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PRIMARY RESEARCH PAPER

Macrobenthos in the central Arabian Gulf: a reflection of climate extremes and variability

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Abstract The arid subtropical ecosystem of the central Arabian Gulf was used to explore the combined effects of low primary productivity, high salinities, and variable temperatures on the composition and structure of benthic macrofauna at 13 sites encircling the Qatar Peninsula in winter and summer (or late spring) of 2010 and 2011. The low abundance, biomass, and remarkably high species turnover may be a reflection of the oligotrophic, thermally variable, hypersaline coastal environment. The number of species and within-habitat diversity was lowest in the highest salinities but increased with finer-grained sediments and lower salinity. A remarkable temporal variation in species composition observed may reflect insufficient primary production to sustain new populations recruited from the seasonal exchange of water from the adjacent Sea of Oman. Low abundances accompanied by continued replacement of species may be a "new model" for extremely arid conditions associated with global warming.

Keywords Macrobenthos · Zooplankton · Phytoplankton · Biodiversity · Community composition · Climate changes

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Introduction

The remarkable progress over the last few decades in the synecology of benthic assemblages has produced an array of models that predict the structure and composition of benthic communities over a wide set of

conditions (Sanders, 1968; Pearson & Rosenberg, 1978; Menge & Sutherland, 1987; Snelgrove & Butman, 1994; Hyland et al., 2005; Gray & Elliott, 2009). No specific criteria have emerged, however, that provide predictive power for tropical and subtropical arid regions with little access to fresh water, salinities above normal sea water, and limited nutrients. The purpose of this analysis is to generate quantitative information on the characteristics of the infauna that are experiencing extremes in environmental conditions of temperature and salinity when food supplies are low, as encountered in the Arabian Gulf (AG) (Coles & McCain, 1990; Sheppard et al., 2010; ROPME, 2012; Quigg et al., 2013; Al-Ansari et al., 2015) or similar habitats (Lamptey & Arma, 2008; Magni et al., 2009).

Few coastal habitats undergo full ranges of multiple physical conditions (from benign to harsh) on a regular basis and thus studies focusing on effects of multiple climate change-related stressors have been scant. In this paper, we utilized the unique subtropical, hyper-arid ecosystem of the central AG to explore the combined effects of high temperature, high salinity, high rates of desert-derived dust and sand, and low primary production on coastal benthos.

The AG is a semi-enclosed, marginal sea surrounded by an extremely arid landmass (Fig. 1). The Gulf's subtropical location, shallow depth (average

$\sim$36 m), and extreme air temperature (up to 50°C) contribute to significant seasonal water temperature fluctuations (11–36°C) (Coles & McCain, 1990; Sheppard et al., 2010). High temperature in summer and dry wind (the Shamal) in winter result in strong evaporation ($\sim$2 m year^{-1}). Salinity can range from 39 over most of the Gulf up to 70 in the shallow embayment between Saudi Arabia and Qatar (Gulf of Salwa) (Sheppard et al., 2010). The dense water south of Bahrain and in the southern shallows off the United Arab Emirates (UAE) drive the dense bottom outflow following the coastline of eastern Qatar and the UAE; the replacement Indian Ocean Surface Water (IOSW) through the Strait of Hormuz along the Iranian coastline forms a Gulf-wide anticlockwise circulation (Kämpf & Sadrinasab, 2006). In summer, lateral density differences intensify the bottom outflow and thus magnify the surface inflow. The intensified IOSW pushes the low salinity front to the NE coast of Qatar (Kämpf & Sadrinasab, 2006). Sedimentation of airborne sand is immense, amounting to 100 tonnes per km^2 per year (Khalaf et al., 1986); hence, fine-grained sediments cover most of the Gulf, except for a belt of coarse-grained material that extend from Bahrain, NE of Qatar, to offshore of the UAE. This coarse-grained material is a reflection of strong bottom currents along the axis of the basin (Massoud et al., 1996; Kämpf & Sadrinasab, 2006).
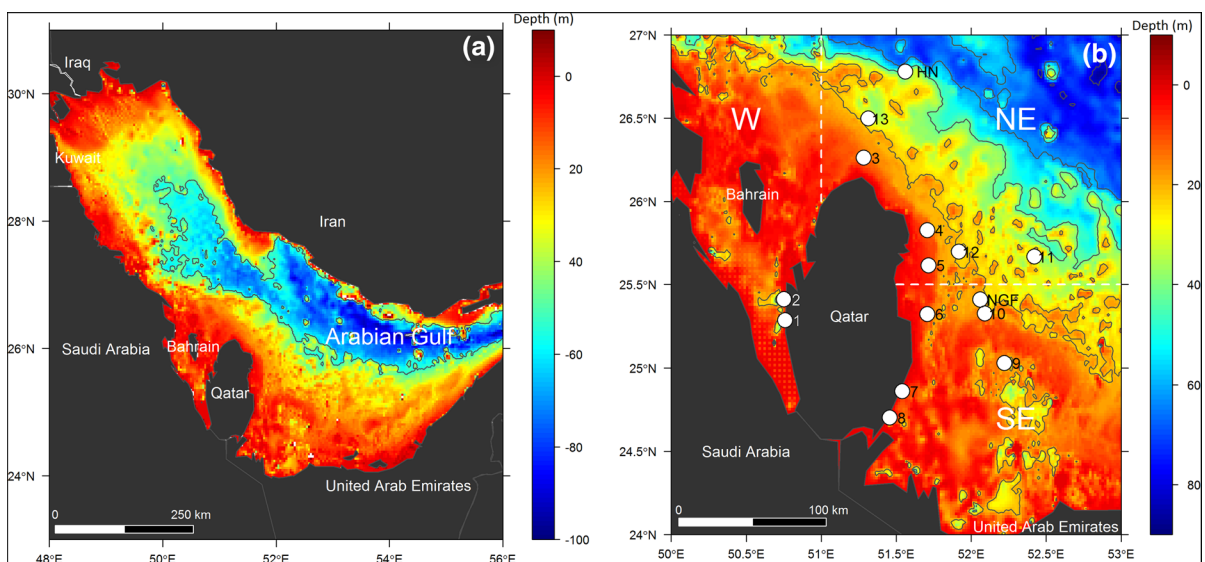

Fig. 1 **a** Map of the AG. *Gray line* 50-m isobaths. *Color palate* water depth (m). **b** Field sampling locations encircling the western (W), northeastern (NE), and southeastern margins (SE) of the Qatar Peninsula. *Gray line* 20-m isobaths

Previous benthic studies in the AG have concentrated on the northwestern extension of the basin (Coles & McCain, 1990; Al-Khayat, 2005; Joydas et al., 2011, 2012). Seagrasses are common and undoubtedly contribute to local fisheries (Price & Coles, 1992; Erftemeijer & Shuail, 2012). No studies to date, however, have explicitly tested whether the unique spatial and temporal variabilities in the AG have exerted environmental controls on the benthic communities or included the potential linkages between benthos and planktonic assemblages. Hence, in this study, we sampled macrobenthos, zooplankton and phytoplankton simultaneously in Feb 2010, July 2010, Feb 2011, and May 2011 across the west, northeast, and southeast off the Qatar Peninsula with contrasting environmental conditions. It was assumed that the abundance and composition of the plankton could influence macrobenthos assemblages. Likewise, because the basin is relatively shallow, benthos could also contribute to the health and diversity of the pelagic biota. A broader goal of this study was to contribute to the understanding of the potential synergistic effects of multiple environmental stressors upon the coastal benthos in response to climate change in an arid environment.

Methods

Sampling

The sampling strategy amounted to 4 sampling periods (Feb 2010, July 2010, Feb 2011, and May 2011) at 13 locations encircling the western (W), northeastern (NE), and southeastern (SE) margins of the Qatar Peninsula, with pairs of locations placed nearshore and offshore (Fig. 1) using the Qatar University's (QU) R/V *Miktabar Al Bihar*. The strategy was to contrast the cool (Feb) vs. hot seasons (May/July), as well as the regions with hypersalinity (W), strong hydrodynamics, frontal influences (NE), and more feeble current conditions (SE). Moreover, two additional locations (NH and NGF) were sampled in July 2010 to detect possible influence of the summer salinity front intruding from the Arabian Sea. At each sampling, vertical profiles included temperature (Temp), salinity (Sal), dissolved oxygen (DO), and pH were measured with an YSI 6920 V2 Multiparameter Water Quality Sonde. Discrete water samples for chlorophyll a concentration (Chla), total dissolved solids (TDS), and nutrients were collected with a Niskin bottle on the surface (1 m depth) and bottom (<1 m above the seafloor). Nutrients included particulate (PN), dissolved organic (DON) and dissolved inorganic nitrogen (DIN) [ammonium (NH_4), nitrate (NO_3), and nitrite (NO_2)], total (TP) and dissolved inorganic phosphorous (DIP), and silicate (Si). Total dissolved nitrogen (TDN) was calculated by combining DON and DIN, and total nitrogen (TN) by combining PN and TDN. Detailed description of the instrumentation and laboratory methods can be found in Quigg et al. (2013).

Pairs of phytoplankton (0.5 m diameter and 67 μm mesh) and zooplankton tows (0.5 m diameter and 120 μm mesh) were taken on the surface (1 m depth) at each location. The zooplankton densities per volume of water and species composition were estimated by dividing the catch by the total water volume filtered (estimated from flow meter). Complete information on phytoplankton and zooplankton collections are available in Quigg et al. (2013) and Nour Al Din et al. (In preparation).

