

Seasonal Fisheries Changes in Low-Rainfall Mangrove Ecosystems of Iran

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Abstract To determine the role of mangroves for fisheries in the arid region of the Persian Gulf, we investigated fish community structure and trophic diversity in intertidal creeks with and without mangroves. Fish community abundances and biomass were compared across habitats and seasons. To identify variations in overall community trophic niches among habitats and seasons, we measured niches with size-corrected standard ellipse areas (SEA_c) calculated from C and N stable isotope values. Although there was a slightly greater species richness occurred in mangrove creeks, we found a general similarity in the diversity patterns in creeks with and without mangroves. Also, there were no consistent differences in fish abundance or biomass for mangrove vs. non-mangrove fish collections. Community trophic diversity measured as SEA_c also showed no significant difference between mangrove and non-mangrove sites. Instead, strong seasonal patterns were observed in the fish assemblages. Winter samples had consistently higher fish abundance and biomass than summer samples. Winter SEA_c values were significantly higher, indicating that the fish community had a larger isotopic niche in winter than summer. Overall, we found that seasonality was much stronger than habitat in determining fish community structure and trophic diversity in the mangrove and non-mangrove ecosystems of Qeshm Island, Iran.

Keywords Fish community structure · Isotopic niche size · Mangrove · Non-mangrove · Qeshm Island · Iran

Introduction

Mangrove forests are highly productive coastal ecosystems with high rates of primary production that help support complex local food webs (Blaber 2007; Chong 2007; Alongi 2014). Over the past 50 years, one third of the world's mangrove forests have been destroyed by human disturbance through urban development, farming, and pollution, and the remaining mangrove forests are under continuing threat from these factors (Alongi 2002). Rationales for conserving mangrove ecosystems are partly based on hypotheses that mangroves are important for fisheries (Fry and Ewel 2003). High abundance of juvenile fish in mangroves has been attributed to the diversity and availability of food sources in this habitat (Robertson and Duke 1987; Laegdsgaard and Johnson 2001), and primary producers such as microphytobenthos, macroalgae, and phytoplankton have been identified as sources of nutrition for many fish in mangrove ecosystems (Nagelkerken et al. 2008). But a number of other variables are also known to influence mangrove-associated fish assemblages. High structural complexity and shelter from predation have been recognized as major factors responsible for the greater abundance of mangrove-associated fish (Blaber 2000; Manson et al. 2005; Verweij et al. 2006). Overall, clear tests of how mangroves influence fish communities and fisheries sustainability are relatively rare.

Most studies have examined the role of mangroves as fish habitat from the perspective of either community structure or trophic diversity. Community approach studies have documented greater abundance of juvenile species in mangroves than in other nearshore habitats, e.g., in Australia (Robertson and Duke 1987; Laegdsgaard and Johnson 1995), Malaysia

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(Chong et al. 1990) and the Caribbean (Nagelkerken and Velde 2002). However, any changes in the trophic web may have strong effects on the whole community and result in major changes to ecosystem structure and function (Williams et al. 2002; Duffy 2003). The analysis of trophic structure can be used to complement the commonly used community descriptors, by giving a different set of quantitative measures of community structure (Bersier et al. 2002; Kaartinen and Roslin 2012). Newsome et al. (2007) emphasized that stable isotope analysis can provide quantitative information on animal food use and trophic niche sizes. We used a combination of community descriptors and isotopic niche estimates as a more holistic approach to determining the habitat use and function of mangrove fish assemblages.

While some studies show that mangrove organic matter provides important nutrition to aquatic communities (Giarrizzo et al. 2011; Zagars et al. 2013; Abrantes et al. 2015), other studies do not show a strong nutritional linkage between mangroves and fish assemblages, especially in the Gulf region (Al-Maslamani et al. 2012; Shahraki et al. 2014). A recent stable isotope study of the contribution of carbon sources supporting mangrove food webs suggested that the direct importance of mangrove litter as assimilated food was surprisingly low for Persian Gulf mangroves (Shahraki et al. 2014). Also, possible nutritional use of mangroves was less than use of other primary producers for benthic and epibenthic invertebrates in the Gulf region (Al-Zaidan et al. 2006; Al-Maslamani et al. 2012). These results suggest that attributes of an arid environment, in other words, the dearth of rainfall, may reduce production and use of mangrove litter in aquatic food webs. Therefore, there was a need to assess the role of mangroves for fisheries in the Persian Gulf region.

