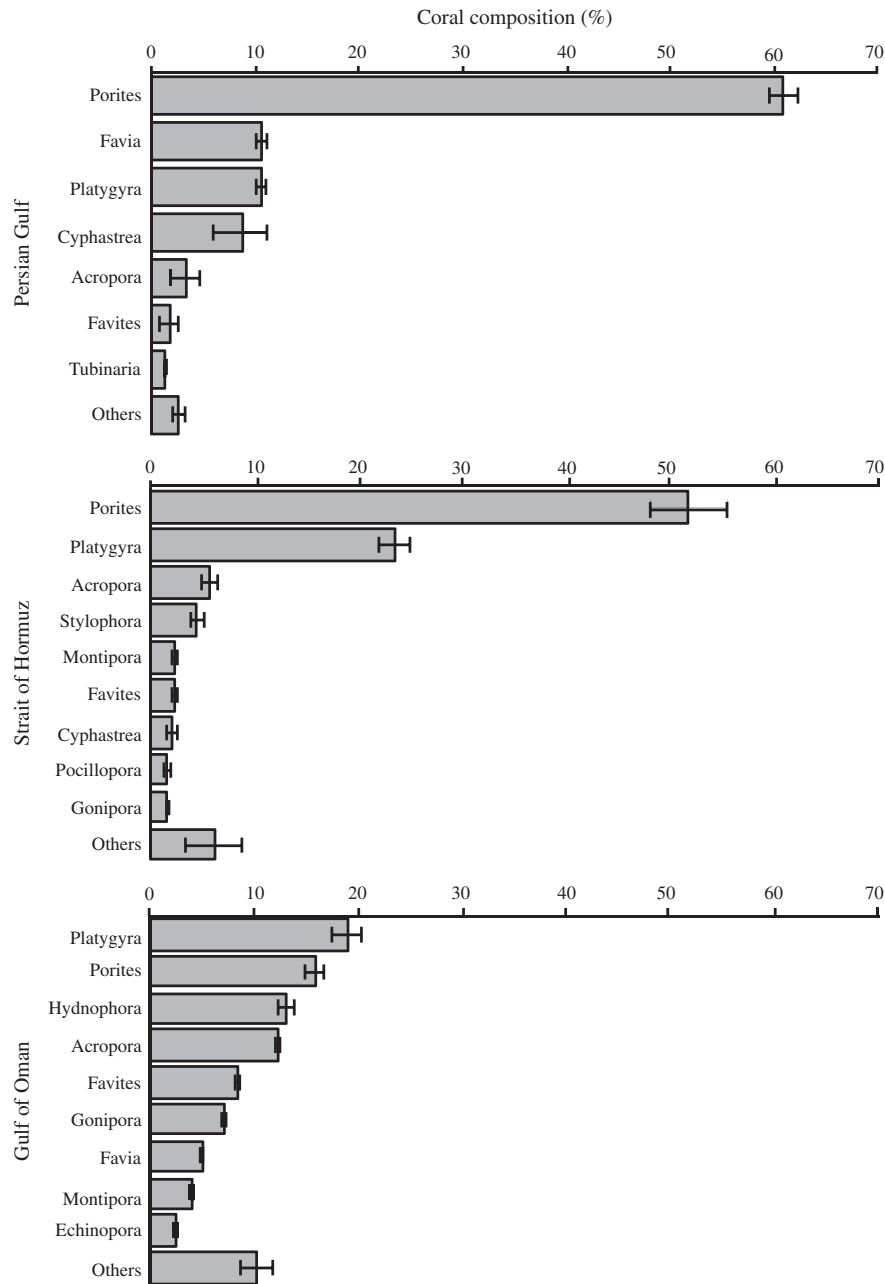


Fig. 4. Coral community patterns: percentage of coral at each location broken down by dominant genera: Persian Gulf (top), Strait of Hormuz (middle), and Gulf of Oman (bottom).

Gulf). Wind direction at this location was predominantly to the east and northeast (Fig. 5); however, the orientation of the coastline at individual sites meant that some sites were dominated by along-shore winds, while others were dominated by offshore winds.