Five 0.1 m^{-2}-van Veen grab samples were taken per site. Small (10–50 ml) subsamples were taken for grain size and organic carbon in the sediments. The grain size (Sand, Silt and Clay) was determined using the combined sieving and settling rate techniques (Folk, 1968), and total organic carbon (TOC) was determined by combustion at 500°C following removal of carbonate with HCl. The five samples were sieved at sea through 0.5 mm sieves and fixed in 10% buffered formalin and sea water solution. A total of 17 surface (water properties and nutrients) and 22 bottom environmental parameters (water properties, nutrients, sediment characteristics, and depth) were recorded (Fig. 1; Table 1) during the Qatar National Priority Research Program (NPRP). All data are achieved and can be requested from the QU Environmental Study Center (ESC).

Data analysis

Due to high correlations among DON, TDN, and TN ($r > 0.94$), as well as between salinity and TDS ($r > 0.99$), TDN, TN, and TDS were not included in the analysis to avoid spurious correlations. The environmental data were logarithm (base of 10) transformed, centered (subtracted from the mean), and normalized (divided by the standard deviation) to reduce the data skewness. Environmental ordination used Principal

Table 1 Mean and standard deviation (bracket) of bottom water properties from four cruises and northeastern, southeastern, and western margin of the Qatar Peninsula

	Cruise				Region			Overall
	Feb-10	Jul-10	Feb-11	May-11	NE	SE	W	All
N	12	15	13	13	25	21	7	53
Chl.a (µg/L)	0.89 (0.52)	1.39 (0.43)	1.57 (1.92)	0.65 (0.41)	1.43 (1.41)	0.99 (0.52)	0.57 (0.38)	1.14 (1.06)
DIN (µM)	0.23 (0.19)	0.42 (0.36)	0.41 (0.17)	0.84 (0.96)	0.36 (0.26)	0.49 (0.77)	0.86 (0.46)	0.48 (0.56)
DIP (µM)	0.66 (0.52)	0.47 (0.17)	0.56 (0.07)	0.31 (0.07)	0.52 (0.39)	0.46 (0.17)	0.55 (0.13)	0.5 (0.29)
DON (mM)	0.24 (0.06)	0.27 (0.05)	0.62 (0.09)	0.65 (0.05)	0.45 (0.22)	0.43 (0.19)	0.45 (0.16)	0.44 (0.2)
NH4 (µM)	0.19 (0.18)	0.15 (0.34)	0.28 (0.14)	0.13 (0.17)	0.15 (0.18)	0.14 (0.13)	0.44 (0.42)	0.19 (0.23)
NO2 (µM)	0.04 (0.05)	0.21 (0.12)	0.11 (0.03)	0.31 (0.07)	0.15 (0.12)	0.17 (0.13)	0.26 (0.14)	0.17 (0.13)
NO3 (µM)	0 (0.01)	0.06 (0.07)	0.03 (0.07)	0.15 (0.18)	0.06 (0.09)	0.02 (0.04)	0.17 (0.22)	0.06 (0.11)
PN (µM)	73.83 (93.93)	73.58 (37.56)	47.56 (44.79)	28.61 (36.21)	45.78 (42.03)	66.67 (77.45)	62.21 (36.74)	56.23 (58.13)
Si (µM)	0.78 (0.29)	1.05 (0.51)	2.73 (2.21)	1.89 (0.41)	1.31 (0.97)	1.9 (1.71)	1.83 (1.28)	1.61 (1.35)
TDN (mM)	0.24 (0.06)	0.27 (0.05)	0.62 (0.09)	0.65 (0.05)	0.45 (0.22)	0.43 (0.19)	0.45 (0.16)	0.44 (0.2)
TN (mM)	0.32 (0.11)	0.35 (0.06)	0.67 (0.1)	0.68 (0.05)	0.5 (0.21)	0.5 (0.17)	0.52 (0.17)	0.5 (0.19)
TP (µM)	1.05 (0.53)	2.1 (0.32)	1.83 (0.27)	1.76 (0.52)	1.7 (0.6)	1.74 (0.6)	1.7 (0.24)	1.71 (0.56)
Temp (C)	19.76 (0.78)	29.9 (2.94)	18.69 (1.04)	29.26 (1.13)	24.47 (5.36)	24.87 (5.53)	24.27 (7.33)	24.61 (5.55)
TDS (g/L)	41.75 (3.24)	41.45 (4)	42.91 (3.6)	42.09 (3.55)	40.15 (1.04)	41.78 (1.98)	50.72 (0.69)	42.03 (3.57)
Salinity	43.52 (3.89)	42.95 (4.79)	44.89 (4.32)	43.74 (4.25)	41.51 (1.26)	43.43 (2.36)	54.21 (0.8)	43.75 (4.29)
pH	8.12 (0.17)	8.62 (0.27)	7.78 (0.16)	7.99 (0.46)	8.22 (0.49)	8.13 (0.35)	7.88 (0.37)	8.15 (0.43)
DO (mM)	0.43 (0.01)	0.35 (0.04)	0.45 (0.01)	0.35 (0.02)	0.39 (0.05)	0.39 (0.05)	0.38 (0.05)	0.39 (0.05)
TOC (%)	0.31 (0.1)	0.46 (0.16)	0.42 (0.15)	0.44 (0.16)	0.32 (0.1)	0.45 (0.13)	0.65 (0.08)	0.41 (0.15)
Sand (%)	92.78 (9.67)	83.7 (20.57)	89.87 (15.25)	87.48 (20.08)	96.08 (10.74)	76.78 (19.24)	96.51 (2.23)	88.03 (17.23)
Silt (%)	6.24 (8.1)	13.57 (16.39)	8.95 (13.09)	11.32 (17.7)	3.27 (7.76)	20.1 (16.48)	3.49 (2.23)	10.36 (14.44)
Clay (%)	0.98 (1.7)	2.73 (4.57)	1.18 (2.21)	1.2 (2.39)	0.65 (3.03)	3.12 (3)	0 (0)	1.61 (3.09)

n number of samples

Component Analysis (PCA) which projects the multivariate data in reduced dimensions. A PC axis is a linear combination of the values (coefficients) for each environmental variable. These coefficients were then used as coordinates to plot vectors on the PC1 and PC2 axes, with the *length* indicating a variable's importance and *direction* (away from the center) representing increasing environmental values.

Species abundance of macrobenthos (this study) and zooplankton (Nour Al Din et al., In preparation) were square-root transformed to accentuate the importance of rare species. Phytoplankton (Quigg et al., 2013) was recorded based on species presence and absence for each sampling. The transformed environmental data were converted to inter-sample Euclidean distance, while the biotic data were converted to Bray–Curtis dissimilarity (Bray & Curtis, 1957) and then subjected to nonmetric multidimensional scaling (nMDS), in which the sample placements indicate relative

dissimilarities in assemblage composition. The shortest geographic distances between sampling stations were calculated using R package "gdistance" (Etten, 2012). The inter-sample environmental and geographic distances were used as a proxy to characterize the benthic habitats and inherited spatial information, respectively. Relationships between the biotic dissimilarities and abiotic distances were examined using Spearman's rank correlations based on the Mantel test (Legendre & Legendre, 2012). Partial Mantel test was used to examine bio-environmental relationships while accounting for the spatial variation or environmental heterogeneity (Legendre & Legendre, 2012). The best subset and the individual environmental variables (highest correlations with faunal dissimilarities) were selected from all possible combinations.

Relationships among faunal dissimilarities (phytoplankton, zooplankton, and macrobenthos), environmental distances, and least-cost geographic distances

were examined with path analysis (Legendre & Legendre, 2012). The environmental variables were broken down into groups that include surface and bottom water properties (Temp, Salinity, DO, and pH), surface and bottom nutrients (DIP, DON, NH_4, NO_2, NO_3, PN, Si, and TP), and sediment properties (TOC, Sand, Silt, and Clay). An initial path model was established with single headed arrows indicating causal relationships and double-headed arrows showing the correlation between the matrices. A correlation matrix among the groups of variables (based on Mantel test) were decomposed to standardized path coefficients using a structural equation model (SEM) based on maximum likelihood with R package "lavaan" (Rosseel, 2012). The goodness-of-fit between the modeled and observed correlations was examined by a Chi-square test with $P > 0.05$ suggesting that the path model was not significantly different from reality. A final parsimonious path model was derived by subsequently comparing the competing models using Akaike's information criteria (AIC) and Bayesian information criteria (BIC), for which the model with the lowest AIC or BIC is retained. Because the correlations between dissimilarity or distance matrices may violate the SEM assumption of stochastic independence, Partial Mantel tests (9,999 permutations) were employed using R package "ecodist" (Goslee & Urban, 2007) to verify the significance of each path coefficient following Leduc et al. (1992).

Temporal (time of sampling) and spatial variability (geographic region) on the bottom environmental distances and macrobenthos dissimilarities were considered using two-way cross permutation multivariate analysis of variance (PREMANOVA). The same two-way design was also used to examine univariate environmental variables and community properties with permutational ANOVAs using R package "lmPerm" (Wheeler, 2010). The following parameters were measured to compare the diversity within a sampling unit (or alpha diversity) including: (1) Number of species (or species density) per sample; (2) Shannon–Weaver (1949) diversity index (H'); (3) Expected number of species from randomly selected n individuals ($E(S_n)$) (Sanders, 1968; Hurlbert, 1971); (4) Simpson's (1949) index (D) (because D emphasizes the dominance, the complement of D ($D' = 1 - D$) was expressed); and (5) Pielou's (1975) evenness measure (J'). Species density, H', and $E(S_{50})$ were used to measure the richness aspect of the

assemblages, while D' and J' were used to measure the evenness of the assemblages (Magurran, 2004). If significant main effects were detected, pair-wise one-way PERMANOVAs (or permutational ANOVAs) were performed to determine which factors were significantly different. To avoid a Type 1 error (false positive), a Bonferroni correction was applied to reduce the significance thresholds to $\alpha = 0.01$ (for pair-wise tests among sampling times) and $\alpha = 0.02$ (for the tests among regions).

