



# Crustaceans functional diversity in mangroves and adjacent mudflats of the Persian Gulf and Gulf of Oman

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## ABSTRACT

The effects of mangrove vegetation on functional features of crustacean assemblages were investigated using the Biological Traits Analysis (BTA). The study was carried out at four major sites in the arid mangrove ecosystem of the Persian Gulf and Gulf of Oman. Samples of Crustacea and associated environmental variables were taken seasonally (February 2018 and June 2019) from two habitats: a vegetated area with both mangrove trees and pneumatophores, and an adjacent mudflat. In each site, functional traits for the species were assigned using seven categories based on bioturbation, adult mobility, feeding habits and life-strategy traits. The results showed that the crabs (*i.e.*, *Opusia indica*, *Nasima dotilliformis* and *Ilyoplax frater*) were widely distributed across all sites and habitats. The vegetated habitats supported higher taxonomic diversity than the mudflats, which highlights the importance of mangrove structural complexity for crustacean assemblages. Species inhabiting vegetated habitats were characterized by stronger presence of conveyor building species, detritivore, predator, grazer, lecithotrophic larval development, body size of 50–100 mm, and swimmer trait modalities. While, mudflat habitat enhanced the occurrences of surface deposit feeder, planktotrophic larval development, body size of <5 mm, and life span of 2–5 years. The results of our study showed that taxonomic diversity increased from the mudflats to the mangrove vegetated habitats. However, functional diversity did not differ between habitats. The significant differences in species and functional trait composition were observed between vegetated habitats and adjacent mudflats, stressing that different habitats may harbor different species and trait sets, likely as a result of habitat complexity. The use of taxonomic and functional attributes generate complementary information that can help us to reach more efficient conclusions in terms of biodiversity conservation and ecosystem functionality in mangrove ecosystems.

## 1. Introduction

Mangroves are productive ecosystems distributed throughout tropical and sub-tropical coastlines of the world (Donato et al., 2011; Spalding et al., 2010). Mangroves provide important spawning, nursery, and feeding habitats for invertebrates, fishes, and terrestrial species (Kon et al., 2007; Kruitwagen et al., 2010). On a larger scale, mangroves mitigate climate change by sequestering a significant amount of organic carbon in sediment and biomass pools (Donato et al., 2011; Jennerjahn, 2020). On small a scale, by reducing tidal velocity and wave surges, mangroves protect the coastlines from erosion (McIvor et al., 2012). Structural complexity, which is a key characteristic of mangroves, is produced by a multi-dimensional net of mangrove canopy, trunks, twigs,

areal roots, and mangrove debris that provide a variety of microhabitats to marine invertebrates. Several studies highlight the importance of habitat structural complexity for taxonomic diversity and abundance of marine invertebrates, as well as for the functioning of coastal environments (Boström et al., 2010; Fonseca et al., 2011; Villéger et al., 2008). Structural complexity, arranged by mangrove vegetation, promotes the abundance of associated fauna by providing substrate for recruitment, and preventing from predation by larger fish or crabs (Kiruba-Sankar et al., 2018; Tomiczek et al., 2020). Furthermore, the complex architecture of trunks and aerial roots increases the surface area available for colonization by benthic algae that are important food resources for higher trophic levels in mangrove food webs (Hemmati et al., 2021; Vorsatz et al., 2021). Several studies compared macrofauna

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communities in mangrove and adjacent habitats and revealed that different habitats may contribute differentially to the functioning, biomass, and diversity (Checon et al., 2017; Corte et al., 2021; Meijer et al., 2021). There is a general consensus that structurally heterogeneous habitats provide a wider range of niches, and different ways of exploiting environmental resources and thus increase taxonomic diversity (Kathiresan and Bingham, 2001). Investigations on the influence of mangrove vegetation on invertebrate functional diversity and consequent changes in the ecosystem functioning are still rare, with little evidence having emerged recently (Bernardino et al., 2018; Checon et al., 2017; Corte et al., 2021; Freitas and Pagliosa, 2020; Leung and Cheung, 2017).

Crustaceans represent an important group of macrofauna in mangroves of the Persian Gulf accounting for 25–55% of the total species density (Delfan et al., 2021; Vahidi et al., 2020). The crustaceans associated with mangrove forests is typically dominated by burrowing decapods such as sesarimid crabs and fiddler crabs. By consuming significant amounts of mangrove detritus and microbial mats, crustaceans highly promote decomposition processes and prevent loss of nutrients (Kristensen, 2008). For example, leaf-eating sesarimid crabs consume mangrove leaves as their major food source (Thongtham and Kristensen, 2005). Crabs process 9–100% (an average of 57%) of the annual leaf litter in mangrove forests (Nordhaus et al., 2006). In addition, through ingestion and gut passage, the fragmentation of litters provides easier access for colonization by bacteria, and thus recycling of nutrients (Kristensen et al., 2017). Besides, the burrowing species affect sediment topography and biogeochemistry, change particle size distribution, and promote the biogeochemical reactions in mangrove sediments (Kristensen et al., 2017; Nordhaus et al., 2019). Thus crustaceans exhibit a wide range of representative traits, which have significant roles in regulating the functioning of mangrove benthic ecosystems (Al-Khayat and Jones, 1999; Nordhaus et al., 2019).

Classically, biodiversity refers to species richness, abundance, and distribution of organisms in a defined, physical environment. However, characterizing biodiversity solely by taxonomic diversity overlooks the various other types of variability that living organisms exhibit, notably the functional facets of diversity (Cardinale et al., 2012; Wong and Dowd, 2015). Over the past decade, functional diversity has been identified as a key component of biodiversity because it considers the variation of functional traits occurring across ecological communities of a given ecosystem based on the activities of organisms, and thus functions (e.g., behavior, feeding and bioturbation activities) (Corte et al., 2021; Lam-Gordillo et al., 2021; Shojaei et al., 2021). Functional traits reflects how species interact with the environment and individuals of other species, giving a greater mechanistic understanding of how species may respond to environmental change (Degen et al., 2018; Loreau et al., 2001; Nasi et al., 2020b). Biological Trait Analysis (BTA) is a useful analytical approach proposed for describing the ecological functioning of terrestrial and marine ecosystems. BTA combines abundance or biomass data with information on life traits of the species to characterize the ecological functioning of an ecosystem (Bremner et al., 2006; Shojaei et al., 2015). BTA was first applied in studies on terrestrial plants (McIntyre et al., 1995) and freshwater organisms (Dolédéc et al., 1996). Over the past decade, an increasing number of studies have applied BTA to marine benthic assemblages in relation to several environmental variables (e.g. Shojaei et al., 2021), hypoxia events (Gogina et al., 2014), dredged material disposal (Bolam et al., 2020), nutrient enrichment (Douglas et al., 2017) and riverine influence (Nasi et al., 2020b). Mangroves worldwide face several threats, including deforestation, pollution, changed hydrodynamic, and sea-level rise (Jennerjahn, 2020). Although many countries have deployed conservation measures, mangrove forests are declining at a global rate of approximately 0.2% per year (Richards et al., 2020). Thus, the knowledge on the functioning of mangrove systems is essential for quantifying biodiversity loss, understanding the future change in ecosystem services, and informing conservation objectives and management plans. In the Persian Gulf and

Gulf of Oman, the distribution of mangroves presents the northern biogeographical boundary of mangroves in the Indian Ocean (Akbari et al., 2022). They are subjected to extreme environmental pressure such as high salinity and temperature fluctuations, thus, living at the edge of their physiological tolerances to environmental conditions (Akbari et al., 2022).

We studied crustacean assemblages to illustrate the link between coastal habitats complexity, seasonal variations, and crustacean species and functional diversity to point out the ecological values of mangroves in the face of their increasingly threatening environment. Here, we hypothesized that: *i*) crustacean assemblages in mangrove habitats would have a higher species and functional diversity than assemblages in the adjacent mudflats, *ii*) habitat complexity driven by features associated with mangrove trees influences the species and trait composition of crustacean assemblages.

## 2. Material and method

### 2.1. Study sites

We selected four mangrove sites along the northern coast of the Persian Gulf and Gulf of Oman *i.e.*, Nayband (NY), Qeshm (QE), Khamir (KH), and Sirik (SK), where dense mangrove occurred naturally (Fig. 1; Supplementary data 1, Table S1). They are located at the northernmost latitudinal limit of mangrove forests in the Indian Ocean. The forests consist mostly of the *Avicennia marina*, due to its tolerance of high salinity and wide temperature extremes (Delfan et al., 2021). These mangroves are intertidal and none has any significant freshwater input other than small seasonal rivers and rain. Due to the climate-geophysical conditions, the development of the forests is lower when compared to that of the tropics, which is mainly evidenced by the mean tree height between 3 and 5 m and mean diameter at breast height of 0.14 m (Delfan et al., 2021). Tall mangrove trees (>4 m) are restricted to seaward areas in the Persian Gulf and Gulf of Oman. Indeed, only at seaward locations the low salinity and high levels of nutrients maintain stands of large trees.

NY mangrove forest (27°27'47.6"N 52°39'32.4"E), covering 611 ha, has been preserved as Iran first national marine reserve since 2004 (Owfi, 2018). NY hosts one of the most northerly mangrove forests in the world (Delfan et al., 2021). The climate in the area is arid with a mean rainfall of <200 mm yr<sup>-1</sup> and an annual mean air temperature of 27.2 °C (2011–2020), with minimum and maximum temperatures of 11.5 °C to 42.3 °C in January and July, respectively (IRIMO, 2021). The mangrove is under a semidiurnal regime with a maximum tidal amplitude of >2 m. QE mangrove forest (26°48'25.2"N 55°42'31.4"E) represents the largest mangrove forest of the region, with an area of about 3900 ha, contributing 40% to the mangrove coverage of Iran. The QE mangrove forest is composed of mostly monospecific stands of *Avicennia marina*, with scattered small patches of planted *Rhizophora mucronata*, which cover a total area of 100 ha. The annual mean air temperature is 27.2 °C (2011–2020), with minimum and maximum temperatures of 12.16 °C and 35.86 °C in January and July, respectively (IRIMO, 2021). The mean rainfall level is about 80.3 mm year<sup>-1</sup> that mainly occurs in winter. The tide is semidiurnal, with a tidal range of 1–3 m at neap tides and 3–4 m at spring tides (Reynolds, 2002).

KH mangrove forest (26°58'43.7"N 55°38'25.4"E) covers an area of approximately 1750 ha is divided into three different sections called Mardo, Khamir, and Lashtaqan. There are two small seasonal rivers discharges into the forest, and tidal water exchange with the open sea occurs through the Khuran Channel (Shahraki et al., 2014). The estuary is tidally dominated with semidiurnal tides that range in height between 3 and 5 m above mean low water. The annual mean air temperature in KH is 29.1 °C (2011–2020), with a minimum of 13.1 °C, and a maximum of 37.9 °C in January and July, respectively (IRIMO, 2021). QE and KH sites are listed in the Ramsar Convention for wetland protection and were recognized as biosphere reserves in 1977 by the Coordination

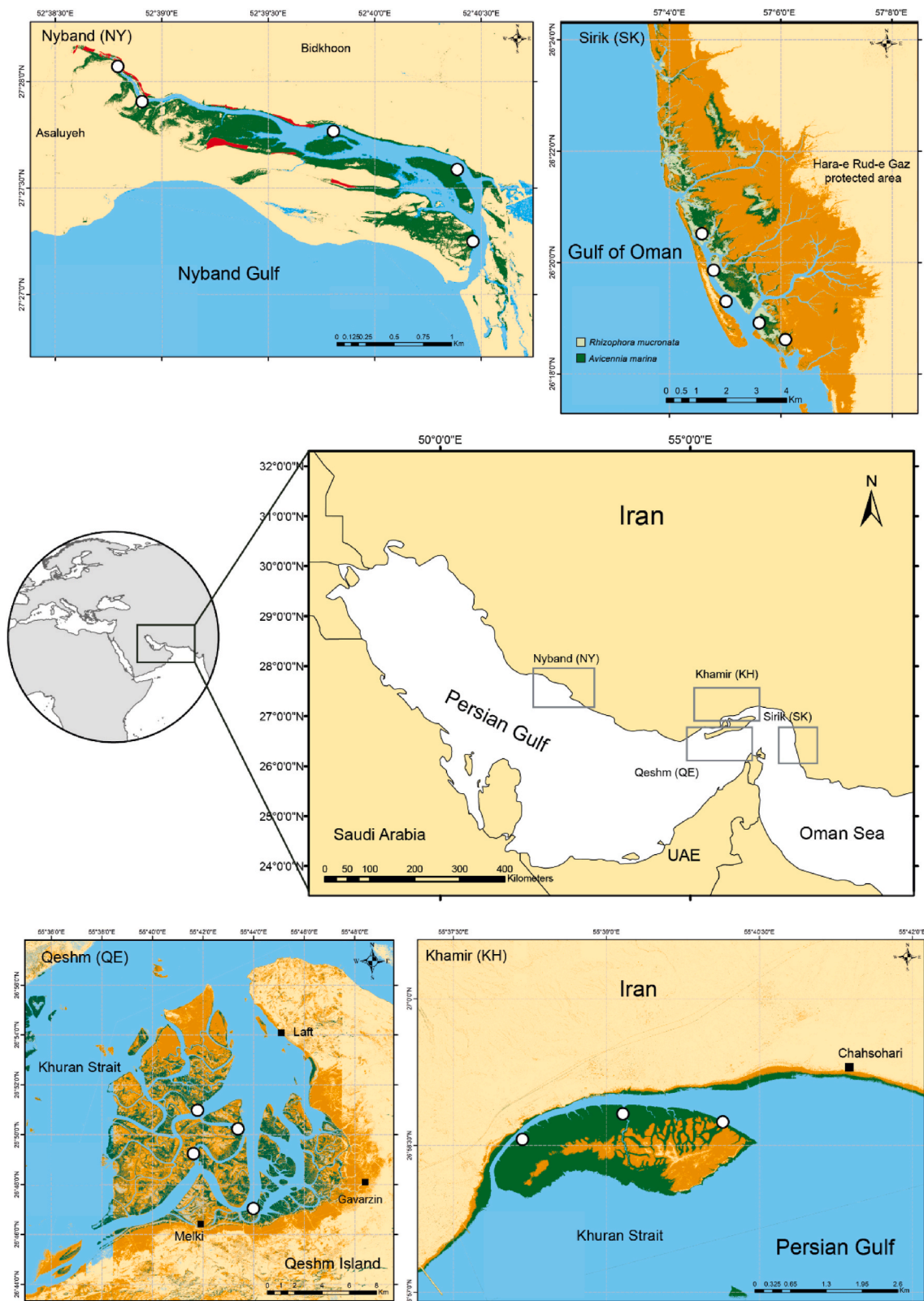


Fig. 1. Map showing four mangrove ecosystems and the positions of the sampling sites of Crustacea in the Persian Gulf and Gulf of Oman.