3.4. Relationship between benthic groups, coral reef communities and environmental variables

Maximum chlorophyll-*a* concentration, maximum temperature, % time of along-shore currents, and mean cross-shore wind speeds best explained the spatial variation in benthic community patterns ($\rho = 0.587$, $p < 0.001$). These four variables explained 59% of the variation in benthic groups, while adding other variables did not improve the strength of the relationship. Maximum chl-*a*

alone was the best single environmental predictor for differences in benthic groups ($\rho = 0.379$, $p < 0.01$). Other important variables explaining spatial variation in benthic group patterns when considered alone were maximum salinity ($\rho = 0.341$) and minimum chlorophyll-*a* ($\rho = 0.271$), and chlorophyll-*a* range (0.271).

LINKTREE analysis of benthic groups showed a first split (split 1; Fig. 6a) between two sites in the Strait of Hormuz (sites 8 and 9) from all other sites, associated with mean cross-shore wind speeds. The second split (split 2) separated all sites in the Persian Gulf and the remaining two sites in the Strait of Hormuz (sites 7 and 10) from all sites in the Gulf of Oman on the basis of differences in maximum chl-*a* concentration, and maximum temperatures (Fig. 6a). The third split (split 3) distinguished sites 7 and 10 in the Strait of Hormuz based on measures of maximum chl-*a*, maximum temperature and mean cross-shore wind speeds, compared

Table 4

Physical metrics for the southern Persian Gulf, Strait of Hormuz and Gulf of Oman.

Location Position	Persian Gulf 55°E, 25°N	Strait of Hormuz 56°E, 26°N	Gulf of Oman 59°E, 23°N
<i>SST (°C)</i>			
Mean annual temperature	27.97 (±1.49)	28.27 (±1.03)	27.72 (±0.79)
Mean warmest month	34.50 (±0.04) August	32.75 (±0.22) July	31.37 (±0.32) July
Mean coldest month	20.44 (±0.17) January	23.31 (±0.07) February	23.59 (±0.05) February
Annual temperature range	14.05	9.43	7.78
<i>Salinity (psu)</i>			
Mean annual salinity	40.86 (±0.23)	37.15 (±0.17)	36.67 (±0.32)
Mean highest salinity month	42.07 (±0.34) February	37.54 (±0.18) July	36.77 (±0.04) July
Mean lowest salinity month	39.19 (±0.65) May	36.76 (±0.20) April	36.59 (±0.01) February
Annual salinity range	2.88	0.78	0.22
<i>Chlorophyll-a (mg m⁻³)</i>			
Mean annual chl-a	1.70 (±0.65)	2.25 (±0.17)	2.76 (±0.44)
Mean highest chl-a month	2.44 (±0.06) September	3.19 (±0.40) February	8.17 (±0.26) February
Mean lowest chl-a month	1.07 (±0.05) March	1.06 (±0.32) May	0.40 (±0.03) May
Annual chl-a range	1.36	2.51	7.77
<i>Currents (m s⁻¹)</i>			
Mean long-shore speed (m s ⁻¹)	0.024 (±0.002)	0.04 (±0.008)	0.06 (±0.016)
Mean cross-shore speed (m s ⁻¹)	0.017 (±0.001)	0.013 (±0.004)	0.02 (±0.006)
% time of along-shore current	48.8%	72.5%	80%
<i>Winds (m s⁻¹)</i>			
Mean long-shore speed (m s ⁻¹)	1.97 (±0.13)	1.80 (±0.09)	2.98 (±0.23)
Mean cross-shore speed (m s ⁻¹)	2.35 (±0.06)	1.72 (±0.09)	1.98 (±0.08)
% Time of cross-shore wind	66.3%	53.2%	40.5%

with all sites in the southern Persian Gulf. The fourth split (split 4) between sites in the southern Persian Gulf was associated with differences in mean cross-shore wind speed and % along-shore currents. Splits 5–7 on the dendrogram separated the sites in the Gulf of Oman from each other on the basis of differences in maximum chl-*a*, cross-shore wind speeds and % along-shore currents (Fig. 6a).