Total species richness (or gamma diversity) (Magurran, 2004) across sampling times and geographic regions was compared using species accumulation curves. The curves were estimated by randomly accumulating samples (without replacement). The mean and 95% confidence interval of the accumulation curves were estimated by randomization (100 iterations). The average faunal similarities within different sampling times and geographic regions were broken down to percent contribution of each species using two-way cross Similarity Percent Contribution (SIMPER). The species with highest contributions were reported as the characteristic species.

Statistical analyses used software R 3.0 (R Core Team, 2013) with custom R scripts. Throughout the paper, the mean value and standard deviation are reported as "mean ± SD." Univariate Pearson correlation coefficient with permutation test used custom R functions "corPerm.R" from Pierre Legendre (http://adn.biol.umontreal.ca/~numericalecology/Rcode/). Multivariate analysis used PRIMER 6 & PERMANOVA (Clarke & Gorley, 2006; Anderson et al., 2008) and R package "vegan" (Oksanen, 2013) unless otherwise indicated. Geostatistical analysis and GIS mapping used R packages "sp" (Bivand, 2013) and "raster" (Hijmans & Etten, 2012). A path diagram was constructed using R package "semPlot" (Epskamp, 2013). All relevant data are within the paper and its supporting information files.

Results

Bottom environmental conditions

No statistical variation in sediment grain sizes (%Sand, %Silt, %Clay) was observed across sampling times. The grain sizes were also fairly homogeneous between the W and NE regions (96.1–96.5% sand,

3.3–3.5% silt, 0–0.7% clay, Table 1), but both were significantly different from the SE region (76.8 ± 19.24% sand, 20.1 ± 16.48% silt, 3.1 ± 3% clay, ANOVAs, $P < 0.05$). Similarly, total organic carbon (TOC) in the sediments was significantly different among the regions (ANOVA, $df_{2, 39} = 11.1$, $P < 0.001$) but not among the cruises with the highest % TOC in the W (0.65 ± 0.08%) and the lowest in the NE regions (0.32% ± 0.1). The % TOC was inversely correlated with the % sand ($r = -0.5$, $P < 0.001$) and positively correlated with % silt ($r = 0.5$, $P < 0.001$) and % clay ($r = 0.46$, $P < 0.001$) in the sediments.

Salinity varied significantly by region (ANOVA, $F_{2,40} = 99.7$, $P < 0.001$), ranging from a high of 54.7 ± 0.94 at St. 1 on the west side of the Qatar Peninsula down to 40.6 ± 1.17 at St. 11 (S1 Table), the most easterly offshore site. Although mean salinity did vary by cruise, an intrusion of summer low salinity front was evident in the NE regions during the July 2010 sampling (S1 Fig.). Bottom water oxygen concentration was inversely related to temperature, ranging from 0.35 ± 0.04 mM (5.5 ± 0.3 mg l^{-1}) in July 2010 up to 0.45 ± 0.01 mM (6.9–7.2 mg l^{-1}) in Feb 2010 and 2011. Chlorophyll *a* was highest in NE region (1.43 ± 1.41 µg l^{-1}) and lowest in the W region (0.57 ± 0.38 µg l^{-1}), showing significant cruise and regional effects (ANOVA, $P < 0.05$).

The first two PCA axes of the bottom environmental properties (19 variables, excluding TDN, TD, and TDS, Table 1) explained 43.5% of the total variation (Fig. 2). The pH made the highest contribution to the "best fitting" plane (PC1 and PC2 axes), followed by DO, DON, NH$_4$, Temp, TOC, DIN, Si, and Salinity. The sample ordination was clearly separated by cruises (Fig. 2) corresponding to a significant temporal effect in PERMANOVA (Time, $P < 0.001$, Table 2) with all cruise pairs being significantly different from each other ($P < 0.01$). The cool versus hot periods can be visualized by the separation of February versus May/July samples. Between sampling years, the environmental conditions for 2011 were characterized by higher DON/DIN/Si/Salinity and vice versa for the 2010. Between the cool versus hot periods, the February sampling had higher % sand/ DO/NH$_4$, while the May and July had higher pH/ Temp/NO$_2$/TOC. Moreover, a significant regional main effect was detected by PERMANOVA (Region, $P < 0.001$, Table 2) with significant differences
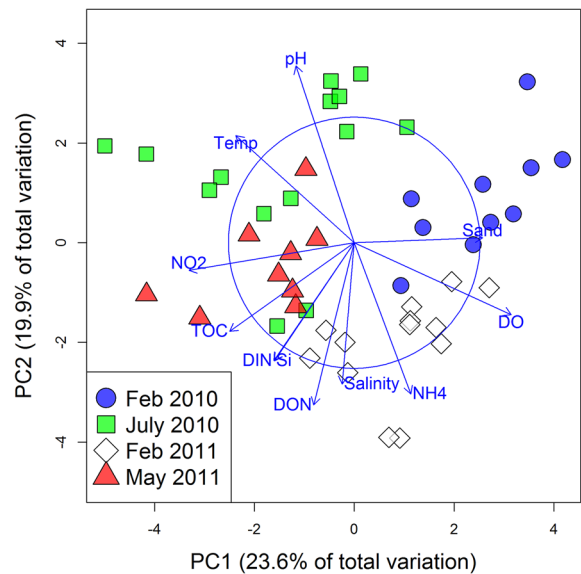

Fig. 2 Principal components analysis (PCA) of bottom environmental variables. *Symbols* are different times of sampling. The vectors (with *arrow*) are the top ten variables with highest PC loadings on PC1 and PC2 axes with vector length and direction indicating the variable importance and increasing values, respectively. The *great circle* vector length of 0.3

between all region pairs ($P < 0.02$). The regional effects, however, appeared to be subordinate compared to the cruise (temporal) effects because the regional grouping was not obvious.

Biological patterns and bio-environmental relationships

Density

Overall mean density of macrofauna was 1,045 ± 859 ind. m^{-2} (Table 3). Polychaetes, the dominant taxon, accounted for 34.7 ± 20.98% of the mean density, followed by gastropods, nematodes, amphipods, bivalves, ostracodes, and cirripeds (Table 4). The mean density ranged from a high of 1,861 ± 1,429 ind. m^{-2} at St. 5 down to as few as 374 ± 201 ind. m^{-2} at St. 1 off the western sites (S2 Table). In fact, the lowest densities were recorded at St. HN and St. NGF in July 2010 (266–316 ind. m^{-2}). These two sites were only visited once and thus reported separately. The highest recorded density occurred at St. 5 in May 2011 (3,745 ± 1,293 ind. m^{-2}, $n = 4$), in which a bivalve species, *Ervilia purpurea* (Smith,

Table 2 Two-way permutation multivariate analysis of variance (PERMANOVA) and permutation analysis of variance (ANOVA)

Variable	Term	df	SS	MS	F	Pr($>F$)
Environ. dist.	Time	3	429.67	143.22	14.80	<0.001***
	Region	2	176.93	88.46	9.14	<0.001***
	Time: region	6	38.81	6.47	0.67	0.951
	Residuals	41	396.65	9.67		
Faunal dissim.	Time	3	2.94	0.98	4.39	<0.001***
	Region	2	1.78	0.89	3.99	<0.001***
	Time: region	6	1.68	0.28	1.26	0.013*
	Residuals	38	8.47	0.22		
Density	Time	3	0.90	0.30	6.21	0.009**
	Region	2	0.58	0.29	6.00	0.008**
	Time: region	6	0.14	0.02	0.49	0.915
	Residuals	38	1.84	0.05		
Number of species	Time	3	1706.32	568.77	1.56	0.218
	Region	2	16493.19	8246.59	22.63	<0.001***
	Time: region	6	1332.68	222.11	0.61	0.716
	Residuals	38	13846.57	364.38		
Shannon index	Time	3	1.69	0.56	1.50	0.219
	Region	2	6.70	3.35	8.92	<0.001***
	Time: region	6	1.75	0.29	0.78	0.584
	Residuals	38	14.26	0.38		
E(S50)	Time	3	86.92	28.97	0.91	0.573
	Region	2	528.58	264.29	8.26	<0.001***
	Time: region	6	124.21	20.70	0.65	0.959
	Residuals	38	1215.89	32.00		
Simpson's index	Time	3	0.10	0.03	3.42	0.036*
	Region	2	0.10	0.05	5.37	0.008**
	Time: region	6	0.06	0.01	1.07	0.398
	Residuals	38	0.35	0.01		
Pielou's index	Time	3	0.13	0.04	2.67	0.065
	Region	2	0.12	0.06	3.62	0.040*
	Time: region	6	0.08	0.01	0.81	0.692
	Residuals	38	0.63	0.02		

Environ. Dist. environmental distance, *Faunal Dissim.* faunal dissimilarity

* $P < 0.05$

** $P < 0.01$

*** $P < 0.001$

1906), dominated with 62.8% of the total. *E. purpurea* also dominated at St.12, adjacent to and east of St. 5 in February 2010, February 2011, and May 2011, contributing 20.2–26.5% of the total organisms, but dropped to less than 0.5% in July 2010.

The overall macrofaunal densities followed a positive relationship with zooplankton densities ($r = 0.34$, $P = 0.013$, Fig. 3a) and a negative relationship with total organic carbon (TOC) in the sediments ($r = -0.29$, $P = 0.046$, Fig. 3b). Densities increased linearly with dissolved oxygen concentrations (DO) ($r = 0.3$, $P = 0.032$, Fig. 3c) but followed

unimodal patterns with salinity (Fig. 3d). With the exception of the TOC and DO, no linear relationship was found between the macrobenthos density and other bottom environmental variables.