**Table 1**

Functional traits and the corresponding modalities of Crustacea with their definitions and the relation of the respective trait to ecosystem functions. A label is given for each category.

Trait	Modalities	ID	Definition	Function
Bioturbation	Biodiffuser	BIBD	Vertical or horizontal redistribution of the sediment over a short distance (François et al., 1997).	Nutrient cycling/ regeneration Habitat formation/ provision
	Conveyor building	BICO	Translocation of sediment from depth within the sediment to the surface during subsurface deposit feeding or burrow excavation and defecation (Bolam and Eggleton, 2014; Gibson et al., 2001).	
	Regenerator	BIRE	Excavator species that dig into sediment and continuously maintain their burrows, and by doing so transfer sediment from depth to the surface. (Kristensen et al., 2012).	
	Superficial modifier	BISM	Species that move sediment particles through living and feeding activities at the sediment surface ( Bernard et al., 2019).	
Living habit	Burrow dweller	AHBD	Species live in permanent or temporary burrows in the sediment (Degen and Faulwetter, 2019).	Nutrient cycling/ regeneration Food web dynamics Carbon sequestration Habitat formation/ provision Bioturbation
	Free living	AHFL	Species that are able to move freely within or on the sediments and are not limited to restrictive structure at any time (Degen and Faulwetter, 2019).	
Body size (mm)	<5 mm	SO < 5	The maximum reported size the species can reach during adult stage (Bolam and Eggleton, 2014).	Nutrient cycling/ regeneration Carbon sequestration Productivity Habitat formation/ provision
	5–10 mm	SO10		
	10–50 mm	SO50		
	50–100 mm	SO100		
Feeding habit	Surface deposit feeder	FDSD	Species that ingest particles associated with sediments or ingest the sediment particles themselves and strip off nutrition in the form of material associated with the sediment grains (Dannheim et al., 2014).	Nutrient cycling/ regeneration Carbon sequestration
	Sub-surface deposit feeder	FDSS	Species that remove food fragments from within the substratum. (Dannheim et al., 2014)	
	Suspension/Filter Feeder	FDSF	Species that feeding on particulate organic matter and material suspended in the water including plankton (Degen et al., 2018; Shojaei et al., 2021).	
	Detritivore	FDDE	Species that feed on fragmented plant detritus.	
	Predator/scavenger	FDPS	Species that feeds by preying on other organisms or feeding upon dead animals (Bolam and Eggleton, 2014; Lincoln et al., 1982).	
	Grazer/scrapper	FDGS	Species that scrape and/or graze algal matter from surfaces or feed on leaves and other parts of plants (Delfan et al., 2021).	
Larval development	Direct development	LDDD	Larvae have no larval stage and eggs develop into juvenile forms (Degen and Faulwetter, 2019).	Nutrient cycling/ regeneration Food web dynamics
	Lecithotrophic	LDLE	Larvae are pelagic for several weeks and feed on yolk reserves (Degen and Faulwetter, 2019).	
	Planktotrophic	LDPL	Larvae are pelagic for several weeks and feed and grow in the water column (Bolam et al., 2020; Degen and Faulwetter, 2019).	
Adult mobility	Burrower	AMBU	Species that live or actively move within the sediment (Degen et al., 2018; Törnroos and Bonsdorff, 2012).	Nutrient cycling/ regeneration Productivity Bioturbation
	Crawler	AMCR	Species that move limitedly along the sediment via movements of its legs and appendages (Degen and Faulwetter, 2019; Frid and Caswell, 2016).	
	Swimmer	AMSW	Species that actively swim in the water column (Frid et al., 2008).	
Life span (year)	<2 years	LS < 2	The maximum reported lifespan of the adult stage in years (Bolam et al., 2020).	Food web dynamics Nutrient cycling/ regeneration Carbon sequestration
	2–5 years	LS2–5		
	>5 years	LS > 5		

Note: Traits linked to key functions are based on Bremner et al. (2006); Brey (2012); Brown et al. (2004); Clare et al. (2015); Frid and Caswell (2016) and Norkko et al. (2013).

Council of the Man and Biosphere Program (MaB) of UNESCO.

SK mangrove forest (26°19'58.6"N 57°05'20.9"E) covers an area of 370 ha and is located on the coast of the Gulf of Oman. SK is the only site that both species *i.e.*, *R. mucronata* and *A. marina* naturally occur, of which the latter is dominant accounting for 65% of the total mangrove coverage in the region (Mafi-Gholami et al., 2020). The annual mean air temperature in SK is 28.1 °C (2011–2020), with a minimum of 12.6 °C, and a maximum of 41.9 °C in January and June, respectively (IRIMO, 2021). The mean rainfall level is about 147 mm year<sup>-1</sup> that mainly occurs in winter. The mangrove is under a diurnal regime that range in height between 3 and 5 m above mean low water.

## 2.2. Sampling of Crustacea

Benthic samples were collected from the four mangrove sites during two different seasons in February 2018 and June 2019. In each study site, five transects were placed randomly. Transects were divided into two plots (10 × 10 m), including mangrove vegetated habitats and adjacent mudflats. In all sampling sites, mangrove trees and dense pneumatophores dominated the vegetated habitats, whereas the mudflat habitats are characterized by the absence of mangrove trees and located seaward of the vegetated habitats. Plots were centered about 10 m from the forest fringe to avoid edge effects that could affect the community composition. Three random replicates separated by ~3 m were taken from each plot. At each plot, we sampled both epifaunal and infaunal crustaceans. Infauna (*e.g.* *Alpheus* sp.) as well as those species hidden in burrows (*e.g.* *opusia indica*) were collected using 25 × 25 cm metal frame down to the depth of 20 cm. The samples were washed through a 500 µm mesh sieve and retained fauna were preserved in 70% ethanol until further processing. The metal frame had high edges (~15 cm) that prevented epifaunal crustaceans from escaping from the surface layer of sediment. These species were handpicked until there were none visible to the naked eye. The plots in each study site sampled on the same day and during the low tide. For each sample, the crustaceans were sorted and identified to the possible lowest taxonomic level. The number of each species and the size of each sample were then recorded.

## 2.3. Environmental data

At each sampling event, temperature (°C), salinity, pH, and Electrical conductivity (EC, S/m) were measured in situ using portable devices. Three subsamples of sediments were taken from each plot using plastic tubes (internal diameter: 5 cm, depth: 10 cm) for the determination of the sediment chemistry and grain size analysis. The cores were sectioned in layers of 5–10 mm and dried at 55 °C. The sediment Organic Carbon (OC) and Total Nitrogen (TN) contents were determined (as % dry weight of the sediment) following the methods of Walkley and Black (1934) and micro-Kjeldahl method (Bremner, 1960), respectively. The Walkley-Black method determines soil organic carbon (OC) by oxidizing carbon with acidic dichromate. The oxidation step is followed by titration of excess dichromate with ferrous sulfate. The OC is calculated from the difference between the total dichromate added and the amount of dichromate left unreacted after OC oxidation (Walkley and Black, 1934). Finally, the percentage of clay, silt, and sand was measured using the hydrometer method (Bouyoucos, 1962).

## 2.4. Species traits

To assess the trait composition of crustaceans in the mangrove ecosystem, 7 functional traits sub-divided into 25 modalities were selected representing morphological, behavioral, and physiological features of crustaceans (Table 1). Species often exhibit different trait modalities depending on resource availability and environmental conditions. To account for a species ability to display trait modalities, the fuzzy coding procedure was selected to score species traits. Fuzzy coding allows describing the affinity of a species to multiple modalities, using

discrete numbers. In our case, the scoring range of 0–3 was adopted with 0 describing no affinity for the given trait modality, 1 or 2 expressing partial affinity, and 3 reflecting total affinity. Information on crustacean traits were collected from own observations, online databases (*e.g.* <http://polytraits.lifewatchgreece.eu>; <https://www.marinespecies.org>) and peer-review literature (Supplementary data 2, Table S1). If trait information was unavailable at species level, data was inferred from related species or the closest taxonomic level. The resultant data *i.e.*, species by trait matrix revealing the abundance of functional traits for each site/time combination. To analyze changes in trait composition, the functional identity as Community-level Weighted Mean (CWM) of trait category expression was calculated, where a community was defined as the species assemblage in each replicate sample (Nasi et al., 2018). CWM gives an indication of the trait strategies of a species in response to environmental data and represents the expression of a trait by species in a given community, weighted by the abundance of species expressing that specific trait (Nasi et al., 2018).

## 2.5. Statistical analysis

Species richness, Shannon-Wiener diversity index ( $H'$ ), and Pielou's evenness index ( $J'$ ) of the crustacean assemblages were calculated using the DIVERSE function (Clarke and Gorley, 2006). Two multivariate functional indices were calculated to assess different components of the functional diversity, namely functional richness (FRic), functional evenness (FEve), and Rao's quadratic entropy (FRao) (Laliberté et al., 2014). FRic estimates the amount of trait space occupied by the given species in the assemblages (Villéger et al., 2008). FRic is independent from species abundance and can thus be used as a proxy of the range of functional traits represented in an assemblage (Mason et al., 2005; Van der Linden et al., 2016). FEve highlights if functional traits are evenly allocated in the trait space (Villéger et al., 2008). FEve is maximized by an even distribution of both species and abundances in the trait space (Mason et al., 2005; Van der Linden et al., 2016). FRao is a measure of functional diversity based on species abundance and their functional differences (Rao, 1982). Species and functional diversity was measured separately for each core, and total diversity was calculated by taking the mean of these values (Leps et al., 2006).

Three-way permutational multivariate analysis of variance (PERMANOVA) was used to test for the effects of sites (NY, QE, KH and SK), habitats (vegetated habitat and mudflat) and seasons (summer and winter) used as fixed factors on taxonomic diversity (species richness, Shannon-Wiener diversity index, and Pielou's evenness index) and functional diversity (functional richness, functional evenness, and Rao's quadratic entropy) and CWM. For multivariate analysis, the abundance and abundance-weighted-trait data were  $\ln(x+1)$  transformed to balance the importance of common and rare taxa and traits. A three-way PERMANOVA was also used to test for the effects of factors on species and trait composition, with the same design as described above. PERMANOVA comparisons of species and functional diversity used the similarity matrix based on Euclidean distance. While, PERMANOVA comparisons of species and trait composition used the similarity matrices based on Bray–Curtis coefficients. In all PERMANOVA tests, the statistical significance of variance ( $p = 0.05$ ) was tested using a type III sum of squares and 9999 permutations under the reduced model. Similarity of percentages (SIMPER) analyses were used to determine contribution of each species and trait modalities to dissimilarity between fixed factors (Clarke and Gorley, 2006).