Mangroves in this area are the northernmost mangroves in the Indo-Pacific region and are subjected to very low rainfall and high salinities (Al-Khayat and Jones 1999), and the understanding of the relationship between mangroves and fisheries has received little study in this area. Due to the aridity of the coast of Persian Gulf, many intertidal creeks are devoid of mangroves but still may be important habitats for fish. This provides a unique opportunity to evaluate the fisheries support of mangroves by comparing mangrove and non-mangrove habitats. We contrasted possible habitat effects involving mangrove vs. non-mangrove creeks with possible seasonal effects in the study area that experience a large >20 °C seasonal change in water temperatures. Thus this study is aimed at better understanding of the role of mangrove in fisheries in a low rainfall region by addressing the following questions: (1) is the fish assemblage structure similar across habitats (mangrove vs. non-mangrove) and seasons, and (2) does the fish community have similar isotopic niche size across habitats and seasons? We hypothesized that fish community structure is the same in our low-rainfall mangrove and non-mangrove habitats, and also the communities have the same isotopic niche size across habitats.

We tested whether mangroves enhance fisheries support by comparing the community-level fish diversity, abundance, biomass, and trophic diversity across habitats and seasons.

Materials and Methods

Study Sites

The study was carried out at Qeshm Island, Strait of Hormuz, Iranian coast of the Persian Gulf (26.8° N, 55.75° E) (Fig. 1a, b). The northwest of Qeshm Island has the largest mangrove area in Iran of 67.5 km², with a single species of mangrove, *Avicennia marina* (Sheppard et al. 2010; Zahed et al. 2010). Mangrove sampling sites included four intertidal creeks (C1, C2, C3, C4) that drained into a main channel. The mangroves extended 5–50 m inland as a fringe along the creek banks, and were 3–6-m tall. Non-mangrove sites included two intertidal creeks (C5 and C6) (Fig. 1c, d). There are no seagrass beds or coral reefs in the vicinity of the mangrove and non-mangrove creeks. The distance between the two sets of creeks was ca. 4 km.

Mangrove and non-mangrove creeks were similar in many measures. For example, mangrove and non-mangrove creeks had similar average volumes of spring tides, although on neap tides, mangrove creeks had 3.6× the average volume on non-mangrove creeks (Table S1). Salinity averaged 38.3 ± 0.5 (mean \pm standard deviation) in the mangrove site and 40.3 ± 2.3 in the non-mangrove site. Winter water temperatures averaged 19.6 ± 1.5 and 19.6 ± 2 and summer water temperature averaged 33.7 ± 1.4 and 34 ± 2 in mangrove and non-mangrove, respectively. During the whole sampling period, the precipitation rate was zero.

Sample Collection

Fish were sampled by setting block nets (15–25 m in length, 4-m high, 12-mm stretched mesh size) at slack high water during four different combinations of tide and daylight conditions. Depending on creek widths, the lengths of the nets were adjusted between 15 and 25 m to completely block off creek mouths to collect fish exiting creeks on low tides. The block net method is regarded as highly efficient in recording the fish fauna using intertidal habitats (Bozeman and Dean 1980) and has been used previously for fish collection in some mangroves studies, e.g., in South Florida (Thayer et al. 1987) and Brazil (Barletta et al. 2003).

Six nets were deployed simultaneously at low tide along the mouth of the creeks and were buried in the sediment and held in place with wooden stakes. The nets were rolled down to the level of the sediment and left until high tide. Lengths of nets were adjusted to stretch across the entire widths of the tidal creeks. At high tide, the top of the nets were lifted onto wooden stakes. During the following low tide when the creeks