Nevertheless, when animal densities were examined in terms of the dominant taxa, the polychaetes exhibited a significant positive relationships with DO ($r = 0.43$, $P = 0.001$) and % silt ($r = 0.46$, $P = 0.001$) but negative relationships with bottom temperature ($r = -0.43$, $P = 0.002$) and pH ($r = -0.39$, $P = 0.006$). Polychaete density was highest in February (2010 and 2011) when the

Table 3 Mean and standard deviation (bracket) of macrobenthos community characteristics from four cruises and northeastern, southeastern, and western margin of the Qatar Peninsula

	Cruise				Region			Overall
	Feb-10	Jul-10	Feb-11	May-11	NE	SE	W	All
n	56	71	65	47	108	104	27	239
Density (Indiv m^{-2})	1031.4 (710)	677.3 (602.9)	1142.9 (732.8)	1480.4 (1224.4)	1121.8 (963.8)	1118.2 (777.2)	454.8 (363.2)	1044.9 (859)
Numbers of species	30.2 (14.1)	20.3 (10.9)	28.6 (14.2)	30 (13.2)	24.4 (10.7)	33 (14.3)	12.3 (5.2)	26.8 (13. 7)
Shannon–Weaver index	2.7 (0.51)	2.37 (0.6)	2.47 (0.65)	2.43 (0.78)	2.28 (0.6)	2.85 (0.51)	1.91 (0.42)	2.49 (0.64)
Simpson's evenness	0.87 (0.08)	0.84 (0.11)	0.82 (0.13)	0.79 (0.18)	0.79 (0.14)	0.89 (0.08)	0.77 (0.11)	0.83 (0.13)
Pielou's evenness	0.82 (0.1)	0.84 (0.13)	0.76 (0.14)	0.74 (0.19)	0.74 (0.17)	0.84 (0.1)	0.79 (0.12)	0.79 (0.14)
n	11	14	13	12	23	21	6	50
ES50	24.3 (5.1)	24.4 (6.8)	22.8 (6)	21.4 (8.3)	21 (6.9)	26.7 (5)	19.6 (5)	23.2 (6.6)
n	56	71			55	59	13	127
Biomass (g wet wt. m^{-2})	18.5 (22.8)	8.5 (12)			11.2 (15.6)	16.4 (21.4)	4 (4.8)	12.9 (18.2)
Body size (mg wet wt. ind^{-1})	19.2 (25.4)	19.1 (29.4)			19.1 (34.8)	20.4 (21.9)	14.1 (13.3)	19.2 (27.6)

Table 4 Relative abundance (%) and standard deviation (bracket) of the major macrobenthos taxa from four cruises and northeastern, southeastern, and western margin of the Qatar Peninsula

	Cruise				Region			Overall
	Feb-10	Jul-10	Feb-11	May-11	NE	SE	W	All
n	56	71	65	47	108	104	27	239
Polychaeta	39.8 (14.3)	38.3 (24.6)	34 (20.6)	24.2 (18.9)	24.3 (17)	41.5 (19.9)	50.2 (19.9)	34.7 (21)
Gastropoda	4.3 (9.2)	9.6 (14.9)	21.3 (20.4)	18.2 (24.1)	18.1 (22)	7.6 (13.4)	15.4 (17.4)	13.2 (18.8)
Secernentea	21.8 (18.7)	8.9 (14.6)	14 (19.5)	6.3 (8.9)	18.1 (21.3)	7.3 (10.4)	13.1 (12.5)	12.8 (17.1)
Amphipoda	15.1 (12.7)	9.2 (13.8)	11.7 (10.8)	15.2 (18)	12 (13.5)	14.5 (14.5)	5.9 (11.1)	12.4 (13.9)
Bivalvia	4.8 (7.6)	9.4 (11)	6.7 (7.7)	13.5 (17.7)	10.7 (14.6)	5.6 (7.4)	10.2 (9.5)	8.4 (11.6)
Ostracoda	6.7 (5.5)	9.8 (12)	3.8 (4.8)	8.9 (10.9)	5.7 (8.1)	10.5 (10)	1 (2.3)	7.3 (9.2)
Cirripedia	1.7 (7.2)	4.9 (11.9)	2.7 (7.8)	3.4 (10.2)	4.8 (11.1)	2.5 (8.8)	0 (0)	3.3 (9.6)
Tanaidacea	2.2 (3.9)	5 (13)	1.6 (3.6)	3.4 (8.6)	0.6 (1.7)	6.4 (12.1)	0.4 (1.4)	3.1 (8.6)
Cumacea	2.9 (3.9)	2.9 (5.2)	4.1 (7.2)	2.9 (4.1)	3.4 (6.3)	3 (3.7)	3.4 (6.7)	3.2 (5.4)
Echinoidea	0.7 (1.4)	1.9 (5)	0.1 (0.4)	4 (10.3)	2.4 (7.6)	0.9 (2.7)	0.5 (2.8)	1.5 (5.5)

temperature and pH were low and DO was high, but declined in July/May (2010 and 2011) when temperature and pH were high but the DO was low.
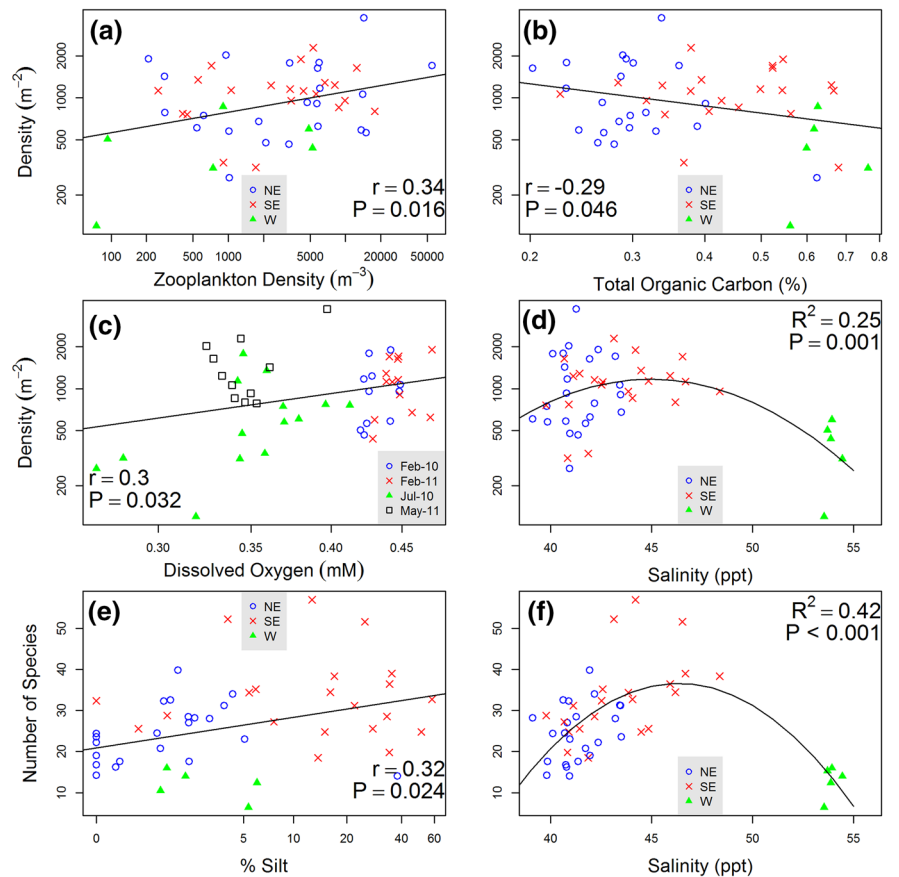
Diversity

A total of 786 macrobenthos species (and taxa) were recovered in this study. The number of species ranged from 11.8 to 13.2 species at St.1 & St.2 on the western shore to 34.8–39 species at St. 7–9 in the southeastern extreme of the study area (S2 Table). The highest species diversity ($E(S_n)$ and H') and evenness (D' and J')

occurred at St. 7–9, while the lowest diversity occurred at St. 5. The number of species at St. 5, however, was not particularly low (26.6 ± 11.6 spp) compared to the global average of all the samples (26.8 ± 13.7), suggesting the low diversity at St. 5 was due to the overwhelming dominance of the bivalve *E. purpurea*.

The number of species was positively correlated with the mean animal density ($r = 0.66$, $P < 0.001$) and % silt in the sediments ($r = 0.32$, $P = 0.024$, Fig. 3e). Similar to the animal density, the number of species was low at the lowest and highest salinity in the NE and W regions, respectively, and high at

Fig. 3 Macrobenthos density as a function of **a** the zooplankton density, **b** total organic carbon (TOC), **c** dissolved oxygen, and **d** salinity and number of species per sample as function of **e** %Silt in the sediments and **f** salinity. The *solid line* shows the linear fit, while the *dashed line* is a quadratic regression fit. The *y axes* for macrobenthos density, zooplankton density, TOC, and % silt axes are in log10 scale

intermediate salinity in the SE region (Fig. 3f). Similarly, statistically significant relationships were found between all diversity indices ($E(S_{50})$, H', D' and J') and % sand ($r = -0.36$ to -0.4, $P < 0.05$), % silt ($r = 0.36$–0.53, $P < 0.01$), and % clay ($r = 0.32$–0.34, $P < 0.05$).