All environmental variables (*i.e.*, temperature, salinity, pH, EC, OC, TN and silt/clay) were transformed ( $\log x+1$ ) and standardized prior to analysis. Multicollinearity among environmental variables was checked using spearman rank correlation coefficients. Variables with correlation-coefficients >0.7 were considered collinear and thus only one of those was retained in the analysis. A principal component analysis (PCA) was performed to compare environmental variables between sampling sites. A combined multivariate approach using a RLQ and fourth-corner

analysis was used to analyze and test the relationship between the environmental variables and functional trait modalities (Dray et al., 2014). The RLQ analysis was used to assess the influence of seasons and different habitats (vegetate and mudflat) on traits occurrences. The RLQ analysis requires the generation of three matrices: the R table, gathers information on the environmental variables from all sites; the L table, constituted by the abundance of each species in each sampling site; and the Q table, composed of trait data provided by the fuzzy-coding procedure of the scoring of each taxa of the twenty-five different trait modalities. A fourth-corner matrix depicting the strength of relations between the distribution of traits and environmental variables is constructed from these three matrices (Dolédec et al., 1996; Dray et al., 2014; Dray and Dufour, 2007). Before running the RLQ analysis, we carried out the three analyses separately on each of the R (environmental variables) (L), abundance and (Q) trait data tables. Thus, a correspondence analysis (CA) was firstly performed on the L table, while a principal component analysis (PCA) was conducted on the R table. Regarding fuzzy-coded trait data, a fuzzy correspondence analysis (FCA) was conducted. These separate analyses were then combined with the RLQ analysis maximizing the covariation between environmental variables and traits. The fourth-corner analysis, on the other hand, tests multiple association between traits and the environmental variables using permutations and thus allows to test the significance of each relationship (Dray et al., 2014). Therefore, RLQ and fourth-corner analyses were used successively. The multivariate analyses were performed using the PRIMER v7 statistical package (Clarke and Gorley, 2006), together with the PERMANOVA + PRIMER add-on package (Anderson, 2014). Functional analysis and RLQ-fourth corner tests were computed in R (ver. 4.1.0; R Development Core Team, 2011) using the packages FD (Laliberté et al., 2014), ade4 (Dray and Dufour, 2007), and ggplot2 (Wickham, 2016).

### 3. Results

#### 3.1. Environmental variables

The values for pH and EC showed significant variation among sites, habitats and seasons (Table 2 and Table 3). The lowest and highest pH values were 7.7 and 8.4 at KH and SK during the summer season. EC at the four sites ranged from 3.4 (SK) – 10.1 (NY) S/m (Table 2). Temperature and salinity were similar between habitats, whereas there were

significant variation over the sites and seasons (Tables 2 and 3). Temperature ranged from a minimum of 23.3 °C in winter season and maximum 33.0 °C in summer season (Table 2). Maximum value of surface water salinity was 42.3 at SK during the summer season and the minimum was 38.7 at NY during winter season. There were differences in OC and TN between sites and habitats. However, the results showed no difference between seasons. The highest and lowest average values of OC and TN were observed at NY vegetated habitats and SK and KH mudflats, respectively. Overall, the sediment was mainly composed of silt, followed by sand and clay, except of the mudflat habitat in Nayband where the sand fraction prevailed followed by silt and clay. NY vegetated habitats recorded the highest silt/clay in the summer. Whilst, the lowest fraction was observed at NY mudflats in winter. The PCA results showed that the first two principal components (PC) explained 56.0% of the data variation (Supplementary data 3, Table S1). EC, TN, and OC were important elements of differences between seasons in the PC1, whereas temperature, salinity and silt/clay and were influential along PC2 (Fig. 2). The PCA revealed a clear segregation of seasons and sites, although sites in the inner Persian Gulf (NY) highly differed from those in the northeast (QE and KH) and Gulf of Oman (SK) (Fig. 2).

#### 3.2. Taxonomic and functional diversity

Three-way PERMANOVA analysis showed that habitat had significant effect on species richness ( $F = 3.30$ ;  $P < 0.01$ ), Pielou's evenness ( $F = 8.52$ ;  $P < 0.01$ ) and Shannon-Wiener diversity ( $F = 4.07$ ;  $P < 0.05$ ). Whilst, only the interaction of habitat-season had significant effect on Pielou's evenness ( $F = 8.38$ ;  $P < 0.01$ ). The analysis indicated that neither factors alone nor their interactions affected functional richness, functional evenness or Rao's quadratic entropy (Fig. 3; Table 4 and Table 5).

#### 3.3. Species and trait composition

A total of 15968 Crustacea specimens (15648 Decapods, and 320 Isopoda) from 19 species (18 Crustacea, 1 Isopoda) were observed across all sites and habitats (Supplementary data 3, Table S2). Average crustacean densities in NY, KH, SK and QE sites were  $35.9 \pm 23.4$ ,  $51.6 \pm 45.3$ ,  $52.9 \pm 49.5$ , and  $55.9 \pm 50.9$  ind.m<sup>-2</sup>, respectively. The highest mean density ( $75.8$  ind.m<sup>-2</sup>) was found at QE mudflats, and the lowest ( $31.4$  ind.m<sup>-2</sup>) was at NY mangrove-vegetated habitat. We found 8288

**Table 2**

Variations in environmental data (mean  $\pm$  SD) between habitats and seasons in different mangrove ecosystems in the Persian Gulf and Gulf of Oman. (OC= Organic Carbon; TN = Total Nitrogen).

	Nayband (NY)				Qeshm (QE)			
	Summer		Winter		Summer		Winter	
	Vegetated	Mudflat	Vegetated	Mudflat	Vegetated	Mudflat	Vegetated	Mudflat
pH	8.06 $\pm$ 0.12	8.26 $\pm$ 0.23	7.98 $\pm$ 0.08	8.28 $\pm$ 0.01	7.49 $\pm$ 0.07	7.72 $\pm$ 0.08	7.51 $\pm$ 0.08	7.74 $\pm$ 0.08
EC	6.14 $\pm$ 0.98	6.77 $\pm$ 1.05	7.86 $\pm$ 1.56	3.89 $\pm$ 2.02	7.85 $\pm$ 1.34	5.41 $\pm$ 1.35	6.93 $\pm$ 2.06	3.54 $\pm$ 1.89
TN (mg/g)	0.07 $\pm$ 0.029	0.03 $\pm$ 0.02	0.08 $\pm$ 0.01	0.02 $\pm$ 0.01	0.05 $\pm$ 0.030	0.03 $\pm$ 0.036	0.04 $\pm$ 0.02	0.02 $\pm$ 0.01
OC (mg/g)	2.38 $\pm$ 0.25	1.19 $\pm$ 0.86	2.38 $\pm$ 0.22	1.29 $\pm$ 0.04	1.11 $\pm$ 0.15	0.47 $\pm$ 0.23	1.03 $\pm$ 0.24	0.24 $\pm$ 0.067
Silt/Clay (%)	2.74 $\pm$ 1.61	1.06 $\pm$ 0.82	1.37 $\pm$ 0.58	0.7 $\pm$ 0.42	1.26 $\pm$ 0.22	2.48 $\pm$ 1.05	1.31 $\pm$ 0.53	2.22 $\pm$ 0.21
SST (°C)	32.92 $\pm$ 2.80	32.63 $\pm$ 2.50	24.78 $\pm$ 0.57	25.1 $\pm$ 0.14	32.33 $\pm$ 0.52	32.42 $\pm$ 0.60	23.54 $\pm$ 0.92	23.88 $\pm$ 0.83
Salinity	40.44 $\pm$ 0.96	40.25 $\pm$ 1.50	38.75 $\pm$ 0.54	39.15 $\pm$ 0.21	41.25 $\pm$ 1.54	41.68 $\pm$ 0.80	41.78 $\pm$ 1.84	40.84 $\pm$ 0.79
	Khamir (KH)				Sirik (SK)			
	Summer		Winter		Summer		Winter	
	Vegetated	Mudflat	Vegetated	Mudflat	Vegetated	Mudflat	Vegetated	Mudflat
pH	7.71 $\pm$ 0.04	7.72 $\pm$ 0.040	7.65 $\pm$ 0.10	7.66 $\pm$ 0.08	8.23 $\pm$ 0.11	8.39 $\pm$ 0.09	8.11 $\pm$ 0.08	8.26 $\pm$ 0.13
EC	6.51 $\pm$ 0.82	5.99 $\pm$ 1.20	4.70 $\pm$ 0.67	5.07 $\pm$ 0.61	6.39 $\pm$ 1.93	3.48 $\pm$ 0.73	6.42 $\pm$ 1.41	3.45 $\pm$ 0.78
TN (mg/g)	0.02 $\pm$ 0.01	0.01 $\pm$ 0.01	0.02 $\pm$ 0.01	0.009 $\pm$ 0.001	0.031 $\pm$ 0.009	0.02 $\pm$ 0.008	0.03 $\pm$ 0.01	0.02 $\pm$ 0.01
OC (mg/g)	0.47 $\pm$ 0.11	0.23 $\pm$ 0.09	0.47 $\pm$ 0.10	0.38 $\pm$ 0.19	0.76 $\pm$ 0.34	0.22 $\pm$ 0.11	0.79 $\pm$ 0.26	0.37 $\pm$ 0.16
Silt/Clay (%)	2.35 $\pm$ 1.21	2.23 $\pm$ 0.53	1.69 $\pm$ 0.19	1.79 $\pm$ 0.13	2.14 $\pm$ 0.93	1.11 $\pm$ 0.65	2.13 $\pm$ 1.04	1.80 $\pm$ 1.05
SST (°C)	32.58 $\pm$ 0.69	32.15 $\pm$ 0.58	24.4 $\pm$ 0.22	23.33 $\pm$ 0.29	30.79 $\pm$ 0.54	31.48 $\pm$ 0.40	23.81 $\pm$ 0.57	23.45 $\pm$ 0.46
Salinity	41.78 $\pm$ 0.96	40.52 $\pm$ 1.03	40.48 $\pm$ 1.13	42.17 $\pm$ 0.29	42.3 $\pm$ 0.78	41.87 $\pm$ 1.08	40.68 $\pm$ 0.57	40.87 $\pm$ 0.47

**Table 3**

Results of one-way PERMANOVA for comparing environmental variables across sites, habitats and seasons in different mangrove ecosystem in the Persian Gulf and Gulf of Oman. Bold values highlight statistical significance.

Environmental variables	Site	Habitat	Season	Site × Habitat	Site × Season	Habitat × Season	Site × Habitat × Season
pH	<b>0.0001</b>	<b>0.0001</b>	<b>0.0069</b>	<b>0.0288</b>	0.2708	0.8984	0.9700
EC (s/m)	<b>0.0001</b>	<b>0.0001</b>	<b>0.0002</b>	<b>0.0013</b>	<b>0.0297</b>	0.7006	0.1642
TON (mg/g)	<b>0.0001</b>	<b>0.0039</b>	0.7495	0.7458	0.5870	0.9820	0.8217
OC (mg/g)	<b>0.0001</b>	<b>0.0001</b>	0.8209	0.0676	0.4954	0.5557	0.7007
Silt/Clay (%)	0.5920	0.6831	0.1366	<b>0.0017</b>	0.0888	0.1988	0.2932
Temperature (°C)	<b>0.0001</b>	0.9004	<b>0.0001</b>	0.2757	<b>0.0277</b>	<b>0.0476</b>	0.3717
Salinity (psu)	<b>0.0001</b>	0.4749	<b>0.0039</b>	0.7513	<b>0.0042</b>	<b>0.0340</b>	<b>0.0257</b>

specimens from 15 species in the vegetated habitat. Whilst, 7680 specimens from 17 species were found in mudflats. Four species were exclusive for the vegetated habitat, and three species were exclusive for the mudflats. The most abundant crustacean family was Camptandriidae (*Opusia indica*, *Nasima dotilliformis* and *Manningis arabicum*) follow by Dotillidae (*Ilyoplax frater*, *Ilyoplax stvensi* and *Scopimera crabcicuda*), Alpheidae (*Alpheus lutosus*, *Athanas iranicus* and *Alpheus euphosyne*) and Sesarmidae (*Parasesarma persicum* and *Nanosesarma sarii*). The most abundant species in vegetated habitats were *O. indica* ( $173.0 \pm 57.8$  ind.  $m^{-2}$ ), *N. dotilliformis* ( $89.7 \pm 32.6$  ind.  $m^{-2}$ ) and *Ilyograpsus rhizophorae* ( $61.8 \pm 23.6$  ind.  $m^{-2}$ ). Whereas the predominant crustacean species in mudflat habitats were *O. indica* ( $392.9 \pm 117.8$  ind.  $m^{-2}$ ), *I. frater* ( $139.0 \pm 41.9$  ind.  $m^{-2}$ ) and *S. crabcicuda* ( $118.86 \pm 26.89$  ind.  $m^{-2}$ ). Three-way PERMANOVA analysis (Table 6) on species composition revealed that all the main effects (sites: Pseudo-F = 8.90,  $P < 0.001$ ; habitat: Pseudo-F = 8.78,  $P < 0.001$ ; season: Pseudo-F = 5.47,  $P < 0.001$ ) as well as all binary interactions (sites × habitat: Pseudo-F = 2.60,  $P < 0.05$ ; sites × season: Pseudo-F = 3.12,  $P < 0.001$ ; habitat × season: Pseudo-F = 2.65,  $P < 0.05$ ) were significant. Subsequent pairwise comparisons displayed significant differences in species composition for all the levels of the three factors *i.e.*, sites, habitat and season. The results of SIMPER analyses (Supplementary data 3, Table S3 - Table S5) based on species abundance data revealed the highest dissimilarity between NY and KH (88.1%, average dissimilarity), were driven primarily by *O. indica* (15.3%) and *Eurycarcinus orientalis* (13.3%). The differences in species abundance between habitats (82.4%, average dissimilarity) were driven primarily by *O. indica* (7.7%) and *I. rhizophorae* (11.8%). While, differences in species abundance between seasons (79.3%, average

dissimilarity) were driven primarily by *O. indica* (18.6%), and *N. dotilliformis* (12.4%). Three-way PERMANOVA analysis (Table 6) on trait composition revealed that all the main effects were significant (sites: Pseudo-F = 3.14,  $P < 0.01$ ; habitat: Pseudo-F = 3.60,  $P < 0.05$ ; season: Pseudo-F = 3.97,  $P < 0.05$ ) as well as the one interaction term (sites × season: Pseudo-F = 2.18,  $P < 0.05$ ). Subsequent pairwise comparisons display significant differences in trait composition for all the levels of the sites (except for between QE and KH and QE and SK), habitat ( $t = 1.89$ ,  $P < 0.05$ ) and season ( $t = 1.99$ ,  $P < 0.05$ ). The results of SIMPER analyses (Supplementary data 3, Table S6 - Table S8) based on CWM data revealed the highest dissimilarity between NY and KH (28.3%, average dissimilarity), were driven primarily by *SO10* (10.1%) and *BIRE* (6.7). The differences in CWM data between habitats (25.8%, average dissimilarity) were driven primarily by *SO10* (7.7%), *BIRE* (7.4%). While, differences in CWM data between seasons (25.4%, average dissimilarity) were driven primarily by *BIRE* (8.0%), *SO50* (7.3%).