Temperature range, minimum salinity, maximum chl-*a*, and the % time of along-shore currents best explained the spatial variation in coral community structure among locations ($p = 0.683$, $p < 0.001$). These four variables explained 68% of the variation in coral community patterns among the locations. When the analysis was restricted to a single environmental variable, temperature range was the best predictor for differences in coral community patterns, and explained the majority of the variation between locations ($p = 0.543$, $p < 0.01$). Other important variables explaining the spatial variation in coral community patterns when considered alone were chl-*a* range ($p = 0.394$), maximum salinity ($p = 0.435$) and maximum temperature ($p = 0.479$); however the latter two showed significant correlations with each other.

LINKTREE analysis of coral communities showed a first split (split 1; Fig. 6b) dividing sites into those associated with a high temperature range and high minimum salinity (all southern Persian Gulf sites and Strait of Hormuz sites 7–9) and those associated with a low temperature range and low salinity minimum (encapsulating all Gulf of Oman sites, and site 10 in Strait of Hormuz). On the left of the tree, the second split in the data was associated with a fine-scale change in temperature range, with sites 8 and 9 (Strait of Hormuz) associated with temperature range < 9.5 °C, while all Persian Gulf sites and Strait of Hormuz site 7 associated with temperate range > 9.5 °C (split 2; Fig. 6b). Higher maximum chl-*a* concentrations (i.e., greater primary productivity) and temperature range were important in differentiating coral communities at site 7 in the Strait of Hormuz from communities at all sites in the Persian Gulf (split 3; Fig. 6b). The distinction between communities in the Persian Gulf (split 4) was related to differences in % time of along-shore currents. On the right side of the tree, split 5 distinguished site 10 in the Strait of Hormuz from all sites in the Gulf of Oman on the basis of temperature range. Splits 6 and 7 dif-

ferentiated the remaining Gulf of Oman sites on the basis of chl-*a* concentration and % time of along-shore current, respectively.

4. Discussion

Benthic groups and coral communities in the northeastern Arabian Peninsula differed significantly among the southern Persian Gulf, Strait of Hormuz, and the Gulf of Oman, associated with distinct sub-regional patterns in community structure. Similar to previous regional studies (e.g., Sheppard, 1987; Sheppard and Sheppard, 1991), there were substantial differences in the abundance, composition and species diversity within benthic groups and coral communities between locations. Community similarity values for corals were similar to previously reported values (Sheppard and Sheppard, 1991; Sheppard et al., 1992), suggesting that coral community structure in the Strait of Hormuz and Gulf of Oman are most similar, and that southern Persian Gulf and Gulf of Oman communities the least similar. In contrast, benthic groups in the Strait of Hormuz showed higher community dissimilarity values compared with groups in the southern Persian Gulf and the Gulf of Oman.

Dissimilarities among benthic groups in the northeastern Arabian Peninsula were driven mainly by differences in the abundance of three benthic groups: hard coral; soft coral; and the combination of sand, pavement and rubble (SPR). Collectively, these three benthic groups contributed most to the dissimilarity between locations. Benthic groups in the southern Persian Gulf and Gulf of Oman were dominated by SPR, which accounted for more than 50% of the benthos. In contrast, less than 20% of the benthic groups in the Strait of Hormuz contained SPR. Such differences likely explain why benthic groups in the southern Persian Gulf and Gulf of Oman were less dissimilar (i.e., lower dissimilarity values) to each other, then when compared to groups in the Strait of Hormuz. Much of these two regions are dominated by uncolonizable soft substrates (i.e., sand and mud), compared to the Strait of Hormuz, which has substantial rocky substrate (Sheppard et al., 2000). Consequently, at sites around the northern and eastern Musandam (i.e., Strait of Hormuz), coral cover and the presence of true reefs