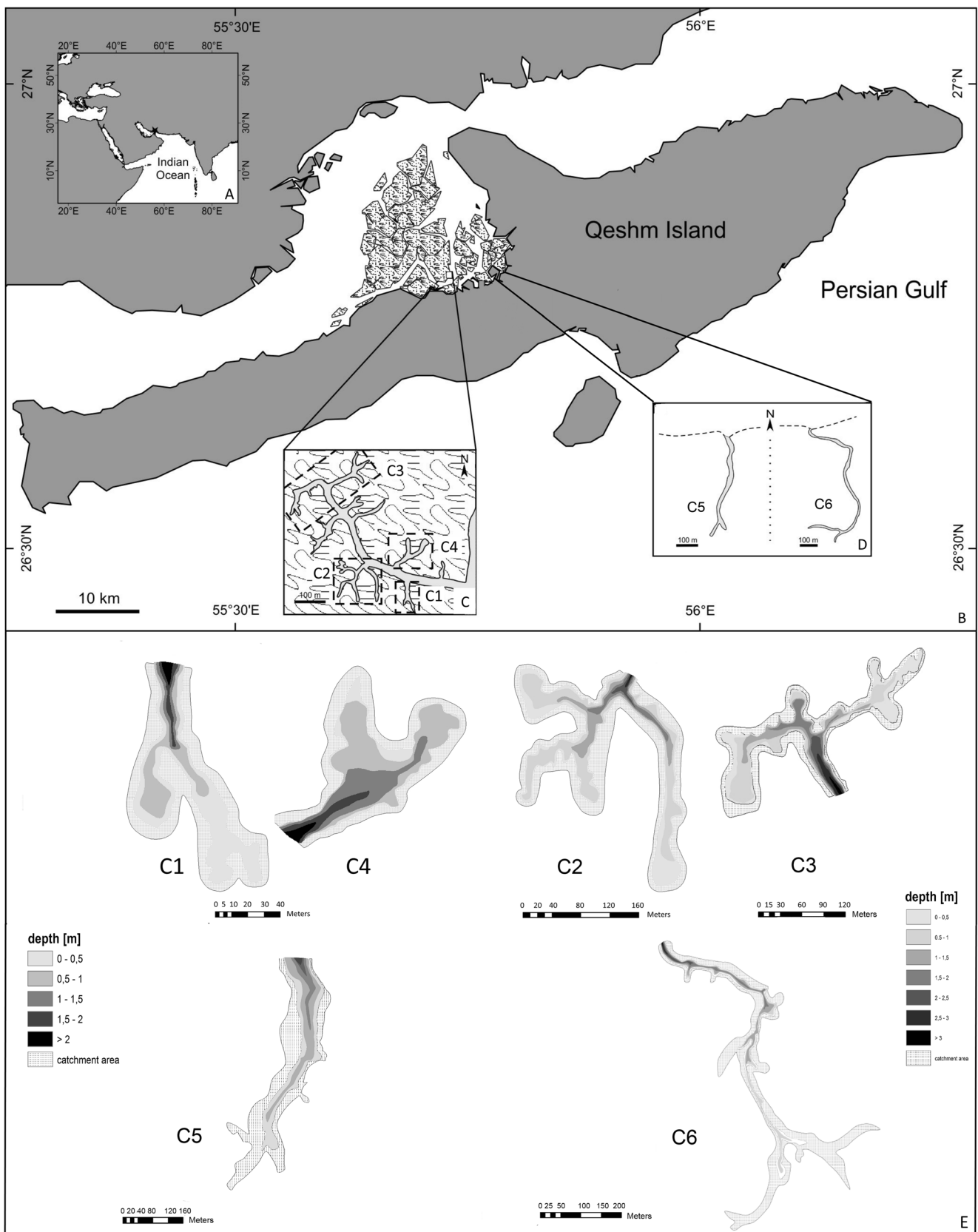


Fig. 1 Study area in Qeshm Island, Iran. Location of the study area in the region (A), sampling sites (mangroves in light gray) (B), mangrove site (with four intertidal creeks) (C), non-mangrove site (with 2 intertidal bare creeks) (D), bathymetric maps of creeks 1, 2, 3, 4, 5, and 6 (E)

were almost empty, the fish were collected. Prawns were also collected simultaneously by the nets with 2-mm mesh size. A total of 96 and 32 block net samples were taken from mangrove and non-mangrove intertidal creeks in winter (December and February) and summer (August) 2011–2012. December sampling was carried out only in mangrove creeks, and these results have been excluded from this comparative study.

All fish and prawns were transported on ice to the laboratory. Specimens were identified to the lowest possible taxonomic level (Fischer and Bianchi 1984; Kuronuma and Abe 1986; Assadi et al. 1997), counted, and weighed ($g \pm 0.1$). Fish total length was measured to the nearest 0.1 cm and analyzed in class intervals of 2.5 cm, except for five large-sized species (see species names with # symbols, Table 1 below) where a 10-cm class interval was used. Abundance estimates were based on the number of individual fish collected.

Bathymetric surveys of the creeks were carried out at the end of the sampling period to assess the local topography with respect to tidal inundation and drainage patterns. A survey included measuring water levels at different horizontal transects for each creek using a tape measure, GPS, and a compass, then drawing approximate inundation areas on a grid map in the field. This information was used with GIS software to produce a bathymetric map of each creek (Fig. 1e). Abundance and biomass for each species per sample were converted to abundance and biomass per m^2 by dividing total values by respective inundation area for each creek. The inundation areas and volumes of water of the creeks are presented in Table S1.

Carbon and nitrogen isotopic values of various potential basal food sources (mangrove leaves, microphytobenthos, plankton, particulate organic matter, sediment organic matter, and macrobenthos) and fishes were measured to estimate the trophic diversity in mangrove and non-mangrove sites. Details of this data set have been published previously (Shahraki et al. 2014).

Data Analysis

Since the objective of the present study was to determine habitat, creek, and seasonal effects rather than tide-diel variations, statistical analyses were performed for each site per season. We used the EstimateS software (Colwell 2009) to produce the rarefaction curves and estimate species richness.

To assess whether intertidal fish assemblages differed in abundance or biomass between habitats, creeks, and seasons, three-way PERMANOVA (permutational multivariate analysis of variance) models were used with the factors: habitat (fixed, two levels: mangrove and non-mangrove), creek (random, six levels, C1, C2, C3, C4, C5, C6) nested in habitat and season (fixed, two levels, winter and summer).