The comparisons of the CWM values between habitats showed that there was a significant differences in functional traits between mangrove and mudflat (Fig. 4, Table 7). Species inhabiting vegetated habitats were characterized by stronger presence of conveyor building species, detritivore, predator, grazer, lecithotrophic larval development, body size of 50–100 mm, and swimmer trait modalities. While, mudflat habitat had more influence of surface deposit feeder, planktotrophic larval development, body size of <5 mm, and life span of 2–5 years (Table 7, Fig. 4). We did not detect significant relationships between environmental variables and the variation trends in trait composition (fourth-corner analysis,  $P > 0.05$ ). However, the RLQ analyses showed clear separation in trait distribution among sites and habitats (Fig. 5a and b). For summer sampling, the first RLQ axis accounted for 70.7%, whereas the second axis represented 17.2% of the total variance of RLQ analysis (87.9%) (Table 8). Salinity the predominant elements of the positive part of RLQ1 axis, related with *body size 10 – 50 mm* and *burrow dweller* modalities. These associations largely matched the characteristics of the *O. indica*, species dominant in mudflat habitat of SK area (Fig. 6c). Conversely, in the negative part of RLQ1 increasing values of OC, TN and EC corresponded to high occurrences of many modalities like *body size 5 – 10 mm*, *detritivore surface deposit feeder*, and *free living* modalities (Fig. 6a and b). They were associated with the crab *D. avarus* and *A. lutosus* and *E. intergrifrons*, highly abundant at NY area (Fig. 6c). The positive part of RLQ2 revealed that *regenerator* modality corresponded to higher pH value (Fig. 6a). The negative part of RLQ2 showed that silt/clay was associated with *body size <5 mm* and *biodiffuser* modalities (Fig. 6b). The main corresponding taxa were *M. arabisum* and *I. frater* (Fig. 6c). For winter sampling the RLQ analysis distinguished the NY areas from the rest of the sites (Fig. 5b). The first RLQ axis accounted for 72.5%, whereas the second axis represented 14.4% of the total variance of RLQ analysis (86.9%). In the positive part of RLQ1, high salinity corresponded to high occurrences of *adult longevity 2–5 years*, *body size 10–50 mm* and *planktotrophic* modalities, mainly expressed by the crab *O. indica* (Fig. 6d, e and 6f). OC, TN and EC were the predominant elements of the negative part of RLQ1, related principally with *grazer/scrapper*, *life span >5 yrs* and *direct development* modalities, principally

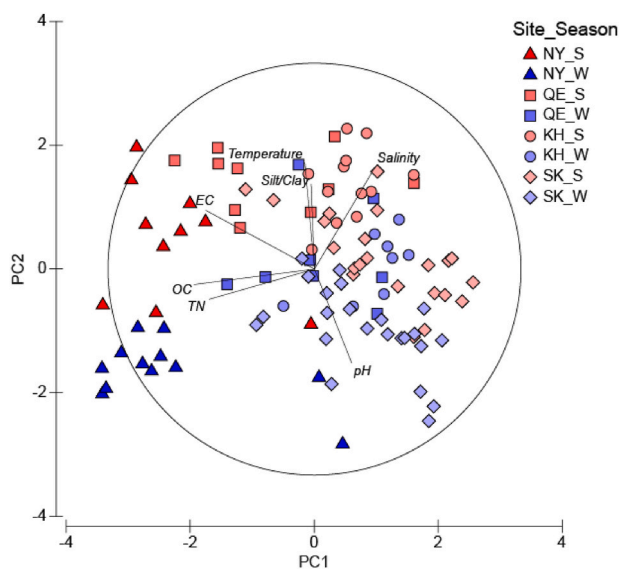
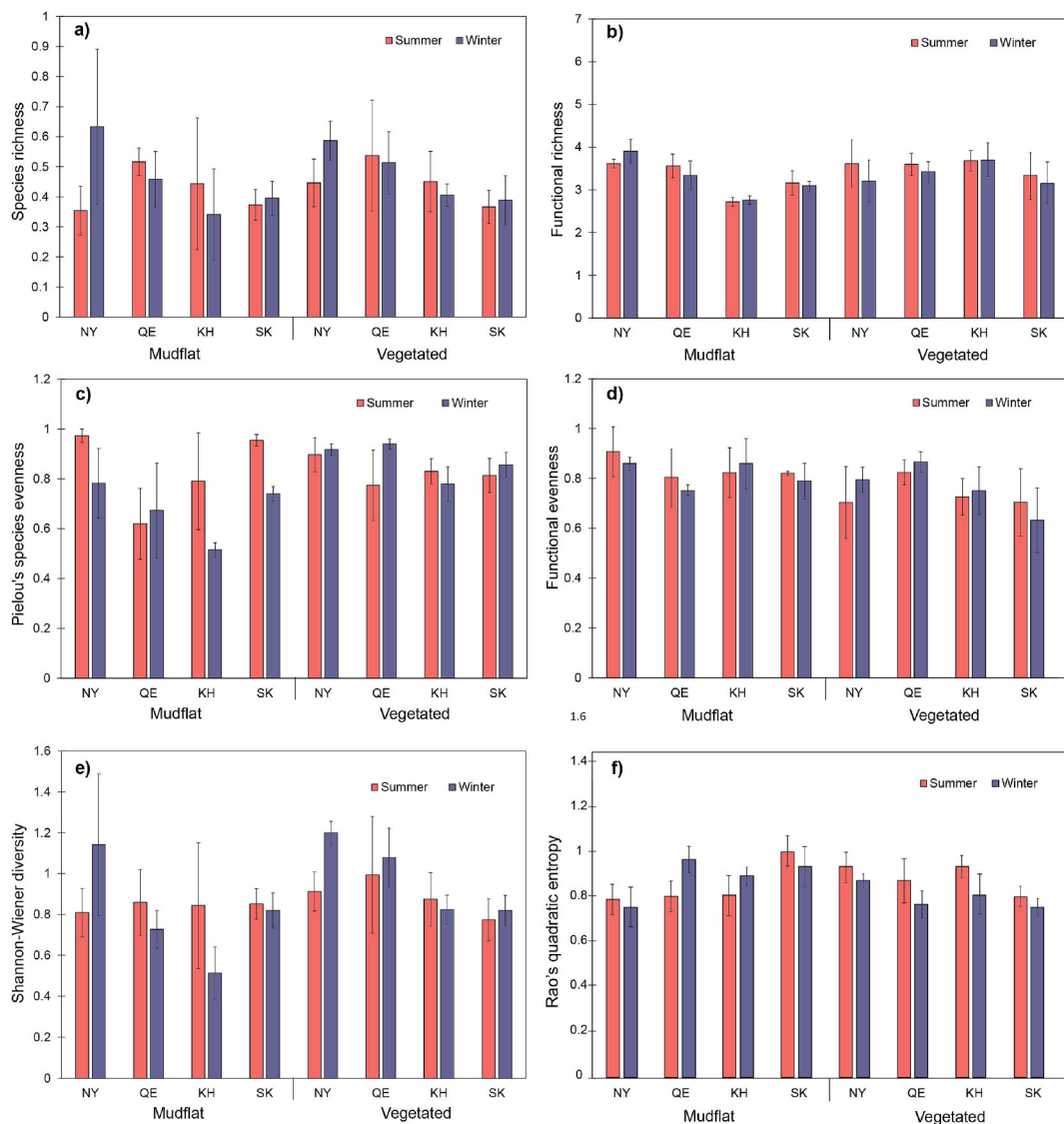


Fig. 2. Principal component analysis (PCA) ordination of environmental variables from sampling sites in the Persian Gulf and Gulf of Oman. S = summer, and W = winter. See Fig. 1 for site abbreviations.



**Fig. 3.** Mean (+1 SE) taxonomic and functional diversity indices of the Crustacea in vegetated and mudflat habitats of different mangrove ecosystem in the Persian Gulf and Gulf of Oman in summer and winter; (a) species richness, (b) functional richness, (c) Pielou's evenness, (d) functional evenness, (e) Shannon-Wiener diversity, (f) Rao's quadratic entropy. See Fig. 1 for site abbreviations.

**Table 4**

Results of three-way PERMANOVA for comparing taxonomic diversity indices of the Crustacea across sites, habitats and seasons in different mangrove ecosystem in the Persian Gulf and Gulf of Oman. Factors: site (levels: NY, QE, KH and SK), habitat (levels: vegetated and mudflat) and season (levels: winter and summer). Bold values highlight statistical significance.

Index	Species Richness		Shannon-Wiener diversity		Pielou's species evenness	
	F	P	F	P	F	P
	Site	1.238	0.298	0.854	0.447	2.292
Habitat	<b>3.304</b>	<b>0.007</b>	<b>4.076</b>	<b>0.041</b>	<b>8.522</b>	<b>0.004</b>
Season	0.654	0.421	0.027	0.865	2.007	0.167
Site × Habitat	2.430	0.069	1.022	0.418	1.991	0.119
Site × Season	0.240	0.863	0.460	0.701	1.342	0.268
Habitat × Season	1.976	0.168	2.149	0.126	<b>8.380</b>	<b>0.006</b>
Site × Habitat × Season	1.088	0.360	0.159	0.934	0.168	0.922

observed in vegetated habitat of NY area (Fig. 6e). These associations largely matched the characteristics of the crabs, *E. integrifrons*, *O. antennatus* and *S. crabicauda* (Fig. 6e). The positive part of RLQ2 revealed

**Table 5**

Results of three-way PERMANOVA for comparing functional diversity indices of the Crustacea across sites, habitats and seasons in different mangrove ecosystems in the Persian Gulf and Gulf of Oman. Factors: site (levels: NY, QE, KH and SK), habitat (levels: vegetated and mudflat) and season (levels: winter and summer).

Index	Functional richness		Functional evenness		Rao's quadratic entropy	
	F	P	F	P	F	P
	Site	5.377	0.102	0.423	0.738	1.344
Habitat	0.420	0.562	0.364	0.548	2.380	0.132
Season	0.108	0.190	0.002	0.959	0.013	0.910
Site × Habitat	0.470	0.827	2.107	0.116	2.511	0.063
Site × Season	0.846	1.480	0.096	0.962	0.334	0.799
Habitat × Season	0.242	0.426	0.046	0.833	0.860	0.358
Site × Habitat × Season	0.143	0.252	0.117	0.945	0.396	0.756

that *biodiffuser*, *sub-surface deposit feeder* and *burrow dweller* modalities mainly expressed by the *A. iranica*, corresponded to higher temperatures and pH values (Fig. 6d and e). The negative part of RLQ2 showed



**Table 6**

Results of PERMANOVA for comparing species and trait composition of the Crustacea across sites, habitats and seasons in different mangrove ecosystem in the Persian Gulf and Gulf of Oman. Factors: Site (levels: NY, QE, KH and SK), habitat (levels: vegetated and mudflat) and season (levels: winter and summer). Bold values highlight statistical significance.

Groups	Species composition					Trait composition				
	df	SS	MS	Pseudo-F	P (perm)	df	SS	MS	Pseudo-F	P (perm)
Sites	3	61684	20561	8.900	<b>0.000</b>	3	3119.7	1206.6	4.279	<b>0.0001</b>
Habitat	1	20286	20286	8.781	<b>0.000</b>	1	2324.7	2324.7	8.245	<b>0.0001</b>
Season	1	12647	12647	5.474	<b>0.000</b>	1	1879.8	1879.80	6.667	<b>0.0002</b>
Sites × Habitat	3	18024	6008.1	2.601	<b>0.000</b>	3	1715.1	571.69	2.027	<b>0.0285</b>
Sites × Season	3	21685	7228.3	3.129	<b>0.000</b>	3	2166.6	722.21	2.561	<b>0.0045</b>
Habitat × Season	1	6136.1	6136.1	2.656	<b>0.018</b>	1	475.28	475.28	1.685	0.1512
Sites × Habitat × Season	3	9609.9	3203.3	1.386	0.145	3	1214.2	404.73	1.435	0.1617

that TN and silt/clay were associated with *free living*, *regenerator* and *surface deposit feeder* modalities. The main corresponding taxa were crabs *M. arabisum* and *N. dotilliformis* (Fig. 6f).