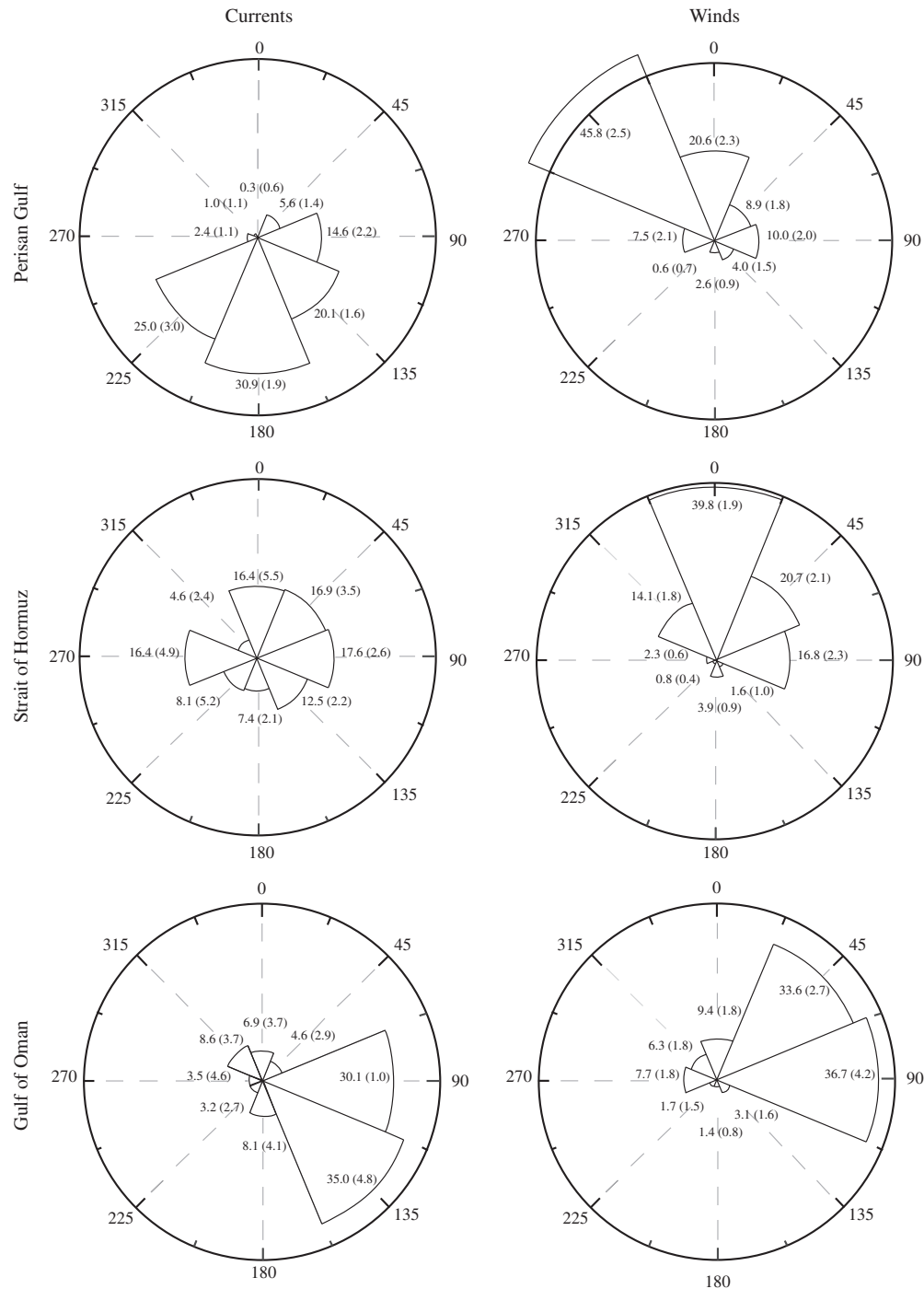


Fig. 5. Rose plot summaries of the currents and wind data for each location. The bearing indicates the direction of motion for both parameters (i.e., oceanographic, not meteorological, convention). The frequency in each quadrant is shown numerically and by the quadrant radius, where the outer circle represents 40%. Mean speed for each quadrant is parenthesized (cm s⁻¹ for currents; m s⁻¹ for wind).

is greater than anywhere else in the northeastern Arabian Peninsula (Sheppard and Salm, 1988; Salm, 1993).