Additionally, with the same set up in PERMANOVA, differences between habitats were tested using Monte Carlo p values, because not enough unique permutations were possible to determine permutational p values for the factor habitat. Monte

Carlo p values provide an approximation of significance based on asymptotic theory and should be used in preference to the permutational p values when the number of unique permutations is <100 (Anderson et al. 2008). Canonical analysis of principal coordinates (CAP) was used as a constrained ordination procedure to visualize fish abundance patterns revealed by PERMANOVA. CAP is a canonical multivariate discriminant analysis which maximizes the differences among a priori-defined groups. The main species responsible for differences were identified based on the strength of their correlation ($|r| > 0.4$) with the CAP axes. Analyses were performed on square-root transformed data to reduce the contributions of quantitatively dominant species to the similarities calculated between samples based on Bray-Curtis distances (Anderson et al. 2008).

Fish abundance and biomass comparisons were made on both a per m^2 basis and on a per sample basis. The per m^2 comparisons maybe more appropriate if fish are resident, and the per sample comparisons more appropriate if fish are transient. Because fish communities likely represent a mix of residents and transients, we considered comparisons ecologically robust when significant differences were found in parallel and significant for both ways of expressing the data (e.g., results were considered ecologically robust when abundance was higher both on a per m^2 basis and also on a per sample basis). Alternatively, if abundance (or biomass) results were not parallel and significant when expressed on a per m^2 and a per sample basis, results were not considered ecologically robust. This logic showed that seasonal differences in abundance and biomass were consistently parallel, significant, and robust for the fish communities, but that the habitat-level differences between mangroves and non-mangroves were usually inconsistent and therefore less robust.

To assess the influence of habitat and season on isotopic niche sizes, we calculated the standard ellipse areas (SEA, expressed in ‰^2) using SIBER (Stable Isotope Bayesian Ellipses in R). These ellipses for bivariate C and N isotope data are analogous to univariate standard deviations, and are calculated from the variance and covariance of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. The resulting ellipses typically contain ca. 40 % of the data and provide a description of the isotopic niche of a population or community (Bearhop et al. 2003; Jackson et al. 2012). A corrected version of the standard ellipse area (SEA_c) is used to correct bias towards underestimation when sample sizes are small (Jackson et al. 2011). SEA_c and SEA values were very similar in this study where n was usually <50 ; SEA_c values are reported here. A Bayesian ellipse estimate (SEA_B) captures all the same properties as SEA_c and was used in probabilistic comparisons (for detailed explanations, see Jackson et al. 2011).

The differences in SEA_B were tested to compare the isotopic niche sizes of potential food sources and fish communities, and to make isotopic niche comparisons of communities across habitats and seasons. For these community-level comparisons, we used the ten most abundant species that occurred

in both mangrove and non-mangrove habitats with relative abundance (RA) of >1 % (species with * in Table 1). Species with RA < 1 % were represented by <10 individuals and usually by only 1–2 individuals; these numbers were too low for the statistical analysis. In some cases, we estimated the SEA_c of fish and also foods, then calculated the (SEA_c-fish)/(SEA_c-food) ratios to see if fish niche changes were related to changes in niche size of food sources.

Table 1 Fish species composition in mangrove and non-mangrove intertidal creeks of Qeshm Island from winter (February 2012) and summer (August 2012). Relative abundance (RA) = 100* total individuals in

Results

Community Overview

A total of 6120 individual fish were caught by 96 block net samples, including 3653 fish from 64 samples in mangrove sites and 2467 fish from 32 samples in non-mangrove sites. A total of 3471 fish were caught in winter

the species/total individuals in the study; Occurrence (M %, NM %) are % samples where individuals of the species occurred in mangrove and non-mangrove habitats