## 4. Discussion

### 4.1. Species and functional diversity

We contrasted the taxonomic and functional diversity of crustacean assemblages in mangroves and adjacent mudflats across different regions in the northern coasts of Persian Gulf and Gulf of Oman. The species number recorded in the present study is high when compared to the previous studies done in the Persian Gulf, which recorded 5 (Vahidi et al., 2020), and 17 (Delfan et al., 2020) crustacean species, respectively. The differences is due to a higher number of sampling locations, which leads to better resolution. However, the species richness was lower than those found in tropical mangroves (e.g., Ashton et al., 2003; Nordhaus et al., 2009). The differences could be attributable to higher temperatures and salinity levels in arid mangroves of the Persian Gulf (Delfan et al., 2021). These stressors are limiting factors commonly known to restrict both abundance and diversity of invertebrates (Shojaei et al., 2021, 2021; van der Wal et al., 2017). This variation could also partly attributed to the sampling methods. During sediment collection, some crabs might escape into the underground deeper than sampled, resulting in an underestimation of crustacean density from this method (Chen et al., 2007).

The results of our study showed that taxonomic diversity increased from the mudflats to the mangrove-vegetated habitats. However, functional diversity did not differ between habitats. These results suggest that while taxonomic diversity of crustaceans may depend on the presence of mangrove structure, functional diversity may show a lesser dependence or none at all. A variety of relationships of taxonomic and functional diversity with habitat gradients have been observed in other mangroves. For example, Leung (2015) found lower functional diversity inside mangrove habitats compared to mudflats. It is important to note that Leung (2015) studied only infaunal assemblages which were limited in mangrove habitats due to the presence of dense root and pneumatophore and sediment with hostile features such as low oxygen penetration. On the contrary, results from Corte et al. (2021), and Leung and Cheung (2017), found that both taxonomic and functional diversity were lowest at sandflats relative to mangrove habitats. The combination of results from the literature and our study suggests that taxonomic diversity cannot always be considered as a good surrogate of functional diversity.

### 4.2. Species and trait composition

Species and trait composition provide information on the range and distribution of species and traits and how they relate to variation in environmental conditions. We found that patterns in species composition among sites, habitats and seasons were generally consistent with patterns in functional trait composition. Previous studies have shown a

variety of relationships between taxonomic and functional trait composition (Bremner et al., 2006; Dolbeth et al., 2013; Wong and Dowd, 2015). Thus, although overall functional diversity may not differ between habitats, different suites of functional traits may be expressed across the mangrove ecosystem. This suggests that, depending on the relative abundance of trait expression, some ecosystem functions derived from crustaceans may differ across habitats (Bremner et al., 2006; Hewitt et al., 2008). Differences in species and trait composition among sites could also be linked to various local environmental factors such as the presence of microalgae, grain size composition and tidal dynamics. This also suggest differential sensitivities of structure and functioning towards environmental drivers (Hewitt et al., 2008).

In this study, we observed different feeding habits in the mangrove and adjacent mudflat habitat which is associated with influx of organic matter (Leung and Cheung, 2017). In the presence of different feeding habits, more diverse pathways of energy flow are expected, likely leading in efficient utilization and transfer of organic matter in the arid mangrove system of the Persian Gulf (Bouillon et al., 2004). Although the carbon and nutrients in the sediment of mangrove ecosystems are derived from a variety of sources, the main source is benthic microalgae in the mangroves of the Persian Gulf (Hemmati et al., 2021). Deposit feeders were the dominant feeding guild across all sites and habitats. Deposit feeders play key roles in multiple ecosystem functions in mangrove ecosystems. Their activities can alter rates of organic matter degradation and nutrient cycling (Kristensen, 2008; Nordhaus et al., 2006). These roles stimulate through nutrient regeneration, and facilitation of biogeochemical cycling through their sediment reworking (Hope et al., 2020).

Burrowing was a predominant trait modality at both habitats. The dominance of burrowers may be an adaptation strategy to avoid harsh environmental conditions and predation (Kristensen, 2008). Burrowers can behaviorally avoid disturbances by actively digging into sediments in which conditions are favorable for survival (Botto and Iribarne, 2000). The burrowing crabs (e.g., *O. indica*, *N. dotilliformis* and *I. frater*) were widely distributed across all sampling sites. The burrowing and feeding habits of these crabs have significant impacts on ecosystem functioning and, thus were considered as ecosystem engineers (Kristensen et al., 2010; Nordhaus et al., 2006; Tomiczek et al., 2020). In addition, this ability makes them good bioturbations through which they cause high rates of turnover of sediments from deeper layers to surface and, thus enhanced sediment oxygenation and nutrient cycling from the activities of crustaceans (Wong and Dowd, 2015).

Crustaceans assemblages at mangrove-vegetated habitats were dominated by grazers/detritivore species, implying enhanced primary production (Wong and Dowd, 2015). This could be due to the presence of sesamid crabs (i.e., *Nanosesarma sarii* and *Parasesarma persicum*) which showed high densities at vegetated habitats. However, the vegetated habitats at NY and QE were different from others as these habitats had a relatively higher abundance of predators caused by the high presence of snapping shrimps (Alpheidae). Crustaceans assemblages at mangrove vegetated habitats also had larger size and longer life span than species inhabiting the neighboring mudflats. Body-size

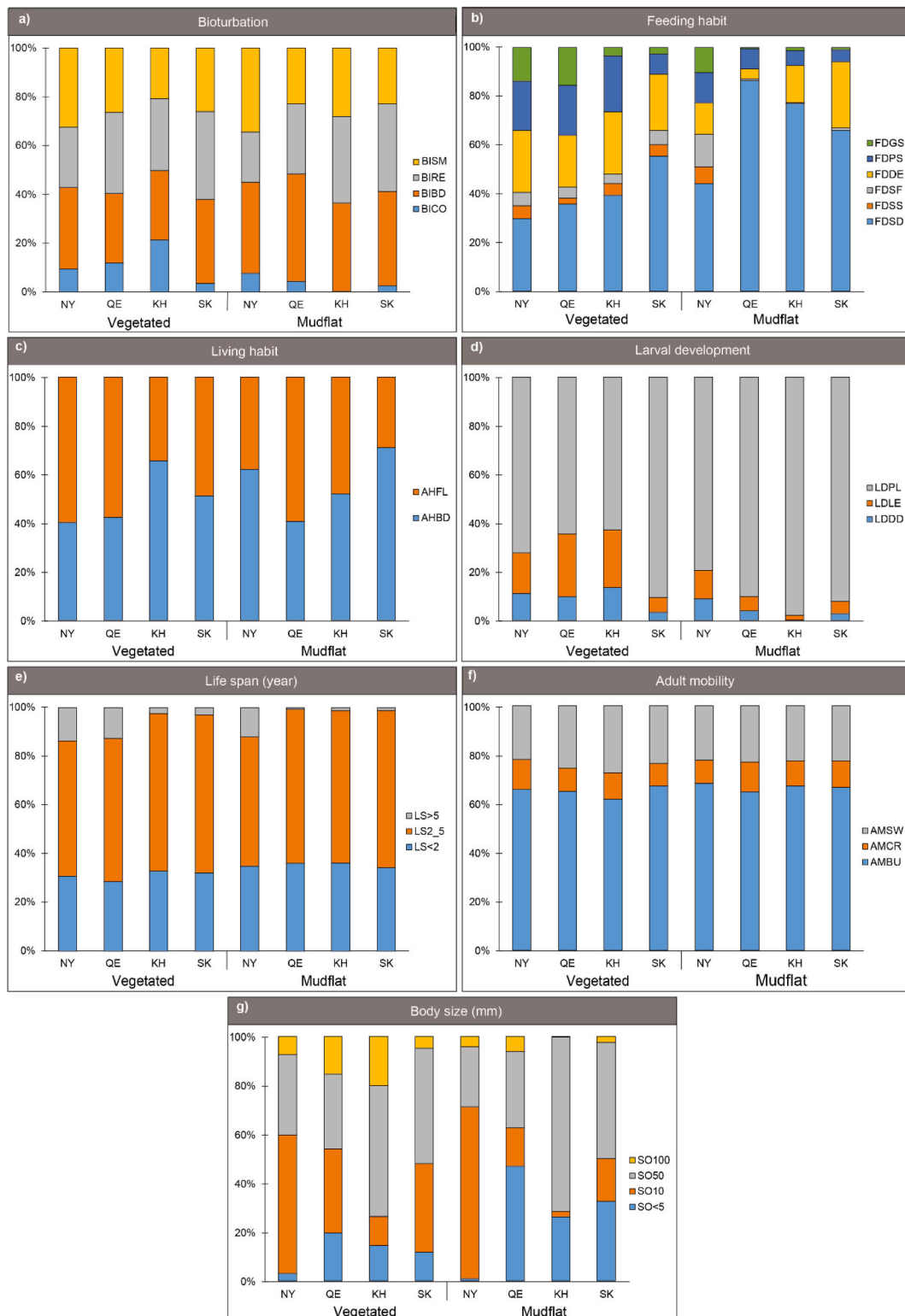
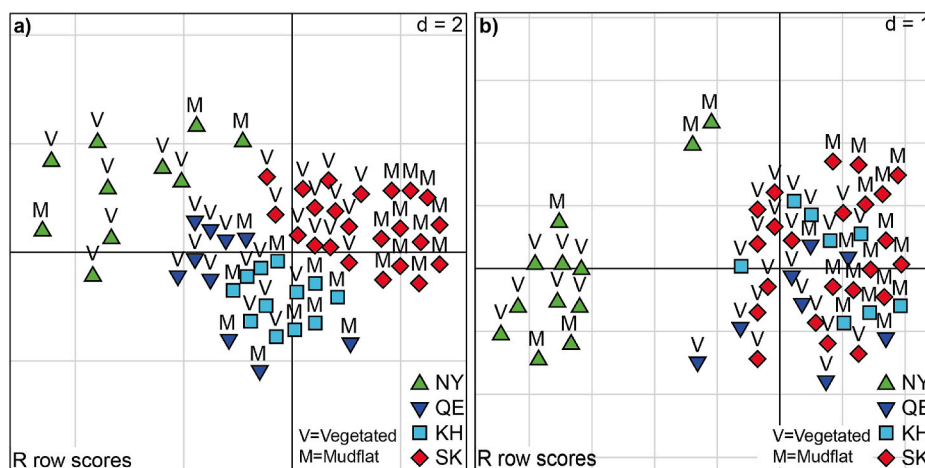


Fig. 4. Community-level Weighted Mean (CWM) of trait modalities of the Crustacea from different habitats and sites in the mangrove ecosystem in the Persian Gulf and Gulf of Oman. Color codes represent the trait affiliation; individual bars represent the trait modality expression. For trait modalities labels see Table 1.

**Table 7**

Results of univariate one-way fixed factor PERMANOVA for comparing CWM trait modalities across sites, habitats, and seasons in different mangrove ecosystem in the Persian Gulf and Gulf of Oman. Bold values highlight statistical significance. See Table 1 for trait modalities codes.

Trait	Trait modality	Site	Habitat	Season	Site × Habitat	Site × Season	Habitat × Season	Site × Habitat × Season
Bioturbation	BICO	0.0724	<b>0.002</b>	0.3918	<b>0.0209</b>	0.8787	0.1396	0.8599
	BIBD	0.6728	0.0934	<b>0.0138</b>	0.4271	<b>0.0147</b>	0.5457	<b>0.0306</b>
	BIRE	0.152	0.5268	<b>0.0002</b>	0.6833	<b>0.0233</b>	0.1714	0.582
Feeding habit	BISM	<b>0.0026</b>	0.9402	0.0626	0.0917	<b>0.0149</b>	<b>0.0018</b>	0.1133
	FSDS	<b>0.0382</b>	<b>0.0012</b>	<b>0.0108</b>	<b>0.0323</b>	<b>0.0006</b>	0.1115	0.2374
	FDSS	0.3287	0.0759	0.457	0.7648	0.3888	<b>0.0177</b>	<b>0.0223</b>
	FDSF	<b>0.0054</b>	0.9405	<b>0.0013</b>	<b>0.0216</b>	<b>0.0044</b>	0.4904	0.1937
	FDDE	0.4639	<b>0.0456</b>	0.1536	0.4996	<b>0.0354</b>	0.7106	0.8363
	FDPS	<b>0.0325</b>	<b>0.0082</b>	0.059	0.4526	0.0976	0.5755	0.3807
Living habit	FDGS	<b>0.0012</b>	<b>0.0222</b>	0.1493	0.1658	0.2627	<b>0.0009</b>	<b>0.0069</b>
	AHBD	<b>0.0009</b>	0.1975	<b>0.0002</b>	<b>0.0093</b>	<b>0.0069</b>	0.1154	0.3732
	AHFL	<b>0.0044</b>	0.0823	<b>0.0024</b>	<b>0.001</b>	0.0853	0.1855	0.7221
Larval development	LDDD	0.1235	<b>0.0096</b>	0.39	0.1022	0.9555	0.0636	0.7888
	LDLE	<b>0.0205</b>	<b>0.0003</b>	0.6685	<b>0.0082</b>	0.2124	0.4814	0.1777
	LDPL	0.0737	<b>0.0131</b>	0.4588	0.0943	0.6861	0.2938	0.5221
Body size	SO < 5	<b>0.0027</b>	<b>0.0076</b>	<b>0.0049</b>	0.258	<b>0.0103</b>	<b>0.0409</b>	0.3199
	SO10	<b>0.0001</b>	0.0952	0.9382	0.4087	0.3647	0.1417	<b>0.0084</b>
	SO50	<b>0.0014</b>	0.7229	<b>0.0048</b>	0.7572	0.0965	0.7406	<b>0.0198</b>
	SO100	0.2286	<b>0.0097</b>	0.059	0.1329	0.6057	0.0936	0.5741
	Adult mobility	AMBU	0.36	0.2931	0.5298	0.4398	0.193	0.5406
Life span	AMCR	0.8397	0.8300	<b>0.0001</b>	0.7328	<b>0.0153</b>	<b>0.0345</b>	0.9804
	AMSW	<b>0.0072</b>	<b>0.0017</b>	0.1535	<b>0.0126</b>	0.3272	0.5092	0.7773
	LS < 2	0.9931	0.2759	<b>0.0008</b>	0.7305	0.2971	0.8951	0.152
	LS2-5	<b>0.0018</b>	<b>0.0411</b>	0.0715	0.1035	0.3817	<b>0.0165</b>	0.4919
	LS > 5	<b>0.0007</b>	<b>0.0433</b>	0.223	0.2031	0.1704	<b>0.0003</b>	<b>0.0144</b>