Coral communities in the southern Persian Gulf were characterized by low species richness, diversity, and evenness, which likely reflect the severe constraints on coral survival in this region associated with extreme environmental conditions (Sheppard et al., 1992; Riegl et al., 2012). Several coral species, including *Montipora*, *Pocillopora* and *Stylophora*, that are common in the Strait of Hormuz and Gulf of Oman (Sheppard and Sheppard, 1991; Claereboudt, 2006), were absent in the present survey. For

example, no *Pocillopora* spp. were recorded, although *Pocillopora damicornis* is reported from neighboring reefs in Bahrain and Saudi Arabia (Fadlallah et al., 1993, 1995). Additionally, *Stylophora pistillata*, which is dominant on many shallow reefs in Tarut Bay, Saudi Arabia (Fadlallah et al., 1995) were completely absent during surveys. Similar to recent studies (Burt et al., 2008; Riegl and Purkis, 2009), reef communities in this study were dominated by poritids and faviids, which accounted for greater than 93% of the total coral cover surveyed. In contrast, *Acropora* species, which formerly dominated these reefs prior to recurrent bleaching events (Riegl, 1999;

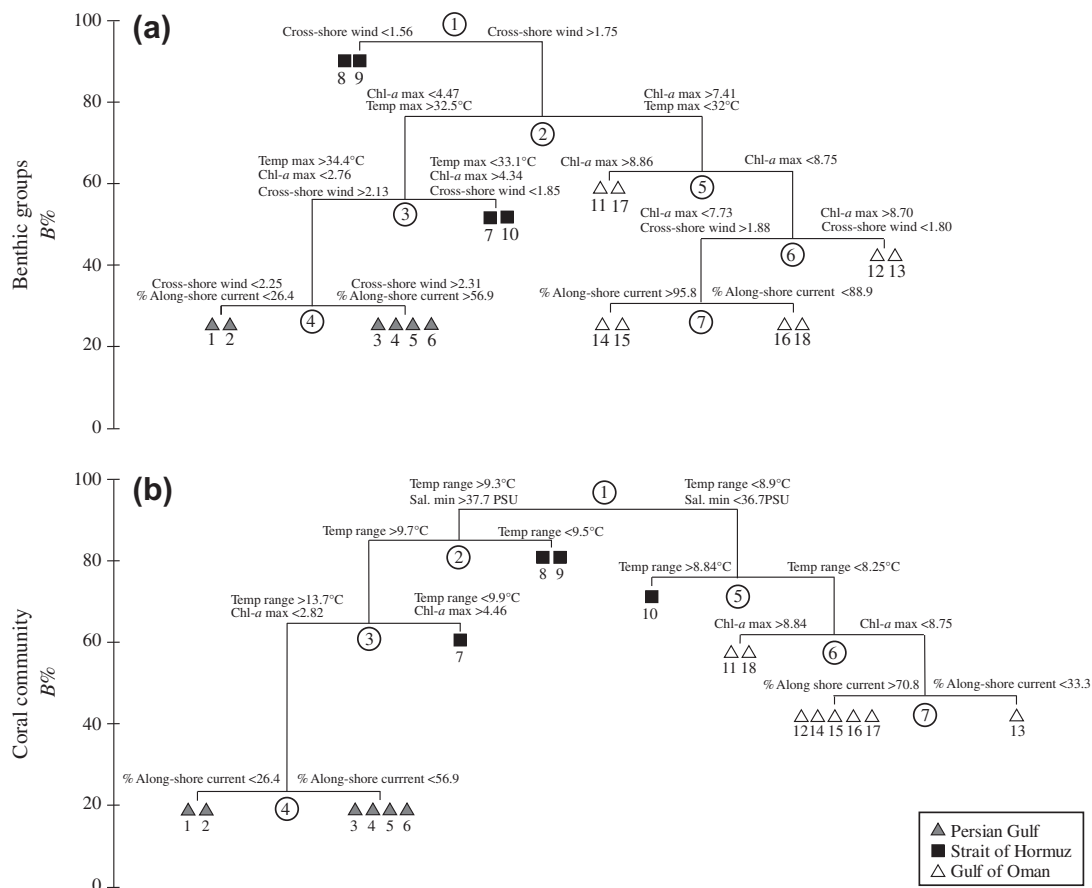


Fig. 6. Linkage tree and associated physical and environmental variable thresholds that relate to the separation of (a) benthic groups and (b) coral communities in the southern Persian Gulf, Strait of Hormuz and Gulf of Oman. Thresholds at the ends of each branch indicate that a left and right path, respectively, should be followed through the tree. B% is the absolute measure of group differences. Numbers under symbols correspond to sites on map (Fig. 1). Chl-a in mg m^{-3} , currents in cm s^{-1} , and winds in m s^{-1} .