	Size range (cm)	RA (%)	Occurrence (M %)	Occurrence (NM %)
Mangrove and non-mangrove				
<i>Scatophagus argus</i> (Scatophagidae)*	2.5–10	2	96	4
<i>Pomadasys kaakan</i> (Haemulidae)*	5–15	2	90	10
<i>Ilisha melastoma</i> (Clupeidae)	5–10	<1	82	18
<i>Sarinella longiceps</i> (Clupeidae)*	5–10	3	88	12
<i>Leiognathus daura</i> (Leiognathidae)*	5–12.5	15	75	25
<i>Thryssa vitirostris</i> (Engraulidae)*	10–15	8	78	22
<i>Acanthopagrus cuvieri</i> (Sparidae)	15–20	<1	79	21
<i>Pentaprion longimanus</i> (Gerreidae)*	5–12.5	8	60	40
<i>Acanthopagrus latus</i> (Sparidae)*	5–15	3	55	45
<i>Eleutheronema tetradactylum</i> (Polynemidae) [#]	20–30	<1	60	40
<i>Scomberoides lysan</i> (Carangidae)	5–10	<1	56	44
<i>Liza klunzingeri</i> (Mugilidae)*	5–20	38	34	66
<i>Pseudorhombus elevatus</i> (Paralichthyidae)	10–15	<1	43	57
<i>Platycephalus indicus</i> (Platycephalidae) [#]	30–40	<1	33	67
<i>Sphyræna putnamiae</i> (Sphyrænidae) [#]	30–40	<1	20	80
<i>Hemiramphus archipelagicus</i> (Hemiramphidae)	12.5–15	<1	33	67
<i>Sillago sihama</i> (Sillaginidae)*	10–17.5	1	19	81
<i>Upeneus sulphureus</i> (Mullidae)	10–15	<1	20	80
<i>Anodontostoma chacunda</i> (Clupeidae)*	5–10	16	7	93
Mangroves only				
<i>Lutjanus johni</i> (Lutjanidae)	5–15	<1	100	0
<i>Plectorhinchus pictus</i> (Haemulidae)	5–15	<1	100	0
<i>Sardinella gibbosa</i> (Clupeidae)	5–10	2	100	0
<i>Scartelaos tenuis</i> (Gobiidae)	5–10	<1	100	0
<i>Bathygobius fuscus</i> (Gobiidae)	5–10	<1	100	0
<i>Epinephelus coioides</i> (Serranidae) [#]	30–40	<1	100	0
<i>Abalistes stellatus</i> (Balistidae) [#]	20–30	<1	100	0
<i>Lutjanus russelli</i> (Lutjanidae)	10–15	<1	100	0
<i>Strongylura stronglura</i> (Belonidae)	10–15	<1	100	0
Non-mangrove only				
<i>Terapon jarbua</i> (Terapontidae)	7.5–10	<1	0	100
<i>Euryglossa orientalis</i> (Soleidae)	12.5–15	<1	0	100
<i>Gerres poieti</i> (Gerreidae)	5–12.5	1	0	100
Crustacean				
<i>Penaeus merguensis</i> (Penaeidae)			100	0

[#] Large-sized species

*Species considered for the SEA

and 2467 fish in summer, with 48 block net samples collected in each season. Generally, small-sized fishes (5–15 cm) dominated in abundance (Table 1). A total of 31 species was caught during the study. The majority of species (19 of 31 species) were found in both the mangrove and non-mangrove ecosystems (Table 1). A total of 1635 prawns of a single species were caught only at mangrove site, including 1490 specimens in winter and 145 specimens in summer.

Fish Diversity

Diversity was generally similar for both seasons and habitats (Fig. 2). The observed number of species was similar at 20–22 species when 2000 individuals were considered for comparisons between mangrove and non-mangrove sites or between winter and summer collections (Fig. 2). The Chao1 species richness estimator reached asymptotic values for fish from different sites (at 28 and 21 species for mangrove and non-mangrove, respectively) and seasons (at 24 and 22 species for winter and summer, respectively), well before all the individuals were collected in each habitat and season.

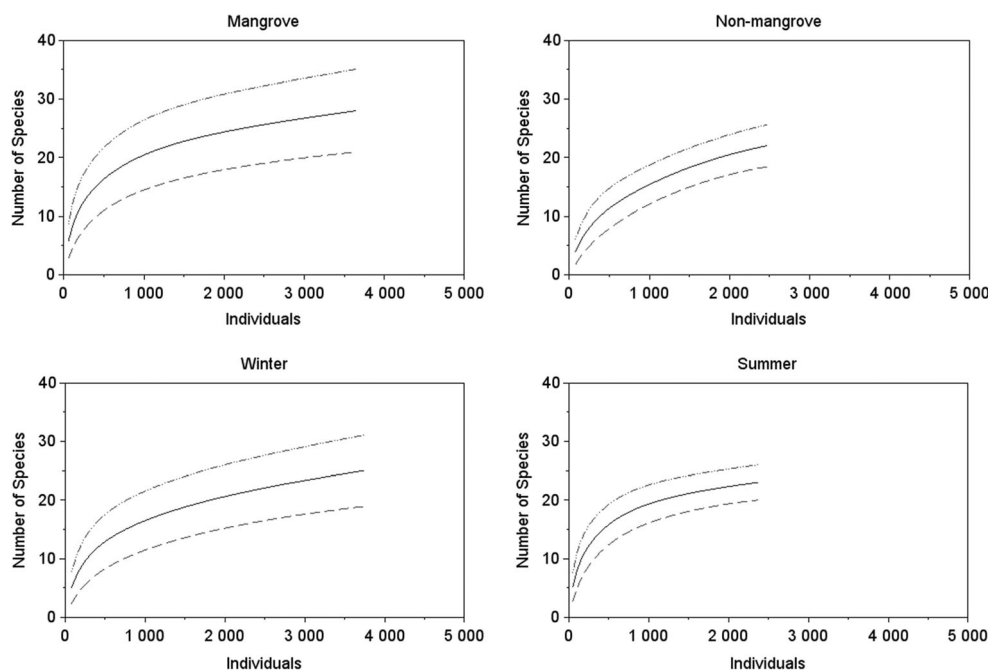
Nine species from seven families were caught only in mangrove creeks, given as follows from most to least abundant: *Sardinella gibbosa* (Clupeidae), *Lutjanus johni* (Lutjanidae), *Plectorhinchus pictus* (Haemulidae), *Bathygobius fuscus* and *Scartelaos tenuis* (Gobiidae), *Lutjanus russelli* (Lutjanidae), *Epinephelus coioides* (Serranidae), *Abalistes stellatus* (Balistidae), and *Strongylura strongylura* (Belontiidae). One species of prawn (*Penaeus merguensis*) also occurred only in the mangrove creeks and at relatively high abundance.