**Fig. 5.** RLQ diagrams defined by two first axes with a projection of sampling sites in summer (a) and winter (B). The d value in the upper right of the corner is the scale of each graph.

distributions have mechanistic links to many ecosystem functions such as energy flow and nutrient cycling, because most rates of ecosystem processes are mechanistically related to biomass through uptake, feeding and physiology (Norkko et al., 2013). Thus, species with larger body size are expected to exert strong influence on the structure and dynamics of local food webs (Corte et al., 2021). Despite this, the predominance of small sized species with the size of <5 mm and 5–10 mm was apparent at NY vegetated habitats, which is a characteristic of disturbed ecosystems (Beche and Resh, 2007; Leung and Cheung, 2017; Shojaei et al., 2021). Small-bodied species require fewer resources to produce offspring than do large-bodied species and so may be better able to maintain population sizes in disturbed habitats (Gollner et al., 2015; Rosenberg, 1995).

**4.3. Environmental variables**

The knowledge of environmental conditions is important for understanding the ecological processes within ecosystems and for

understanding the temporal and spatial variation of biodiversity and function of benthic assemblages (Degen et al., 2018; Nasi et al., 2020a). The ranges of temperature and salinity within this study were similar to those reported in mangrove forests in the Persian Gulf (Delfan et al., 2021; Vahidi et al., 2020). The grain size did not change seasonally, but there was a difference between habitats, which was similar to observations in Qeshm (Delfan et al., 2021) and Nayband mangroves (Hamzavi et al., 2012). In contrast to what we observed, no spatial changes in the sediment texture were reported between sites and habitats in Qeshm Island as observed by other authors (Vahidi et al., 2020). Higher pH observed in summer season could be attributed to the removal of CO<sub>2</sub> by the photosynthetic organisms (Kumar and Khan, 2013). The measured values of organic matter in our study were highest in vegetated habitats which are associated with mangrove trees. This is due to the decomposition of mangrove leaves and increased retention of organic matter in the soil, which subsequently increases the organic matter content in the soil, which subsequently increases the organic matter content (Twilley et al., 1992). In the Nayband mangroves, the higher organic matter content contributed to the improvement of functional diversity,

**Table 8**  
Summary of RLQ analysis.

Summer						Winter					
Cumulative projected inertia (%)						Cumulative projected inertia (%)					
AX 1	AX 1:2					AX 1	AX 1:2				
70.7	87.9					72.5	86.9				
Projected inertia (%)						Projected inertia (%)					
AX 1	AX 2					AX 1	AX 2				
70.7	17.2					72.5	14.4				
Eigenvalues decomposition						Eigenvalues decomposition					
	eig	covar	sdR	sdQ	corr		eig	covar	sdR	sdQ	corr
eig 1	2.437	1.561	1.508	2.275	0.455	eig 1	2.892	1.701	1.790	2.021	0.470
eig 2	0.591	0.769	0.950	1.725	0.469	eig 2	0.573	0.757	0.923	1.536	0.534
Inertia & coinertia R (env)						Inertia & coinertia R (env)					
	inertia	max	ratio				inertia	max	ratio		
eig 1	2.273	2.368	0.960			eig 1	3.203	3.259	0.983		
eig 1 + 2	3.175	3.809	0.834			eig 1 + 2	4.055	4.463	0.909		
Inertia & coinertia Q (traits)						Inertia & coinertia Q (traits)					
	inertia	max	ratio				inertia	max	ratio		
eig 1	5.175	6.423	0.806			eig 1	4.084	6.000	0.681		
eig 1 + 2	8.151	12.377	0.658			eig 1 + 2	6.443	10.486	0.614		
Correlation L (abundance)						Correlation L (abundance)					
	corr	max	ratio				corr	max	ratio		
eig 1	0.455	0.957	0.476			eig 1	0.470	0.960	0.490		
eig 2	0.469	0.859	0.546			eig 2	0.534	0.774	0.690		

especially in vegetative habitats. In this area, we observed an increasing occurrence of functional traits related to feeding habits, especially in summer (see Fig. 6). The balance between macrofauna feeding habits (i. e., suspension and deposit feeders, grazers, and predators) indicates increasing community stability at this site.

Mangroves of the Persian Gulf represent one of the more northerly extremes of mangrove distribution in the Indo-Pacific, and is populated only by *A. marina*, due to its tolerance of high salinity and wide temperature extremes (Delfan et al., 2021; Shahraki et al., 2014; Shojaei et al., 2021). High salinity levels result in physiological stress to mangrove trees, forcing them to allocate more energy to osmotic regulation at the expense of growth (Ball, 2002) potentially affecting mangrove net primary productivity (Ball, 2002; Chowdhury et al., 2019). Crustacea in the mangroves of the Persian Gulf and Oman Gulf have to cope with arid environmental conditions. In the mudflat habitats of all the mangroves studied, the harsh environment led to a reduction in functional diversity, which was observed especially in the Khamir and Sirik mangroves (see Fig. 3). However, this reduction did not affect some ecosystem functions such as nutrient cycling/regeneration and oxygen exchange in deeper sediment layers. In fact, we observed a high abundance occurrence of regenerator and burrower, biodiffuser crustaceans at mudflat habitats. Specifically, biodiffuser modality includes organisms whose activities produce constant and random (i.e. horizontal and vertical) local sediment biomixing over a short distance resulting in particle transport. Among them, gallery biodiffusers which are often found in finer sediments, such as mudflat habitats, where they promote diffusive local biomixing primarily through their burrowing activity in the upper 10–30 cm of sediments (Kristensen et al., 2012).

## 5. Conclusion

We studied the spatial patterns of crustacean assemblages, based on taxonomic and functional diversity in mangroves of the Persian Gulf and Gulf of Oman. The significant differences in species and functional trait composition were observed between vegetated habitats and adjacent mudflats, stressing that different habitats may harbor different species

and trait sets, likely as a result of habitat complexity. This suggests that, depending on the relative abundance of trait expression, some ecosystem functions derived from crustaceans may differ between habitats. The results of current study suggests that taxonomic diversity cannot always be considered as a good surrogate of functional diversity. This has important implications for conservation and management programs that often maintain biodiversity under the implicit assumption that ecological function will also be maintained. The use of taxonomic and functional metrics generate complementary information that can help us to reach more efficient conclusions in terms of biodiversity conservation and ecosystem functionality in mangrove ecosystems.

## CRedit authorship contribution statement

**Rahil Nozarpour:** Conceptualization, Methodology, Data curation and formal analysis, Visualization, Writing original draft. **Mehdi Ghodrati Shojaei:** Conceptualization, Methodology, Formal analysis, Visualization, Funding acquisition, Supervision, Writing - review and editing. **Reza Naderloo:** Conceptualization, Methodology, Writing - review and editing. **Federica Nasi:** Conceptualization, Methodology, Formal analysis, Writing - review and editing. All authors approved the final manuscript for publication and agreed to be accountable for the result presented therein.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data will be made available on request.

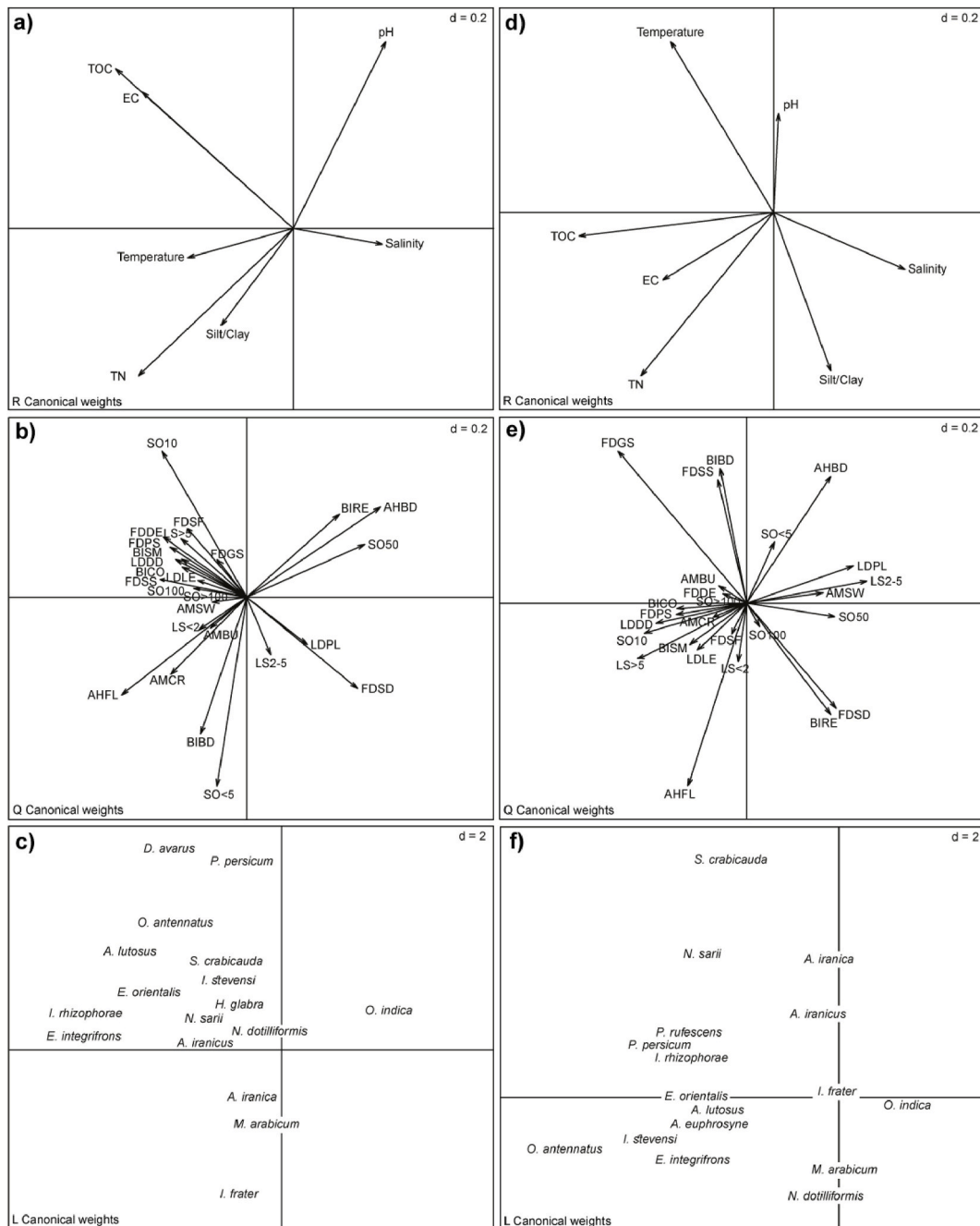


Fig. 6. RLQ diagrams as defined by two first axes with a projection of species, environmental variables, and trait categories from the two sampling periods (a, b, c summer and d, e, f for winter, respectively). The d value in the upper right of the corner is the scale of each graph.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2023.105919>.