Species composition

Macrobenthos species composition was significantly different among sampling time (PERMANOVA, Time, $P < 0.001$) and geographic regions (PERMANOVA, Region, $P < 0.001$); however, a significant interaction was also evident (Time × Region, $P = 0.013$, Table 2). Moreover, the inter-annual variation (between 2010 and 2011) in faunal dissimilarities was stronger than the variations between the cold vs. hot periods (i.e., February vs. May/July) because the two consecutive February samples did not resemble each other anymore than the May or July samples in the same year (MDS, Fig. 4a, b). The cruise

(time) effects were significant between most cruise pairs in the NE and SE (pair-wise PERMANOVAs, $P < 0.01$) but not in the W regions ($P = 0.33$–0.34). Nevertheless, the regional effect was not as strong as the temporal effect, because most of the between-regions comparisons were only marginally different (based on α level $= 0.02$) during the July 2010 and 2011 sampling (PERMANOVAs, $P = 0.024$–0.047).

Faunal dissimilarities were significantly correlated with bottom environmental variables when geographic distances were held constant (Partial Mantel test, $r = 0.3$, $P < 0.001$). The best correlated variable with the faunal dissimilarities was DON ($r = 0.27$, $P < 0.001$), followed by DO, pH, % clay, depth, % sand, NO_3, NH_4, Temp, PN, % silt, salinity, TOC, and NO_2 (Partial Mantel test, $r = 0.13$–0.26, $P < 0.05$, Fig. 5a). When all possible combinations of variables were considered, the best correlated variable subset were depth, DON, NO_2, NO_3, PN, salinity, pH, DO, % silt, and % clay (Partial Mantel test, $r = 0.45$, $P < 0.001$, Fig. 5b). The inter-annual faunal

difference seems to correspond more to the higher DON in 2011 than in 2010 (Fig. 4a), while the seasonal faunal variations may reflect higher DO in February than in May/July difference but this is most likely driven by the temperature (Fig. 4b). Regionally, the faunal difference was correlated with the variations in salinity (Fig. 4c) and sediment grain size (Fig. 4d).

Temporal and spatial dynamics of community characteristics

Significant regional differences (W, NE, and SE) were evident across macrobenthos density, species richness, diversity (H' and $E(S_{50})$), and evenness indices (D' and J') (ANOVAs, Region, $P < 0.05$, Table 2). For example, the eastern regions (NE and SE) consistently had higher densities than the western region (pair-wise ANOVAs, $P < 0.02$, Fig. 6a). The species richness was highest in the SE, followed by the NE and W

regions ($P < 0.02$). The diversity indices (H' and $E(S_{50})$) were significantly higher in the east (NE and SE) than in the west ($P < 0.02$, Fig. 6b), while the evenness indices (D' and J') were higher in SE than in the NE region ($P < 0.02$, Fig. 6c). The temporal effects (among cruises), however, were only significant for the density and evenness D' (ANOVA, Time, $P < 0.05$). The densities were significantly higher in February and May 2011 compared to July 2010 ($P < 0.01$), but the pair-wise ANOVAs for evenness D' were inconclusive ($P > 0.05$).

None of the species accumulation curves approach the asymptote, suggesting that the species will likely increase if more samples were taken (Fig. 6d, e). The accumulation curve (polygons in Fig. 6d) was highest in the SE (608 spp.), followed by the NE (546 spp.) and the W (134 species). The species richness in 2011 (Feb or May, 388–414 spp.) was higher than that in 2010 (Feb or July, 302–324 spp., Fig. 6e).

Fig. 4 Nonmetric multidimensional scaling (nMDS) on square-root transformed macrofauna species abundance based on inter-sample Bray–Curtis dissimilarities. The symbol sizes represent a dissolved organic nitrogen, b temperature, c salinity, and d % silt fraction
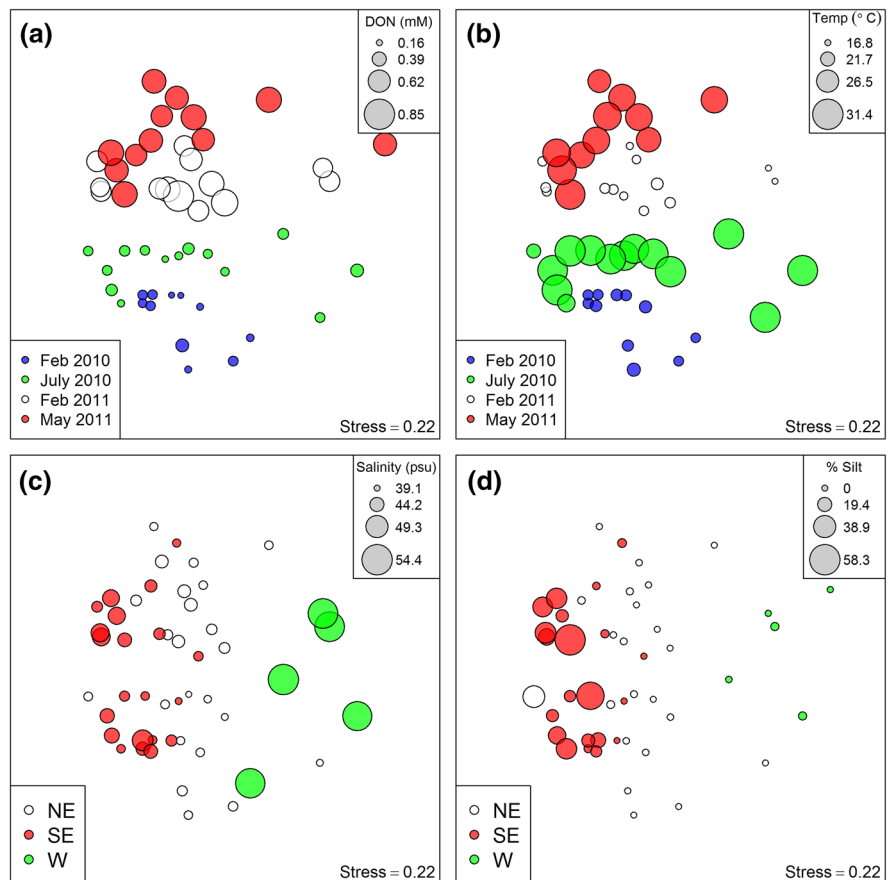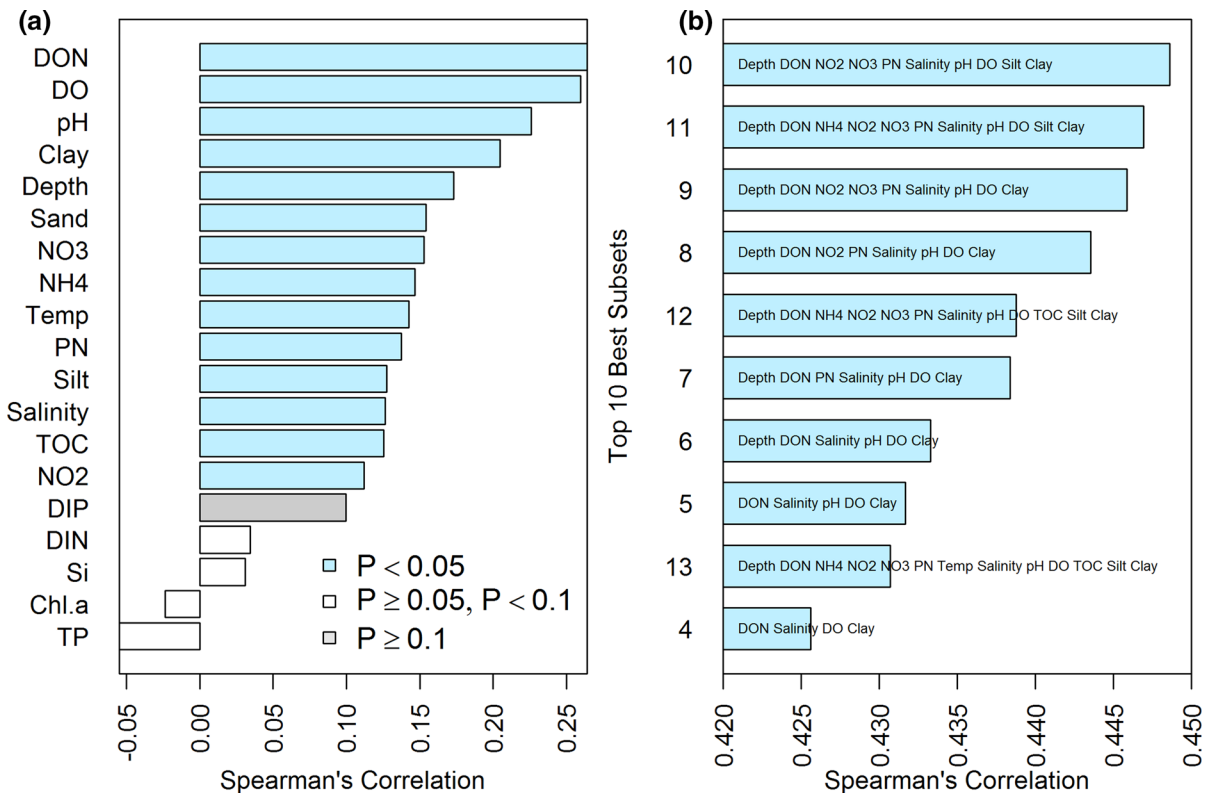
Fig. 5 **a** Partial Mantel test between macrobenthos dissimilarities and individual bottom environmental variables while controlling for the effect of the least-cost distances. **b** Best subsets of bottom environmental variables with the highest correlations to the faunal dissimilarity matrix

Characteristic species contributing >30% of the average similarity within each geographic area are listed in Table 5. The multispecies category Nematoda indet. made the highest contribution in all three regions. Suspension-feeding Bivalvia *E. purpurea* was an important species in the W and NE regions. The carnivorous Polychaeta *Syllis cornuta* Rathke, 1843, and deposit-feeding *Prionospio sexoculata* Augener, 1918, as well as suspension-feeding Amphipoda *Grandidierella exilis* Myers, 1981, were in high numbers in both NE and SE regions. Among cruises, the Nematoda indet. were always an important contributor (7.6–12.4%) to the average faunal similarity (Table 5). *G. exilis* was important in almost all cruises except for the February 2010. Carnivorous Polychaeta *S. cornuta* and *Chrysopetalum debile* (Grube, 1855) were abundant as well in both February 2010 and 2011, while suspension-feeding *E. purpurea* were common in July 2010 and May 2011.