Three fish species from three families were caught only in the non-mangrove creeks: *Gerres poieti* (Gerreidae), *Euryglossa orientalis* (Soleidae), and *Terapon jarbua* (Terapontidae). The ratios of rare vs. common fish species were somewhat higher in mangroves (1.8) than non-mangrove (1.3). Seasonally, these ratios were similar (0.7) for winter and summer.

There were 15 and 13 species which were rare with total individuals comprising less than 1 % of total individuals in mangroves and non-mangroves, respectively; of these rare species in mangroves, 8 were represented by only 1 or 2 individuals (*Sphyræna putnamiae*, *Hemiramphus archipelagicus*, *Upeneus sulphureus*, *Strongylura strongylura*, *L. russelli*, *Abalistes stellatus*, *Epinephelus coioides*, *B. fuscus*) and 6 were represented by less than 10 individuals (*Plectorhinchus pictus*, *Scartelaos tenuis*, *Eleutheronema tetradactylum*, *Scomberoides lysan*, *Pseudorhombus elevates*, *Platycephalus indicus*). Of these rare species in non-mangroves, 10 were represented by only 1 or 2 individuals (*E. orientalis*, *T. jarbua*, *U. sulphureus*, *H. archipelagicus*, *S. putnamiae*, *P. elevates*, *S. lysan*, *E. tetradactylum*, *Acanthopagrus cuvieri*, *Ilisha melastoma*) and 3 were represented by less than 10 individuals (*Scatophagus argus*, *P. indicus*, *Pomadasys kaakan*).

Regarding seasonal results, *G. poieti* was only found in summer, while *Sardinella longiceps* and *S. gibbosa* were only found in winter. Most of these species showing seasonal changes occurred at low (<1 %) relative abundance as rare species, e.g., *S. lysan*, *S. putnamiae*, *P. pictus*, *E. coioides*, and *P. indicus* occurred in summer and *P. elevates*, *A. stellatus*, *S. strongylura*, *T. jarbua*, *E. orientalis*, and *B. fuscus* occurred

Fig. 2 Individual-based rarefaction curves of fish species sampled in different habitats (mangrove vs. non-mangrove) and seasons (winter vs. summer). Dashed lines indicate 95 % confidence intervals



in winter. Detailed species data for each habitat and season are presented in Table S2.

Fish Abundance and Biomass

Total fish abundance (individuals) and biomass per sample and per m^2 was dominated by Mugilidae (*Liza klunzingeri*) in both mangrove vs. non-mangrove habitats. Also, Leiognathidae, Gerreidae, Engraulidae, and Clupeidae were among the most abundant families in both sites. In spite of these similarities, we found inconsistent differences for mean abundance and biomass for mangrove vs. non-mangrove fish collections. These inconsistent differences reflected how the comparisons were made, on a per m^2 or per sample basis (Fig. 3). Thus, fish from mangroves showed higher abundance and biomass per m^2 than fish from non-mangrove sites, but the opposite pattern pertained when data was expressed on a per sample basis, i.e., fish from mangroves showed lower abundance and biomass per sample than fish from non-mangrove sites (Fig. 3). Only biomass data is shown in Fig. 3; additional graphs for abundance and correlations relating abundance and biomass are presented in the Figs. S1 and S2.

PERMANOVA tests showed that all these habitat differences were significant at the 0.004–0.01 level for Monte Carlo p values (Table 2). Thus, the habitat-level comparisons showed significant trends but had opposite directions

depending on how data were expressed. The inconsistent habitat differences were not considered ecologically robust.