## References

- Akbari, N., Shojaei, M.G., Farahani, M.M., Weigt, M., 2022. Stable Isotopes Reveal the Food Sources of Benthic Macroinvertebrates in the Arid Mangrove Ecosystem of the Persian Gulf. *Estuaries and Coasts* 1–13. <https://doi.org/10.1007/s12237-022-01083-9>.
- Al-Khayat, J.A., Jones, D.A., 1999. A comparison of the macrofauna of natural and replanted mangroves in Qatar. *Estuar. Coast Shelf Sci.* 49, 55–63. [https://doi.org/10.1016/S0272-7714\(99\)80009-2](https://doi.org/10.1016/S0272-7714(99)80009-2).
- Anderson, M.J., 2014. Permutational Multivariate Analysis of Variance (PERMANOVA). *Wiley statsref Stat.* <https://doi.org/10.1002/9781118445112.stat07841>. Ref. online 1–15.
- Ashton, E.C., Macintosh, D.J., Hogarth, P.J., 2003. A baseline study of the diversity and community ecology of crab and molluscan macrofauna in the Sematan mangrove forest, Sarawak, Malaysia. *J. Trop. Ecol.* 127–142. <https://doi.org/10.1017/S0266467403003158>.
- Ball, M.C., 2002. Interactive effects of salinity and irradiance on growth: implications for mangrove forest structure along salinity gradients. *Trees (Berl.)* 16, 126–139.
- Beche, L.A., Resh, V.H., 2007. Biological traits of benthic macroinvertebrates in California mediterranean-climate streams: long-term annual variability and trait diversity patterns. *Fundam. Appl. Limnol.* 169, 1–23. <https://doi.org/10.1127/1863-9135/2007/0169-0001>.
- Bernard, G., Gammal, J., Järnström, M., Norkko, J., Norkko, A., 2019. Quantifying bioturbation across coastal seascapes: habitat characteristics modify effects of macrofaunal communities. *J. Sea Res.* 152, 101766 <https://doi.org/10.1016/j.seares.2019.101766>.
- Bernardino, A.F., de Oliveira Gomes, L.E., Hadlich, H.L., Andrades, R., Correa, L.B., 2018. Mangrove clearing impacts on macrofaunal assemblages and benthic food webs in a tropical estuary. *Mar. Pollut. Bull.* 126, 228–235. <https://doi.org/10.1016/j.marpolbul.2017.11.008>.
- Bolam, S.G., Eggleton, J., Barry, J., 2020. Spatial variability of macrofaunal traits across the greater north sea. *J. Sea Res.* 101923 <https://doi.org/10.1016/j.seares.2020.101923>.
- Bolam, S.G., Eggleton, J.D., 2014. Macrofaunal production and biological traits: spatial relationships along the UK continental shelf. *J. Sea Res.* 88, 47–58. <https://doi.org/10.1016/j.seares.2014.01.001>.
- Bostrom, C., Törnroos, A., Bonsdorff, E., 2010. Invertebrate dispersal and habitat heterogeneity: expression of biological traits in a seagrass landscape. *J. Exp. Mar. Biol. Ecol.* 390, 106–117. <https://doi.org/10.1016/j.jembe.2010.05.008>.
- Botto, F., Iribarne, O., 2000. Contrasting effects of two burrowing crabs (*Chasmagnathus granulata* and *Uca uruguayensis*) on sediment composition and transport in estuarine environments. *Estuar. Coast Shelf Sci.* 51, 141–151. <https://doi.org/10.1006/ecss.2000.0642>.
- Bouillon, S., Moens, T., Overmeer, I., Koedam, N., Dehairs, F., 2004. Resource utilization patterns of epifauna from mangrove forests with contrasting inputs of local versus imported organic matter. *Mar. Ecol. Prog. Ser.* 278, 77–88. <https://doi.org/10.3354/meps278077>.
- Bouyoucos, G.J., 1962. Hydrometer method improved for making particle size analyses of soils 1. *Agron. J.* 54, 464–465. <https://doi.org/10.2134/agronj1962.00021962005400050028x>.
- Bremner, J., Rogers, S.I., Frid, C.L.J., 2006. Matching biological traits to environmental conditions in marine benthic ecosystems. *J. Mar. Syst.* 60, 302–316. <https://doi.org/10.1016/j.jmarsys.2006.02.004>.
- Bremner, J.M., 1960. Determination of nitrogen in soil by the Kjeldahl method. *J. Agric. Sci.* 55, 11–33. <https://doi.org/10.1017/S0021859600021572>.
- Brey, T., 2012. A multi-parameter artificial neural network model to estimate macrobenthic invertebrate productivity and production. *Limnol. Oceanogr. Methods* 10, 581–589. <https://doi.org/10.4319/lom.2012.10.581>.
- Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. Toward a metabolic theory of ecology. *Ecology* 85, 1771–1789. <https://doi.org/10.1890/03-9000>.
- Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., 2012. Biodiversity loss and its impact on humanity. *Nature* 486, 59–67. <https://doi.org/10.1038/nature11148>.
- Checon, H.H., Corte, G.N., Silva, C.F., Schaeffer-Novelli, Y., Amaral, A.C.Z., 2017. Mangrove vegetation decreases density but does not affect species richness and trophic structure of intertidal polychaete assemblages. *Hydrobiologia* 795, 169–179. <https://doi.org/10.1007/s10750-017-3128-0>.
- Chen, G.-C., Ye, Y., Lu, C.-Y., 2007. Changes of macro-benthic faunal community with stand age of rehabilitated *Kandelia candel* mangrove in Jiulongjiang Estuary, China. *Ecol. Eng.* 31, 215–224. <https://doi.org/10.1016/j.ecoleng.2007.07.002>.
- Chowdhury, R., Sutradhar, T., Begam, M.M., Mukherjee, C., Chatterjee, K., Basak, S.K., Ray, K., 2019. Effects of nutrient limitation, salinity increase, and associated stressors on mangrove forest cover, structure, and zonation across Indian Sundarbans. *Hydrobiologia* 842, 191–217. <https://doi.org/10.1007/s10750-019-04036-9>.
- Clare, D.S., Robinson, L.A., Frid, C.L.J., 2015. Community variability and ecological functioning: 40 years of change in the North Sea benthos. *Mar. Environ. Res.* 107, 24–34. <https://doi.org/10.1016/j.marenvres.2015.03.012>.
- Clarke, K.R., Gorley, R.N., 2006. *Primer*. Prim, Plymouth.
- Corte, G.N., Checon, H.H., Shah Esmaili, Y., Lefcheck, J.S., Amaral, A.C.Z., 2021. Mangrove fragments as key coastal reservoirs of taxonomic and functional biodiversity. *Biodivers. Conserv.* 30, 1573–1593. <https://doi.org/10.1007/s10531-021-02158-y>.
- Dannheim, J., Brey, T., Schröder, A., Mintenbeck, K., Knust, R., Arntz, W.E., 2014. Trophic look at soft-bottom communities-Short-term effects of trawling cessation on benthos. *J. Sea Res.* 85, 18–28. <https://doi.org/10.1016/j.seares.2013.09.005>.
- Degen, R., Aune, M., Bluhm, B.A., Cassidy, C., Kędra, M., Kraan, C., Vandepitte, L., Włodarska-Kowalczyk, M., Zhulay, I., Albano, P.G., 2018. Trait-based approaches in rapidly changing ecosystems: a roadmap to the future polar oceans. *Ecol. Indic.* 91, 722–736. <https://doi.org/10.1016/j.ecolind.2018.04.050>.
- Degen, R., Faulwetter, S., 2019. The Arctic Traits Database—a repository of Arctic benthic invertebrate traits. *Earth Syst. Sci. Data* 11, 301–322. <https://doi.org/10.5194/essd-11-301-2019-supplement>.
- Delfan, N., Shojaei, M.G., Naderloo, R., 2020. Biodiversity and structure of macrozoobenthos communities in the hara biosphere reserve, Persian Gulf, Iran. *J. Anim. Environ.* 12, 373–380.
- Delfan, N., Shojaei, M.G., Naderloo, R., 2021. Patterns of structural and functional diversity of macrofaunal communities in a subtropical mangrove ecosystem. *Estuar. Coast Shelf Sci.* 107288 <https://doi.org/10.1016/j.ecss.2021.107288>.
- Dolbeth, M., Cardoso, P., Grilo, T., Raffaelli, D., Pardal, M.A., 2013. Drivers of estuarine benthic species distribution patterns following a restoration of a seagrass bed: a functional trait analyses. *Mar. Pollut. Bull.* 72, 47–54. <https://doi.org/10.1016/j.marpolbul.2013.05.001>.
- Dolédéc, S., Chessel, D., Ter Braak, C.J.F., Champely, S., 1996. Matching species traits to environmental variables: a new three-table ordination method. *Environ. Ecol. Stat.* 3, 143–166. <https://doi.org/10.1007/BF02427859>.
- Donato, D.C., Kauffman, J.B., Murdiyasar, D., Kurnianto, S., Stidham, M., Kanninen, M., 2011. Mangroves among the most carbon-rich forests in the tropics. *Nat. Geosci.* 4, 293–297. <https://doi.org/10.1038/ngeo1123>.
- Douglas, E.J., Pilditch, C.A., Kraan, C., Schipper, L.A., Lohrer, A.M., Thrush, S.F., 2017. Macrofaunal functional diversity provides resilience to nutrient enrichment in coastal sediments. *Ecosystems* 20, 1324–1336. <https://doi.org/10.1007/s10021-017-0113-4>.
- Dray, S., Choler, P., Dolédéc, S., Peres-Neto, P.R., Thuiller, W., Pavoine, S., ter Braak, C.J.F., 2014. Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. *Ecology* 95, 14–21. <https://doi.org/10.1890/13-0196.1>.
- Dray, S., Dufour, A.-B., 2007. The ade4 package: implementing the duality diagram for ecologists. *J. Stat. Software* 22, 1–20. <https://doi.org/10.18637/jss.v022.i04>.
- Fonseca, G., Hutchings, P., Gallucci, F., 2011. Meiobenthic communities of seagrass beds (*Zostera capricorni*) and unvegetated sediments along the coast of New South Wales, Australia. *Estuar. Coast Shelf Sci.* 91, 69–77. <https://doi.org/10.1016/j.ecss.2010.10.003>.
- François, F., Poggiale, J.-C., Durbec, J.-P., Stora, G., 1997. A new approach for the modelling of sediment reworking induced by a macrobenthic community. *Acta Biotheor.* 45, 295–319. <https://doi.org/10.1023/A:1000636109604>.
- Freitas, R.F., Pagliosa, P.R., 2020. Mangrove benthic macrofauna: drivers of community structure and functional traits at multiple spatial scales. *Mar. Ecol. Prog. Ser.* 638, 25–38. <https://doi.org/10.3354/meps13260>.
- Frid, C.L.J., Caswell, B.A., 2016. Does ecological redundancy maintain functioning of marine benthos on centennial to millennial time scales? *Mar. Ecol.* 37, 392–410. <https://doi.org/10.1111/maec.12297>.
- Frid, C.L.J., Paramor, O.A.L., Brockington, S., Bremner, J., 2008. Incorporating ecological functioning into the designation and management of marine protected areas. *Hydrobiologia* 606, 69–79. <https://doi.org/10.1007/s10750-008-9343-y>.
- Gibson, R.N., Barnes, M., Atkison, R.J.A., 2001. Functional group ecology in soft-sediment marine benthos: the role of bioturbation. *Oceanogr. Mar. Biol. Annu. Rev.* 39, 233–267.
- Gogina, M., Darr, A., Zettler, M.L., 2014. Approach to assess consequences of hypoxia disturbance events for benthic ecosystem functioning. *J. Mar. Syst.* 129, 203–213. <https://doi.org/10.1016/j.jmarsys.2013.06.001>.
- Gollner, S., Govenar, B., Fisher, C.R., Bright, M., 2015. Size matters at deep-sea hydrothermal vents: different diversity and habitat fidelity patterns of meio-and macrofauna. *Mar. Ecol. Prog. Ser.* 520, 57–66. <https://doi.org/10.3354/meps11078>.