When species contributions to similarity were aggregated by major taxonomic groups, polychaetes were always most important, contributing to 23.9 to 45.9% of the average faunal similarity at all times (Fig. 7a–d). Amphipods were usually second in importance (Fig. 7a, c, d) but were replaced by ostracodes in July 2010 (Fig. 7b). Geographically, polychaetes were the most abundant taxa in the W, NE, and SE regions, respectively (Fig. 7e–g). Molluscs (gastropod and bivalve) came in second in the W region, contributing 38.6% to the average similarity (Fig. 7e). In the NE and SE region, amphipods accounted for 12.5 and 16.6% of the average similarities, respectively (Fig. 7f, g).

Path analysis

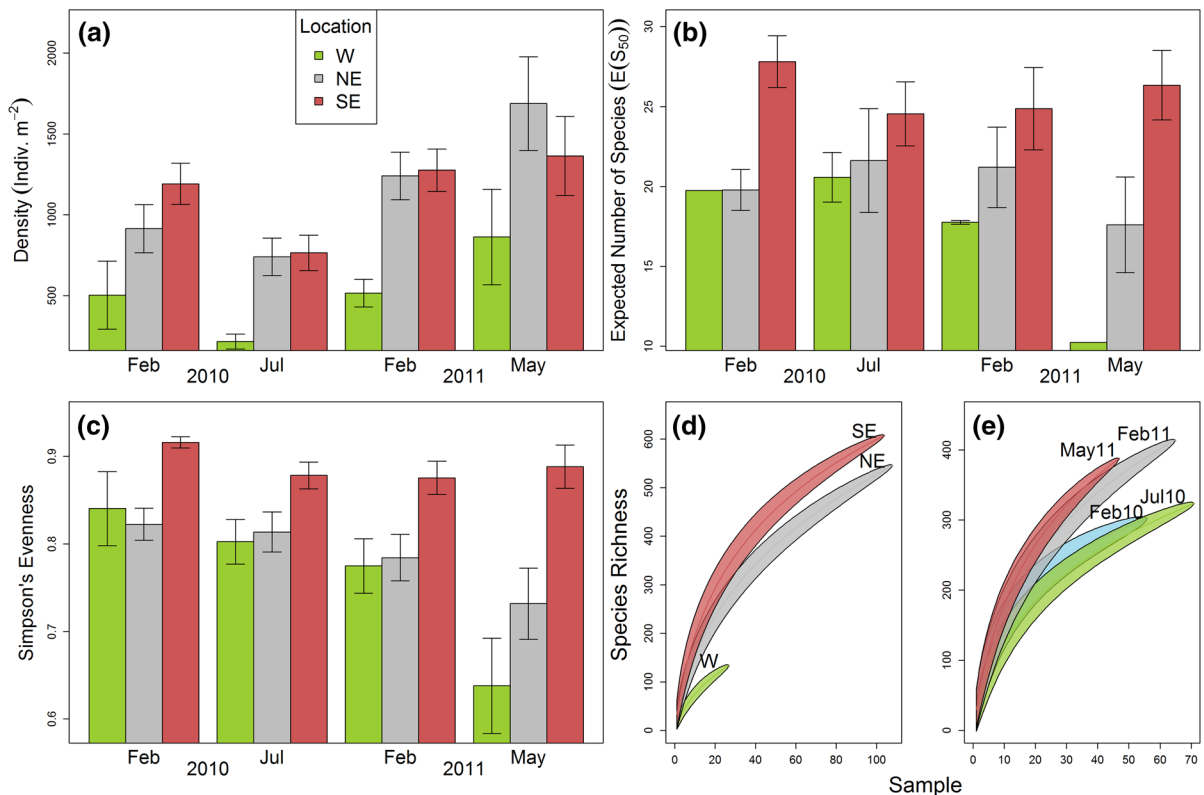Pair-wise Mantel tests were used to construct a correlation matrix (Fig. 8a) among the least-cost

Fig. 6 Macrofauna **a** mean density (individual m^{-2}), **b** expected numbers of species for 50 randomly selected individuals ($E(S_{50})$), **c** Simpson's species evenness index (D'), and **d** species accumulation curves for western, northeastern, and southeastern regions and **e** species accumulation curves for the February 2010, July 2010, February 2011, and May 2011 sampling

geographic distances (Dst), Bray-Curtis dissimilarities of zooplankton (Zoo), phytoplankton (Phy), macrobenthos (Ben), and Euclidean distances of surface nutrients (SNt), bottom nutrients (BNt), surface water properties (SWt), bottom water properties (BWt), and sediment characteristics (Sed). Exact variables included in each group can be found in the Methods section. Based on maximum likelihood, an initial path model was derived from the correlation matrix using structural equation modeling (SEM, Fig. 8b). A Chi-square test indicates that the model relationships were not significantly different from the original correlation matrix ($X^2 = 15$, df $= 24$, $P = 0.87$). By subsequently removing the less influential paths, a parsimonious path model was produced (Fig. 8c, with the lowest AIC and BIC). In the parsimonious model, the proportions of variance explained (R^2) were 24% for Ben and 18% for Zoo and Phy, as well as 5% for BNt and 27% for SNt. Ben was influenced significantly by Dst, Sed, BWt, and Zoo (Partial Mantel Tests,

$P < 0.001$). No statistical evidence supported the influence of Phy on Ben (Partial Mantel test, $P = 0.94$). The composition of Ben significantly influenced BNt and thus subsequently affected the SNt, Phy, and Zoo (Partial Mantel tests, $P < 0.001$). There was no statistical influence of Zoo on SNt (Partial Mantel test, $P = 0.17$). Both Phy and Zoo were significantly influenced by SWt (Partial Mantel test, $P < 0.001$).

Discussion

Variations in density

The standing stocks of macrobenthos density ($1{,}045 \pm 859$ ind. m^{-2}) were low compared to other continental shelves at similar latitudes and depths. Highest benthic metazoan densities are normally encountered in productive continental shelves near

Table 5 Similarity percentage (SIMPER) contribution for benthic macrofauna species

Region	Taxon	Species	Contrib%	Cum.%	Feeding
W: Avg.Sim: 44.2%	Nematoda	Nematoda sp.	10.78	10.78	
	Polychaeta	*Janua* (*Fauveldora*) *kayi*	9.47	20.25	S
	Polychaeta	*Spirorbis spirorbis*	9.14	29.39	S
	Bivalvia	*Ervilia purpurea*	7.33	36.72	S
NE: Avg.Sim: 33.1%	Nematoda	Nematoda sp.	10.73	10.73	
	Gastropoda	*Vermetus triquetrus*	7.94	18.67	H (Saldanha, 2003)
	Bivalvia	*Ervilia purpurea*	3.46	22.13	S
	Polychaeta	*Syllis cornuta*	3.35	25.48	C (MacDonald et al., 2010)
	Polychaeta	*Prionospio sexoculata*	3.01	28.49	D (Pillay et al., 2008)
	Amphipoda	*Grandidierella exilis*	2.8	31.29	S (Barnard et al., 1991)
SE: Avg.Sim: 33.2%	Nematoda	Nematoda sp.	5.33	5.33	
	Ostracoda	*Synasterope* sp.	4.07	9.4	S (Vannier et al., 1998)
	Amphipoda	*Grandidierella exilis*	3.69	13.09	S (Barnard et al., 1991)
	Polychaeta	*Prionospio sexoculata*	2.95	16.04	D (Pillay et al., 2008)
	Malacostraca	*Grandidierella* sp.1	2.76	18.8	S (Barnard et al., 1991)
	Polychaeta	*Nephtys cornuta*	2.73	21.53	C (MacDonald et al., 2010)
	Polychaeta	*Chrysopetalum debile*	2.71	24.24	C (Fauchald & Jumars, 1979)
	Amphipoda	*Ampelisca* cf. *mississippiana* sp.	2.57	26.81	S (Soliman & Wicksten, 2007)
	Polychaeta	*Lumbrinereis gracilis*	2.25	29.06	C (Fauchald & Jumars, 1979)
	Polychaeta	*Syllis cornuta*	2.14	31.2	C (MacDonald et al., 2010)

Percent contributions (Contib%) were examined for the "Region" groups across all "Time" groups using the same two-way layout in the PERMANOVAs and ANOVAs (Table 2). Only species contributed to at least 30% (Cum.%) of the average similarity (Av.Sim) in each geographic location are shown

S suspension feeder, *H* herbivore, *C* carnivore, and *D* deposit feeder

river mouths, such as the northern Gulf of Mexico ($3{,}740 \pm 3{,}349$ ind. m^{-2}) (Nunnally et al., In preparation), in coastal upwelling zones such as NW Africa ($5{,}966 \pm 1{,}636$ ind. m^{-2}, Nichols & Rowe, 1977), or eutrophic coastal regions such as the New York Bight, where over 200,000 ind. m^{-2} were found at a sewage sludge dump site (Rowe, 1971a). Variations in densities and biomass have been attributed to surface primary production and depth (Rowe, 1971b), and thus we presume that in the warm, shallow AG the low densities are most probably a function of low phytoplankton primary production (Quigg et al., 2013).