Seasonal effects were much more consistent. Winter fish assemblages had higher mean biomass and mean abundance in all comparisons made on a per m^2 or per sample basis (Fig. 3), and seasonal effects were all significant at the 0.015–0.023 level (Table 2). Interactions between season and habitat (mangrove vs. non-mangrove) were also significant ($P < 0.05$) in three of four cases (Table 2). The seasonal patterns were partly due to the high abundance of *S. argus* in summer and Clupeidae (*Anodontostoma chacunda*, *S. longiceps*, and *S. gibbosa*) during winter. The rare species (e.g., *Pseudorhombus elevatus*) also contributed to the high biomass in winter. Lastly, creek-level variations were strong in PERMANOVA results with $P < 0.03$ (Table 2), but patterns were not consistent between creeks as shown in Fig. S3. Statistical tests showed no significant interactions between creeks and seasons (Table 2).

A further examination of the significant factors in the PERMANOVA tests of Table 2 was performed using the CAP routine with leave-one-out procedures, and indicated a low overall allocation success for the factor creek (<30 %). Thus, creeks were not identified as consistent factor that could separate samples based on the CAP ordination, despite being significant in PERMANOVA tests. CAP analysis also showed smaller canonical correlation coefficients for the factor habitat and CAP only allocated the samples according to the factor

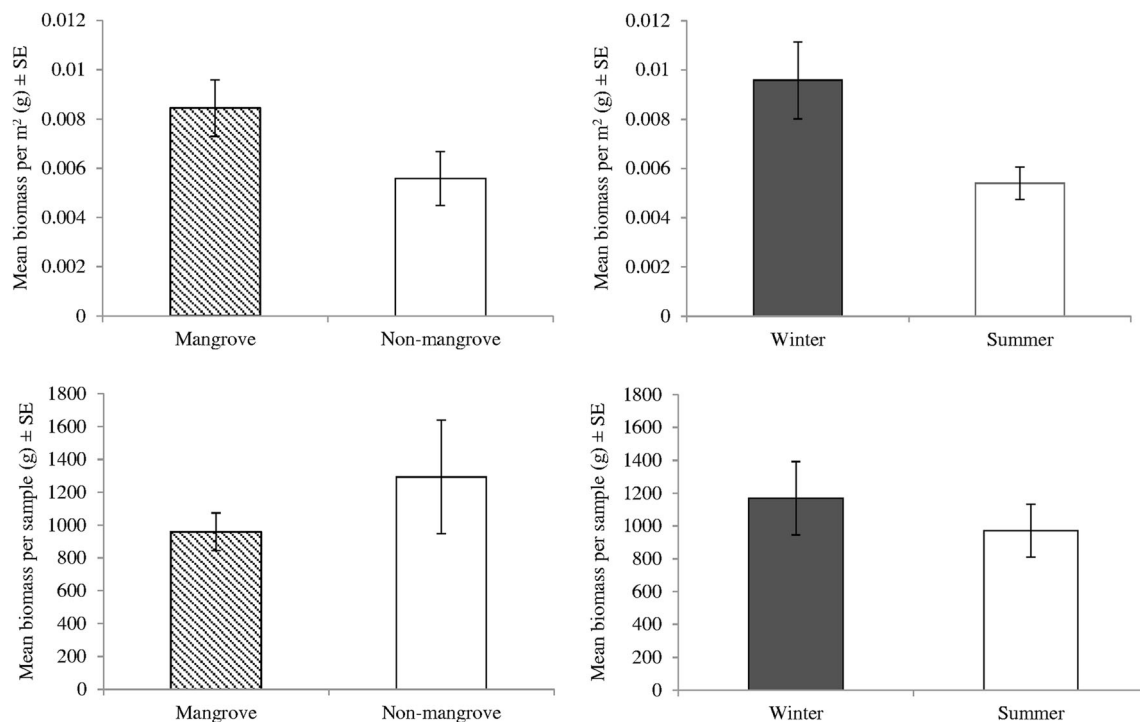


Fig. 3 Mean fish biomass (g) per sample and per m^2 (\pm SE) in different habitats (*left panels*) and seasons (*right panels*). *Left panels* show fish can be more abundant at greater biomass when results are expressed on a per m^2 basis (*top panels*), but the opposite result pertains when results are

expressed on a per sample basis (*bottom panels*). *Right panels* show the consistent seasonal differences between winter and summer fish assemblages, regardless of a per sample or per m^2 basis used to scale the data

Table 2 Results of 3-way PERMANOVA, testing the effects of habitats, creeks, and seasons on biomass and abundance per sample and per m²