George and John, 2000; see also Riegl, 2002, 2003; and related references), represented less than 4% of total cover. Importantly, these findings provide additional evidence to support claims of long-term shifts in community structure in the southern Persian Gulf towards more robust coral species (*Porites* and faviids) that are more resistant to major disturbances (Riegl and Purkis, 2009).

Coral communities in the Strait of Hormuz and Gulf of Oman were characterized by relatively high species diversity and richness, likely due to less extreme physical conditions in these locations (Sheppard, 1987; Sheppard and Sheppard, 1991; Glynn, 1993). Nonetheless, each location represented a distinct community, with 56% dissimilarity in structure, associated with substantial differences in coral cover and community structure. The Strait of Hormuz had almost three times more coral cover than the Gulf of Oman, but had significantly lower species evenness, with communities dominated by poritids and faviids. In comparison, coral communities in the Gulf of Oman were relatively even, and held a much wider range of genera. This study also found that percent live coral cover within both locations was relatively similar with previous estimates (Sheppard and Salm, 1988; Salm, 1993; Glynn, 1993). However, *Acropora* cover within the Strait of Hormuz was substantially lower than previously reported, while Gulf of Oman coral communities showed similar estimates of *Acropora* cover to previous work (Sheppard and Salm, 1988). Sheppard and Salm (1988) reported extensive *Acropora* cover (50–85%) from several sites in the Musandam (i.e., Strait of Hormuz), while Maghsoudlou et al. (2008) reported in early 2007 that reefs in the Musandam had high coral cover in excess of 80% with *Pocillopora*

and *Acropora* the dominant species. Both the Strait of Hormuz and the Gulf of Oman have been impacted by recent disturbance events, including cyclone Gonu (2007) and a large-scale HAB event (2008), which had significant selective effects on branching species (e.g., *Acropora* spp.) (Maghsoudlou et al., 2008; Foster et al., 2011; Bauman et al., 2010). Such differences in *Acropora* cover between locations suggest that there has been substantial re-growth of *Acropora* species within the Gulf of Oman (Maghsoudlou et al., 2008), with limited recovery of these corals within the Strait of Hormuz.

Understanding how reef communities vary across environmental gradients is important for determining how communities will respond to changing environmental conditions (Kleypas et al., 1999). Results from this study showed considerable spatial heterogeneity in oceanic conditions among locations, with strong directional environmental gradients that operate from the Persian Gulf through the Strait of Hormuz to the Gulf of Oman (Reynolds, 1993, 2002; Nezhlin et al., 2007; Piontkovski et al., 2011). Interestingly, the combination of physical variables responsible for explaining differences between benthic groups and coral communities were relatively similar. Differences in benthic groups were best explained by maximum chlorophyll-*a* in combination with maximum temperature, % time of along-shore currents, and mean cross-shore wind speeds. In contrast, differences in coral community structure around the region were best explained by temperature range in combination with minimum salinity, maximum chlorophyll-*a*, and the % time of along-shore currents. Although BEST analysis selected temperature range and maximum chl-*a* as

the single best environmental predictors for differences in patterns of benthic groups and coral community, these could effectively be replaced by the minimum, maximum or range in these parameters respectively, as these variables showed a similar gradient across the three locations.