Within the AG, our estimates are comparable to or somewhat lower than the Manifa-Tanajib Bay of Saudi Arabia ($1{,}867 \pm 1{,}417$ ind. m^{-2}) (Joydas et al., 2011), the northern Saudi coast ($2{,}716 \pm 1{,}723$ ind. m^{-2}, Joydas et al., 2012), Kuwait Bay (summer: $1{,}400$–$3{,}900$ ind. m^{-2}; winter: 700–$2{,}000$ ind. m^{-2}, Bu-Olayan & Thomas, 2005), and an earlier survey along the coast of Saudi Arabia (silt/sand bottom,

670–$3{,}740$ ind. m^{-2}, Coles & McCain, 1990). The recent ROPME (Regional Organization for the Protection of the Marine Environment) winter survey (ROPME, 2012), however, reported a lower estimate (~ 425 ind. m^{-2}) than our reported values but nonetheless a higher density in the northwestern (~ 422 ind. m^{-2}) than in the eastern gulf along the Iranian coast (~ 298 ind. m^{-2}). Thus we conclude that the entire AG is 'food limited.'

Lowest densities were encountered at the highest bottom water temperature (29.9 ± 2.9°C) in July 2010 across all sampling sites (Fig. 6). The density was also depressed during hypersaline conditions year-round on the west coast near Dukhan (54.2 ± 0.8), suggesting that osmotic stress from extreme salinity as well as the meager food supply may affect the benthos. Similarly, in the Saudi Arabian side of the Gulf of Salwa, the benthic communities also experienced large drop in densities when the salinity exceeded 60 and temperature exceeded 35°C in the summer
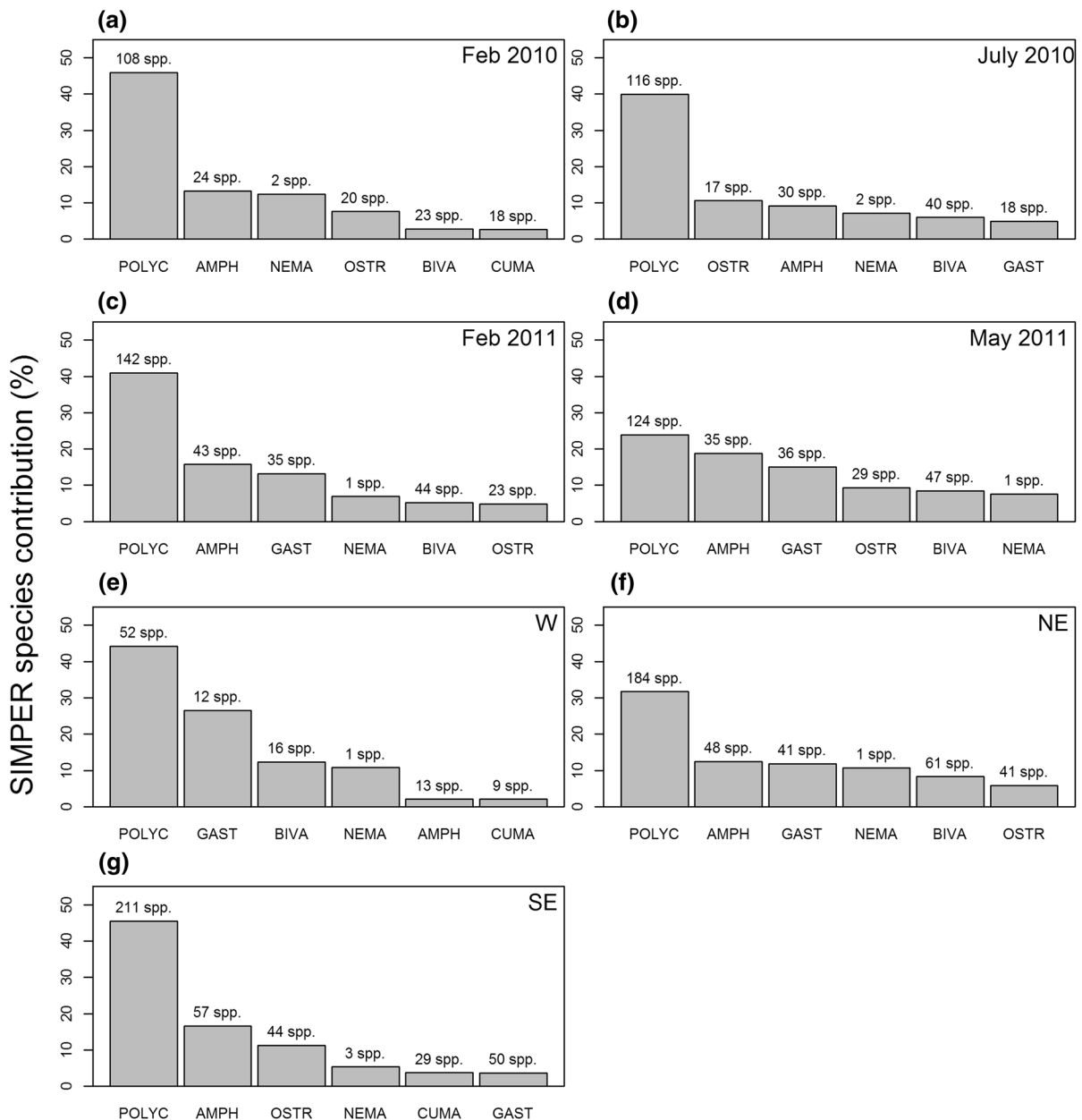
Fig. 7 Cumulative species similarity percent (SIMPER) contributions for **a** February 2010, **b** July 2010, **c** February 2011, **d** May 2011 sampling, **e** western, **f** northeastern, and **g** southeastern regions. The average similarity for specific sampling time and geographic area are broken down to percent similarity contribution (2 way cross SIMPER) for each species. The individual species SIMPER contributions are aggregated to major benthic taxa. *POLYC* POLYCHAETA, *AMPH* AMPHIPODA, *NEMA* NEMATODA, *OSTR* OSTROCODA, *BIVA* BIVALVIA, *CUMA* CUMACEA, *GAST* GASTROPODA

(Joydas et al., 2015). Lowest bottom dissolved oxygen (0.35 ± 0.04 mM or 5.6 ± 0.64 mg l^{-1}) occurred during July 2010 (Table 1). Although none of the locations we sampled would be considered hypoxic (DO < 2 mg l^{-1}), the lower oxygen in summer may

exert stress on macrobenthos due to exponential increases of metabolic rates as a function of temperature (Vaquer-Sunyer & Duarte, 2011). A combination of thermal (Coles & McCain, 1990; Sheppard et al., 2010; Vaquer-Sunyer & Duarte, 2011; Joydas
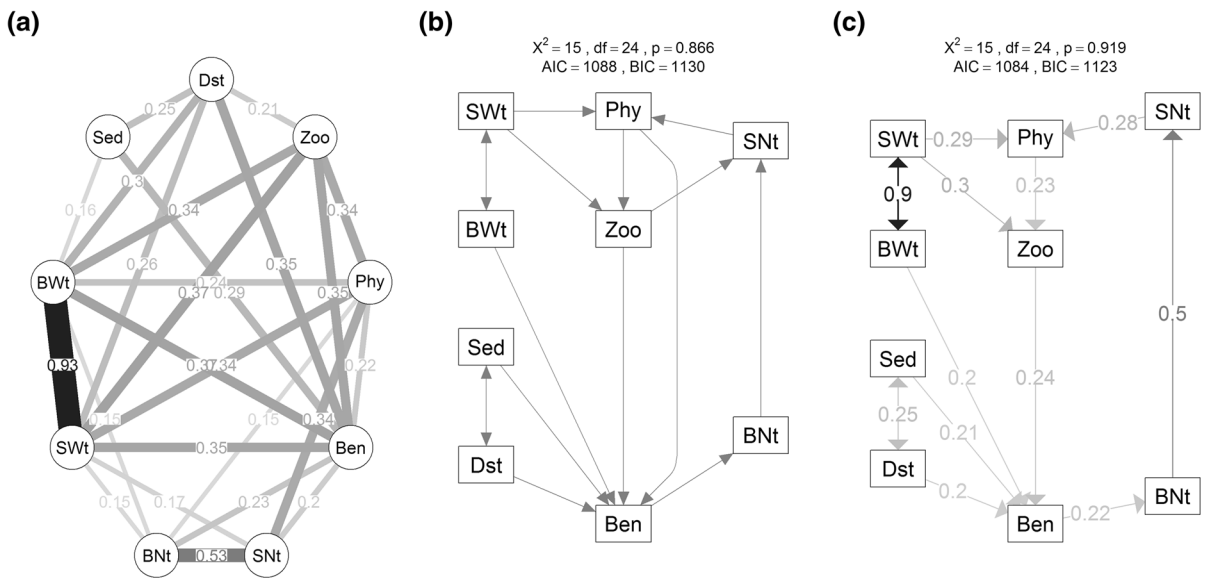
(a)

(b)

(c)

Fig. 8 Path analysis of causal relationships among faunal dissimilarities and environmental and geographic distances. 'Dst' = least-cost geographic distance, 'Zoo' = zooplankton dissimilarities, 'Phy' = phytoplankton dissimilarities, 'Ben' = macrobenthos dissimilarities, 'SNt' = Euclidean distances of surface water nutrients, 'BNt' = Euclidean distances of bottom water nutrients, 'SWt' = Euclidean distances of surface water properties, 'BWt' = Euclidean distances of bottom water properties, 'Sed' = Euclidean distances of sediment characteristics. **a** Mantel correlation matrix among dissimilarity and distance matrices based on Spearman's rank correlation. Only the significant correlations (Mantel test,

$p < 0.05$) were shown. The line width and color scales to the strength of the correlation coefficients. **b** Full conceptual model with direction of *arrows* indicating the influences of Dst, Sed, BWt, Zoo, and Phy on Ben. Feedback paths through the influences of Ben on BNt and then subsequently to SNt, Phy, and Zoo were added to represent benthic-pelagic coupling. Additional paths indicating the influences of SWt on Phy and Zoo, as well as Zoo on SNt, were also added to the model. Finally, the relationships between SWt and BWt and Dst and Sed were set to their Mantel correlations (*double-headed arrow*). **c** The best parsimonious path model giving the lowest AIC and BIC scores

et al., 2015), hypoxic (Vaquer-Sunyer & Duarte, 2008, 2011), and hypersaline conditions (Coles & McCain, 1990; Lamptey & Arma, 2008; MacKay et al., 2010; Sheppard et al., 2010; Joydas et al., 2011, 2015; Dittmann et al., 2015), accompanied by poor supplies of food (Quigg et al., 2013), likely exert synergistic negative effects that result in depressed density.