- Hamzavi, S., Kamrani, E., Salarzadeh, A.R., Salarpoury, A., 2012. The study of seasonal changes of intertidal macrobenthoses in mangrove forests of Basatin Estuary of Nayband Gulf. *J. Appl. Environ. Biol. Sci.* 2, 348–357.
- Hemmati, M.R., Shojaei, M.G., Taheri Mirghaed, A., Mashhadi Farahani, M., Weigt, M., 2021. Food sources for camptandriid crabs in an arid mangrove ecosystem of the Persian Gulf: a stable isotope approach. *Isot. Environ. Health Stud.* 1–13. <https://doi.org/10.1080/10256016.2021.1925665>.
- Hewitt, J.E., Thrush, S.F., Dayton, P.D., 2008. Habitat variation, species diversity and ecological functioning in a marine system. *J. Exp. Mar. Biol. Ecol.* 366, 116–122. <https://doi.org/10.1016/j.jembe.2008.07.016>.
- Hope, J.A., Hewitt, J., Pilditch, C.A., Savage, C., Thrush, S.F., 2020. Effect of nutrient enrichment and turbidity on interactions between microphytobenthos and a key bivalve: implications for higher trophic levels. *Adv. Challenges Microphytobenthos Res. From Cell Biol. to Coast. Ecosyst. Funct.* <https://doi.org/10.3389/fmars.2020.00695>.
- IRIMO, 2021. The Average 10-years Climatic Parameters. Retrieved 19 October 2021, from Iran Meteorological Organization (IRIMO). <https://www.irimo.ir/eng/index.php>.
- Jennerjahn, T.C., 2020. Relevance and magnitude of blue carbon storage in mangrove sediments: carbon accumulation rates vs. stocks, sources vs. sinks. *Estuarine, Coastal and Shelf Science*, 107027. <https://doi.org/10.1016/j.eess.2020.107027>.
- Kathiresan, K., Bingham, L.B., 2001. Biology of mangroves and mangrove ecosystems. *Adv. Mar. Biol.* [https://doi.org/10.1016/S0065-2881\(01\)40003-4](https://doi.org/10.1016/S0065-2881(01)40003-4).
- Kiruba-Sankar, R., Krishnan, P., Roy, S.D., Angel, J.R.J., Goutham-Bharathi, M.P., Kumar, K.L., Ragavan, P., Kaliyamoorthy, M., Muruganandam, R., Rajakumari, S., 2018. Structural complexity and tree species composition of mangrove forests of the Andaman Islands, India. *J. Coast. Conserv.* 22, 217–234. <https://doi.org/10.1007/s11852-017-0588-3>.
- Kon, K., Kurokura, H., Hayashizaki, K., 2007. Role of microhabitats in food webs of benthic communities in a mangrove forest. *Mar. Ecol. Prog. Ser.* 340, 55–62. <https://doi.org/10.3354/meps340055>.
- Kristensen, D.K., Kristensen, E., Mangion, P., 2010. Food partitioning of leaf-eating mangrove crabs (Sesarminae): experimental and stable isotope evidence. *Estuar. Coast Shelf Sci.* 87, 583–590. <https://doi.org/10.1016/j.eess.2010.02.016>.
- Kristensen, E., 2008. Mangrove crabs as ecosystem engineers; with emphasis on sediment processes. *J. Sea Res.* 59, 30–43.
- Kristensen, E., Lee, S.Y., Mangion, P., Quintana, C.O., Valdemarsen, T., 2017. Trophic discrimination of stable isotopes and potential food source partitioning by leaf-eating crabs in mangrove environments. *Limnol. Oceanogr.* 62, 2097–2112. <https://doi.org/10.1002/lno.10553>.
- Kristensen, E., Penha-Lopes, G., Delefosse, M., Valdemarsen, T., Quintana, C.O., Banta, G. T., 2012. What is bioturbation? The need for a precise definition for fauna in aquatic systems. *Mar. Ecol. Prog. Ser.* 446, 285–302. <https://doi.org/10.3354/meps09506>.
- Kruitwagen, G., Nagelkerken, I., Lugendo, B.R., Mgaya, Y.D., Bonga, S.E.W., 2010. Importance of different carbon sources for macroinvertebrates and fishes of an interlinked mangrove–mudflat ecosystem (Tanzania). *Estuar. Coast Shelf Sci.* 88, 464–472. <https://doi.org/10.1016/j.eess.2010.05.002>.
- Kumar, P.S., Khan, A.B., 2013. The distribution and diversity of benthic macroinvertebrate fauna in Pondicherry mangroves, India. *Aquat. Biosyst.* 9, 1–18. <https://doi.org/10.1186/2046-9063-9-15>.
- Laliberté, A.E., Legendre, P., Shipley, B., Laliberté, M.E., 2014. FD: Measuring functional diversity from multiple traits, and other tools for functional ecology. *R Package FD, Version 1.0-12*.
- Lam-Gordillo, O., Baring, R., Dittmann, S., 2021. Taxonomic and functional patterns of benthic communities in southern temperate tidal flats. *Front. Mar. Sci.* 8, 723749. <https://doi.org/10.3389/fmars.2021.723749>.
- Leps, J., de Bello, F., Lavorel, S., Berman, S., 2006. Quantifying and Interpreting Functional Diversity of Natural Communities: Practical Considerations Matter.
- Leung, J.Y.S., 2015. Original research article: habitat heterogeneity affects ecological functions of macrobenthic communities in a mangrove: implication for the impact of restoration and afforestation. *Global Ecol. Conserv.* 4, 423–433. <https://doi.org/10.1016/j.gecco.2015.08.005>.
- Leung, J.Y.S., Cheung, N.K.M., 2017. Can mangrove plantation enhance the functional diversity of macrobenthic community in polluted mangroves? *Mar. Pollut. Bull.* 116, 454–461. <https://doi.org/10.1016/j.marpolbul.2017.01.043>.
- Lincoln, R.J., Boxshall, G.A., Clark, P.F., 1982. *A Dictionary of Ecology, Evolution and Systematics*, vol. 298. Cambridge University Press.
- Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., Tilman, D., Wardle, D.A., 2001. Ecology: biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* 294, 804–808. <https://doi.org/10.1126/science.1064088>.
- Mafi-Gholami, D., Jaafari, A., Zenner, E.K., Kamari, A.N., Bui, D.T., 2020. Spatial modeling of exposure of mangrove ecosystems to multiple environmental hazards. *Sci. Total Environ.* 740, 140167. <https://doi.org/10.1016/j.scitotenv.2020.140167>.
- Mason, N.W.H., Mouillot, D., Lee, W.G., Wilson, J.B., 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos* 111, 112–118. <https://doi.org/10.1111/j.0030-1299.2005.13886.x>.
- McIntyre, S., Lavorel, S., Tremont, R.M., 1995. Plant life-history attributes: their relationship to disturbance response in herbaceous vegetation. *J. Ecol.* 31–44. <https://doi.org/10.2307/2261148>.
- McIvor, A.L., Spencer, T., Möller, I., Spalding, M., 2012. Storm surge reduction by mangroves. *Nat. Coast. Prot. Ser. Rep. 2*. Cambridge Coast. Res. Unit Work. Pap. 35.
- Meijer, K.J., El-Hacen, E.-H.M., Govers, L.L., Lavaleye, M., Piersma, T., Olf, H., 2021. Mangrove-mudflat connectivity shapes benthic communities in a tropical intertidal system. *Ecol. Indicat.* 130, 108030. <https://doi.org/10.1016/j.ecolind.2021.108030>.
- Nasi, F., Auriemma, R., Relitti, F., Bazzaro, M., Cassin, D., Cibic, T., 2020a. Structural and functional response of coastal macrofaunal community to terrigenous input from the Po River (northern Adriatic Sea). *Estuar. Coast Shelf Sci.* 235, 106548. <https://doi.org/10.1016/j.eess.2019.106548>.
- Nasi, F., Ferrante, L., Alvisi, F., Bonsdorff, E., Auriemma, R., Cibic, T., 2020b. Macrofaunal bioturbation attributes in relation to riverine influence: what can we learn from the Po River lagoonal system (Adriatic Sea)? *Estuarine, Coastal and Shelf Science* 232, 106405. <https://doi.org/10.1016/j.eess.2019.106405>.
- Nasi, F., Nordström, M.C., Bonsdorff, E., Auriemma, R., Cibic, T., Del Negro, P., 2018. Functional biodiversity of marine soft-sediment polychaetes from two Mediterranean coastal areas in relation to environmental stress. *Mar. Environ. Res.* 137, 121–132. <https://doi.org/10.1016/j.marenvres.2018.03.002>.
- Nordhaus, I., Hadipudjana, F.A., Janssen, R., Pamungkas, J., 2009. Spatio-temporal variation of macrobenthic communities in the mangrove-fringed Segara Anakan lagoon, Indonesia, affected by anthropogenic activities. *Reg. Environ. Change* 9, 291–313. <https://doi.org/10.1007/s10113-009-0097-5>.
- Nordhaus, I., Toben, M., Fauziyah, A., 2019. Impact of deforestation on mangrove tree diversity, biomass and community dynamics in the Segara Anakan lagoon, Java, Indonesia: a ten-year perspective. *Estuarine, Coastal and Shelf Science* 227, 106300. <https://doi.org/10.1016/j.eess.2019.106300>.
- Nordhaus, I., Wolff, M., Diele, K., 2006. Litter processing and population food intake of the mangrove crab *Ucides cordatus* in a high intertidal forest in northern Brazil. *Estuarine, Coastal and Shelf Science* 67, 239–250. <https://doi.org/10.1016/j.eess.2005.11.022>.
- Norkko, A., Villnäs, A., Norkko, J., Valanko, S., Pilditch, C., 2013. Size matters: implications of the loss of large individuals for ecosystem function. *Sci. Rep.* 3, 2646. <https://doi.org/10.1038/srep02646>.
- Owfi, R.E., 2018. Ecological study of harra forests in the Nayband protected area at bushehr province, Iran. *J. Coast. Zo. Manag.* 21, 1–3. <https://doi.org/10.4172/2473-3350.1000454>.
- R Development Core Team, R., 2011. *R: A Language and Environment for Statistical Computing*.
- Rao, C.R., 1982. Diversity and dissimilarity coefficients: a unified approach. *Theor. Popul. Biol.* 21, 24–43.
- Reynolds, R.M., 2002. *Oceanography. Gulf Ecosyst. Heal. Sustain.*. Backhuys Publ., Leiden. Netherlands 55–64.
- Richards, D.R., Thompson, B.S., Wijedasa, L., 2020. Quantifying net loss of global mangrove carbon stocks from 20 years of land cover change. *Nat. Commun.* 11, 1–7. <https://doi.org/10.1038/s41467-020-18118-z>.
- Rosenberg, R., 1995. Benthic marine fauna structured by hydrodynamic processes and food availability. *NJSR (Neth. J. Sea Res.)* 34, 303–317. [https://doi.org/10.1016/0077-5799\(95\)90040-3](https://doi.org/10.1016/0077-5799(95)90040-3).
- Shahraki, M., Fry, B., Krumme, U., Rixen, T., 2014. Microphytobenthos sustain fish food webs in intertidal arid habitats: a comparison between mangrove-lined and unvegetated creeks in the Persian Gulf. *Estuarine, Coastal and Shelf Science* 149, 203–212. <https://doi.org/10.1016/j.eess.2014.08.017>.
- Shojaei, M.G., Gutow, L., Dannheim, J., Pehlke, H., Brey, T., 2015. Functional diversity and traits assembly patterns of benthic macrofaunal communities in the southern North Sea. In: *Towards an Interdisciplinary Approach in Earth System Science*. Springer, pp. 183–195. [https://doi.org/10.1007/978-3-319-13865-7\\_2](https://doi.org/10.1007/978-3-319-13865-7_2).
- Shojaei, M.G., Gutow, L., Dannheim, J., Schröder, A., Brey, T., 2021. Long-term changes in ecological functioning of temperate shelf sea benthic communities. *Estuar. Coast Shelf Sci.* 249, 107097. <https://doi.org/10.1016/j.eess.2020.107097>.
- Spalding, M.D., Kainuma, M., Collins, L., 2010. *World Atlas of Mangroves; Earthscan with ITTO, ISME, FAO, UNEP-WCMC*.
- Thongtham, N., Kristensen, E., 2005. Carbon and nitrogen balance of leaf-eating sesamid crabs (*Neopisesarma versicolor*) offered different food sources. *Estuar. Coast Shelf Sci.* 65, 213–222. <https://doi.org/10.1016/j.eess.2005.05.014>.
- Tomiczek, T., Wargula, A., Lomónaco, P., Goodwin, S., Cox, D., Kennedy, A., Lynett, P., 2020. Physical model investigation of mid-scale mangrove effects on flow hydrodynamics and pressures and loads in the built environment. *Coast. Eng.* 162, 103791. <https://doi.org/10.1016/j.coastaleng.2020.103791>.
- Törnroos, A., Bonsdorff, E., 2012. Developing the multitrait concept for functional diversity: lessons from a system rich in functions but poor in species. *Ecol. Appl.* 22, 2221–2236. <https://doi.org/10.1890/11-2042.1>.
- Twilley, R.R., Chen, R.H., Hargis, T., 1992. Carbon sinks in mangroves and their implications to carbon budget of tropical coastal ecosystems. *Water, Air, Soil Pollut.* 64, 265–288. <https://doi.org/10.1007/BF00477106>.
- Vahidi, F., Fatemi, S.M.R., Danehkar, A., Mashinchian, A., Nadushan, R.M., 2020. Benthic macrofaunal dispersion within different mangrove habitats in Hara Biosphere Reserve, Persian Gulf. *Int. J. Environ. Sci. Technol.* 17, 1295–1306. <https://doi.org/10.1007/s13762-019-02469-2>.
- Van der Linden, P., Marchini, A., Dolbeth, M., Patrício, J., Veríssimo, H., Marques, J.C., 2016. The performance of trait-based indices in an estuarine environment. *Ecol. Indicat.* 61, 378–389. <https://doi.org/10.1016/j.ecolind.2015.09.039>.
- van der Wal, D., Lambert, G.I., Ysebaert, T., Plancke, Y.M.G., Herman, P.M.J., 2017. Hydrodynamic conditioning of diversity and functional traits in subtidal estuarine macrozoobenthic communities. *Estuar. Coast Shelf Sci.* 197, 80–92. <https://doi.org/10.1016/j.eess.2017.08.012>.
- Villéger, S., Mason, N.W.H., Mouillot, D., 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89, 2290–2301. <https://doi.org/10.1890/07-1206.1>.
- Vorsatz, L.D., Patrick, P., Porri, F., 2021. Quantifying the in situ 3-dimensional structural complexity of mangrove tree root systems: biotic and abiotic implications at the microhabitat scale. *Ecol. Indicat.* 121, 107154. <https://doi.org/10.1016/j.ecolind.2020.107154>.

Walkley, A., Black, I.A., 1934. An examination of the Degtjareff method for determining soil organic matter, and a proposed modification of the chromic acid titration method. *Soil Sci.* 37, 29–38.

Wickham, H., 2016. Package 'ggplot2': Elegant Graphics for Data Analysis, vol. 10. Springer-Verlag New York, pp. 970–978.

Wong, M.C., Dowd, M., 2015. Patterns in taxonomic and functional diversity of macrobenthic invertebrates across seagrass habitats: a case study in Atlantic Canada. *Estuar. Coast.* 382323. <https://doi.org/10.1007/s12237-015-9967-x>. –2336.