Temperature and salinity are often cited as the two most important physical factors structuring benthic groups and coral communities around the northeastern Arabian Peninsula (Sheppard and Sheppard, 1991; Sheppard et al., 1992; Reynolds, 1993; Coles, 2003). Results from this study support that finding but also indicated that chlorophyll-*a* concentrations, surface currents, and wind speeds, in addition to temperature and salinity, were important physical factors in structuring benthic groups and coral communities. It is worthwhile to note that differences in topography across the region may be responsible for coinciding associations between some of these variables. For example, it is reasonable that the much shallower enclosed southern Persian Gulf would experience increased values and ranges of temperature and salinity but not experience deep-water convective mixing or upwelling, whereas the sections of the coastline along the Strait of Hormuz and Gulf of Oman would experience less extreme values of temperature and salinity but could be exposed to enhanced chl-*a* values from convective mixing or upwelling of adjacent deep waters. Previous studies have indicated both higher temperature and salinity in the southern Persian Gulf (Sheppard et al., 1992, 2000), with higher chl-*a* in the Gulf of Oman and Strait of Hormuz due to seasonal upwelling and monsoonal events (Reynolds, 1993; Piontkovski et al., 2011). Importantly this study has isolated specific environmental variables (i.e., chlorophyll-*a* concentrations, surface currents, and wind speeds) that, in addition to temperature and salinity, may influence the composition of benthic groups and coral communities. This has important implications for future ecosystem changes given the predicted long-term changes to multiple oceanic factors as a consequence of on-going climate changes (IPCC, 2007).

Moreover, these factors are also considered likely correlates of resistance and resilience to bleaching events (West and Salm, 2003; Maina et al., 2008), which are expected to become both more frequent and more severe in coming decades (e.g., Hoegh-Guldberg, 1999). For example, recent studies suggest that chlorophyll-*a* may reduce the effects of light by absorbing and scattering thus creating a shading effect (Maina et al., 2008, 2011). Consequently, within regions that have high chlorophyll concentrations the severity and impact of bleaching events may be lower than in areas of low chlorophyll-*a* (McClanahan et al., 2003). Although the gradient in maximum chl-*a* increasing from the Persian Gulf to the Gulf of Oman likely influences coral community structure, it remains unclear whether this is indeed a causal relationship. Furthermore, areas with strong currents and high wind speed, which can enhance vertical mixing of the water column (Skirving et al., 2006), may potentially increase local and regional cooling, thereby reducing the effects of increased sea surface temperature, and the potential for disturbance mediated effects on coral reef communities (West and Salm, 2003). Similar to previous studies, (Reynolds, 1993, 2002; Piontkovski et al., 2011) results from this study indicate upwelling and stronger vertical mixing of the water column in both the Strait of Hormuz and along the coast of Oman. Interestingly, no coral bleaching was reported from either the Strait of Hormuz or Gulf of Oman during the 1998 large-scale coral bleaching event (Wilson and Claereboudt, 2005) that heavily impacted most reefs around the world (see review Baker et al., 2008) and in the southern Gulf (Riegl, 1999, 2002). Moreover, the southern Gulf has a much higher frequency, but also more recent occurrence, of bleaching events over the last three decades compared to the Strait of Hormuz or Gulf of Oman (Wilson and Claereboudt, 2005; Sheppard and Loughland, 2002; Baker et al., 2008).

5. Conclusions

Overall, this work has shown that considerable changes to coral reef community structure have occurred throughout the northeastern Arabian Peninsula over the past two decades. Most dramatic are the apparent changes from *Acropora* dominated to poritids and faviids dominated communities particularly in the southern Persian Gulf and Strait of Hormuz. Sustained and on-going disturbances throughout the region (Maghsoudlou et al., 2008; Sheppard et al., 2010; Sale et al., 2011; Riegl et al., 2011), associated with changing global climate, are likely to continue altering the structure of benthic groups and coral communities, and could potentially increase the deleterious effects on reef ecosystem function. Nonetheless, despite the stark contrasts between reef community structure in the southern Persian Gulf and other locations in this study, these do not necessarily apply to all regions within the Persian Gulf (e.g., coral areas along the coast of Iran, off-shore islands of UAE and Saudi Arabia). Furthermore, although temperature and salinity remain good proxies for distinguishing between coral reef communities across the region, they are not the only physical variables that correlate with the transition of community structure. This work clearly highlights that multiple environmental variables are related to reef community patterns throughout the northeastern Arabian Peninsula. As such there is a critical need to increase our understanding of the range of physical factors that influence the structure of reefs throughout the region, including different areas within the Gulf (e.g., off-shore islands and coast of Iran), and how these conditions may change with sustained climate change.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.marpolbul.2012.10.013>.

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