The positive relationship between benthos and zooplankton abundances (Fig. 3a) but not surface or bottom chlorophyll concentration suggests that the benthos may be more reliant on zooplankton fecal pellets, molts, or carcasses as food than phytoplankton cellular debris, as observed elsewhere in shallow coastal environments (Turner, 2002; Sampei et al., 2009; Frangoulis et al., 2011). The lack of seasonal patterns in Qatar's coastal phytoplankton (Quigg et al., 2013) likely leads to diminishing export of phytodetritus. High temperatures may also increase microbial degradation (Kirchman et al., 2009) and thus decrease the quantity and quality of phytodetritus that reaches

the benthos, leading to an overlap in resource utilization between the zooplankton and macrobenthos (Dauvin & Vallet, 2006).

Variations in diversity

Alpha diversity was positively related to % silt (Fig. 3e) and both were highest in the southeastern region. This pattern was a function of the numerically dominant polychaetes whose density and species numbers also correlated with % silt. Moreover, when polychaetes are excluded from the analysis, the silt-macrofauna (density and species numbers) correlations become nonsignificant ($P > 0.05$). A common generalization is that the suspension feeders prefer sandy substrates because the coarser sediments are associated with high energy environments and more suspended food; in contrast, the deposit feeders prefer silt and clay, where feeble currents allow the fine sediments and labile organic materials to accumulate

on the seafloor. This dichotomy, however, may be over simplified because suspension and deposit feeders co-occur in multiple substrate types and near-bottom flow conditions (Snelgrove & Butman, 1994).

The environmental stress model (ESM) (Menge & Sutherland, 1987) predicts low diversities at the highest and lowest stress levels as a result of intense stress and competitive (or predation) exclusion, respectively. In between these conditions, coexistence gives rise to a unimodal diversity pattern, an attractive explanation for our observed unimodal diversity salinity relationship. Depressed diversity in hyper-saline condition (Fig. 3f, salinity >45) has also been observed elsewhere in the gulf (Coles & McCain, 1990; Joydas et al., 2011, 2015), as well as the other hypersaline coastal environments such as semi-enclose lagoons in South Africa and Mediterranean (Lamptey & Arma, 2008; Magni et al., 2009) or drought-influenced estuaries in South African and Australia (MacKay et al., 2010; Dittmann et al., 2015) with sharp salinity gradients over relatively short geographic distances or over flood and prolonged drought periods.

Benthic-Pelagic coupling

Benthos provide essential nutrient regeneration, particularly rate-limiting nitrogen in the form of NH_4 (Gray & Elliott, 2009; Nunnally et al., 2014), especially in ecosystems as shallow as the AG. We have no direct benthic regeneration measurements in the AG, but the addition of bottom water to incubations of phytoplankton can stimulate surface primary production, suggesting benthic regeneration might be an important source of nutrients (Quigg et al., 2013). Our path model suggests that the zooplankton and benthos contribute to surface and bottom nutrient pools, respectively (Fig. 8). Given the high correlation between the bottom and surface water properties (e.g., temperature, salinity, DO and pH, $r > 0.9$), the water column was well mixed and thus the coupling between benthic nutrient regeneration and primary production in the path model is reasonable (Snelgrove et al., 2000).

Patterns and drivers of assemblage composition

The potential causes of the temporal variability remain ill-defined. It was stronger than the regional variability, and the inter-annual variability (2010 vs. 2011) was stronger than the variability between cold vs. hot seasons (February vs. May/July) (Fig. 4). Note that the range in each of the correlating environmental variables was small, and thus the correlations we described may play a minor role in the remarkable changes in the fauna observed as a function of time. The oxygen was never clearly limiting, the Chl a was always low, salinities were always above that in the open ocean, the inorganic nutrients were always low, the organic matter in the sediments was universally low, and the sediments were always clearly sand, with only a modest admixture of mud-sized material in them. We have had no way to measure the impact of potential burial by the heavy and constant rain of particles from the surrounding desert (Nichols et al., 1978). Clearly, the assemblage composition was not determined by any single factor or even a combination of the factors we list above. In fact, the explanatory powers for most of our analysis were low (i.e., Figs. 3, 5, 8) and thus the causes of the variations in the fauna we observed remain obscure.

Characteristic species of each sampling period and area reflect the 'substrate-feeding type paradigm' (Table 5). For example, in the W and NE regions, the predominant sand (>96%) produced by strong bottom currents along the axis of the AG (Massoud et al., 1996; Kämpf & Sadrinasab, 2006) was characterized by the suspension-feeding Bivalvia E. purpurea (3.5–7.3% of the average faunal similarity). The bivalves, however, declined from the W (12.3%), NE (8.3%) to SE regions (2%), with increased fractions of mud (silt and clay, 3.5–23.2%). In the W region, suspension-feeding serpulid polychaetes, Spirorbis spirorbis (Linnaeus, 1758), Spirorbis sp., and Janua (Fauveldora) kayi (Knight-Jones, 1972) accounted for 23.2% of the average similarity. They attach to macroalgae (e.g., seagrass or algal beds) (Bell et al., 2001) and dead corals (Riegl & Purkis, 2012). The carnivorous polychaetes S. cornuta and Syllis gracilis Grube, 1840 (7.7%) occur under boulders or coral rubble and feed on sessile invertebrates (e.g., hydroids, sponges, bryozoans, and ascidians) (Riegl & Purkis, 2012) that are common substrates in the W region (Sheppard et al., 2010). In the SE region, the sandy mud substrates (Massoud et al., 1996) supported deposit-feeding and carnivorous polychaetes (e.g., P. sexoculata, Nephtys cornuta Berkeley & Berkeley, 1945, C. debile, Lumbrinereis gracilis (Ehlers, 1868),

and *S. cornuta*). Although polychaetes made significant contributions to both W (41.2%) and SE regions (45.5%), their assemblages were composed of distinctly different feeding types (suspension-feeding vs. deposit-feeding/carnivores).

The lack of temporal variation in numbers of species and alpha diversity (Table 2) suggest that whatever drives the temporal variations in abundance and changes in species composition (e.g., synergy of thermal, hypersaline, hypoxic stresses, burial by sand and dust, and low productivity) had little or no effect on the alpha diversity. Most notably, the alpha diversity did not seem to be affected (at least statistically) when the density was significantly depressed in July 2010 or when the assemblage composition was statistically different over time. In fact, only 50.4–57.6% of species recurred between consecutive cruises and only 40.5–38% of species recurred in the same seasons (February or May/July) of consecutive years, suggesting high seasonal and inter-annual species turnover. Moreover, such temporal shifts were also observed when the individual species contributions (to average faunal resemblance) were aggregated to higher taxonomical levels (Fig. 7a–d), suggesting that the rapid temporal faunal turnover also occurred above the species level.

The low abundance and biomass of the benthos appear to be directly related to the oligotrophic nature of the AG, in association with high temperature fluctuations and high salinity. The high temporal species turnover could be source-sink dynamics related to exchange of water masses between the AG and Indian Ocean through the Strait of Hormuz (Kämpf & Sadrinasab, 2006). We suggest that the benthos in the AG is recruited from the meroplanktonic larvae and juveniles within the annual incursion of Arabian Sea water, and this creates the high seasonal and inter-annual faunal turnover rates. The potential 'new' recruits are ephemeral because they are susceptible to the synergistic negative effects of multiple stresses (e.g., high temperature, burial by sand and silt, and hypersalinity), accompanied by very meager phytoplankton productivity, and the community remains an r-regulated assemblage from which a stable, predictable K-regulated benthos cannot be derived: it is unsustainable. While the path model demonstrates that, at the assemblage level, the heterogeneity of plankton parallels the heterogeneity of benthic assemblages both are related to the annual

front of Arabian Sea water that penetrates the AG every summer.

In the context of global climate change, there is no reliable "model" for the effects of persistent stresses under low primary production. Despites their limited spatial extent relative to the world's ocean, such environmental conditions are common in subtropical/tropical arid regions or semi-enclose lagoons, bays, or estuaries under prolonged drought conditions. Multiple lines of evidence suggest that the phytoplankton biomass or productivity have been declining in the past century (Boyce et al., 2010), in the past decade (Gregg & Rousseaux, 2014) and are likely to decline into the future under the climate change scenarios (Steinacher et al., 2010). Whether or not coastal environments are increasingly subjected to multiple persistent stresses with continuing climate change remains to be seen (Harley et al., 2006). Our results provide a modicum of insight into the ecological dynamics of a naturally arid coastal ecosystem, with virtually no or little 'new' sources of organic matter. We suggest that what we observed in the AG is a "new model" for extremely arid environments impacted by global warming and ocean acidification.

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