Biomass per sample	df	SS	MS	Pseudo-F	P(perm)	perms	P(MC)	Abundance per sample	df	SS	MS	Pseudo-F	P(perm)	perms	P(MC)
Habitat	1	11,222	11,222	3.221	0.081	15	0.014	Habitat	1	13,391	13,391	4.12	0.054	15	0.003
Season	1	7555.8	7555.8	4.5085	0.015	998		Season	1	9600.5	9600.5	4.9082	0.016	996	
Creek (Habitat)	4	13,937	3484.1	1.792	0.006	998		Creek (Habitat)	4	13,001	3250.3	1.7139	0.014	998	
Habitat x Season	1	4710.9	4710.9	2.811	0.07	997		HabitatxSeason	1	7084.2	7084.2	3.6218	0.037	997	
Creek (Habitat) x Season	4	6703.6	1675.9	0.862	0.664	999		Creek (Habitat) x Season	4	7824	1956	1.0314	0.412	998	
Residual	84	163,320	1944.3					Residual	84	159,300	1896.5				
Total	95	209,670						Total	95	214,110					
Biomass per m ²	df	SS	MS	Pseudo-F	P(perm)	perms	P(MC)	Abundance per m ²	df	SS	MS	Pseudo-F	P(perm)	perms	P(MC)
Habitat	1	11,945	11,945	4.0799	0.067	15	0.004	Habitat	1	16,115	16,115	5.1394	0.071	15	0.001
Season	1	8341.5	8341.5	5.0361	0.023	997		Season	1	7707.7	7707.7	4.0688	0.018	999	
Creek (Habitat)	4	11,711	2927.8	1.5134	0.025	998		Creek (Habitat)	4	12,543	3135.6	1.6583	0.016	998	
Habitat x Season	1	5420	5420	3.2722	0.038	999		Habitat x Season	1	10,173	10,173	5.37	0.012	997	
Creek (Habitat) x Season	4	6625.4	1656.3	0.8562	0.693	998		Creek (Habitat) x Season	4	7577.4	1894.3	1.0018	0.486	997	
Residual	84	162,510	1934.6					Residual	84	158,840	1890.9				
Total	95	208,720						Total	95	217,080					

Biomass and abundance per sample (top matrix) and biomass and abundance per m² (bottom matrix). Difference were considered to be significant when *P* < 0.05 (italic values)

season (Fig. 4). Summer samples were divided from the winter samples along the CAP1 axis. Two species (*S. argus* and *P. pictus*) were correlated with the summer and three species *Leiognathus daura*, *S. longiceps*, and *Pentaprion longimanus* were correlated with winter (Fig. 4). Detailed CAP results are presented in Table S3.

Isotope Niche Diversity

The standard ellipses based on fish carbon and nitrogen isotope compositions showed some differences in niche size among sites and seasons (Fig. 5). The standard ellipse sizes for ten most abundant species were more variable between seasons than habitats, with winter ellipses estimated to be significantly larger than summer ellipses at the 96 % probability indicated by SEA_B (Table 3). Mangrove and non-mangrove fish assemblages showed a much lower 30 % probability of difference based on SEA_B (Table 3). To examine whether the seasonal comparisons for fish were due to a larger food isotope variability, we calculated standard ellipses using isotopic values of all potential basal food sources sampled (Fig. 5). Food isotope variability was similar in mangrove vs. non-mangrove sites, but significantly less diverse in winter than in summer (probability of 99 %; Table 3). Density plots showing the credibility intervals of the standard ellipses areas (SEA) for fish and food sources are presented in Fig. S4.

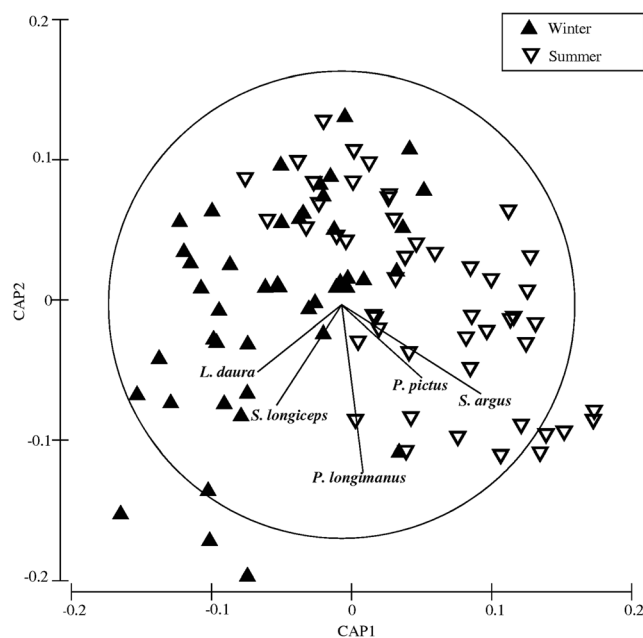


Fig. 4 Canonical analysis (CAP) yielded two axes regarding factor season, with squared canonical correlations of $\delta_1^2 = 0.63$ and $\delta_2^2 = 0.50$. Symbols represent biomass (g m⁻²) for individual block net samples and vectors show individual species correlations with the two CAP axes where $|r| > 0.4$. See Table 1 for full species names

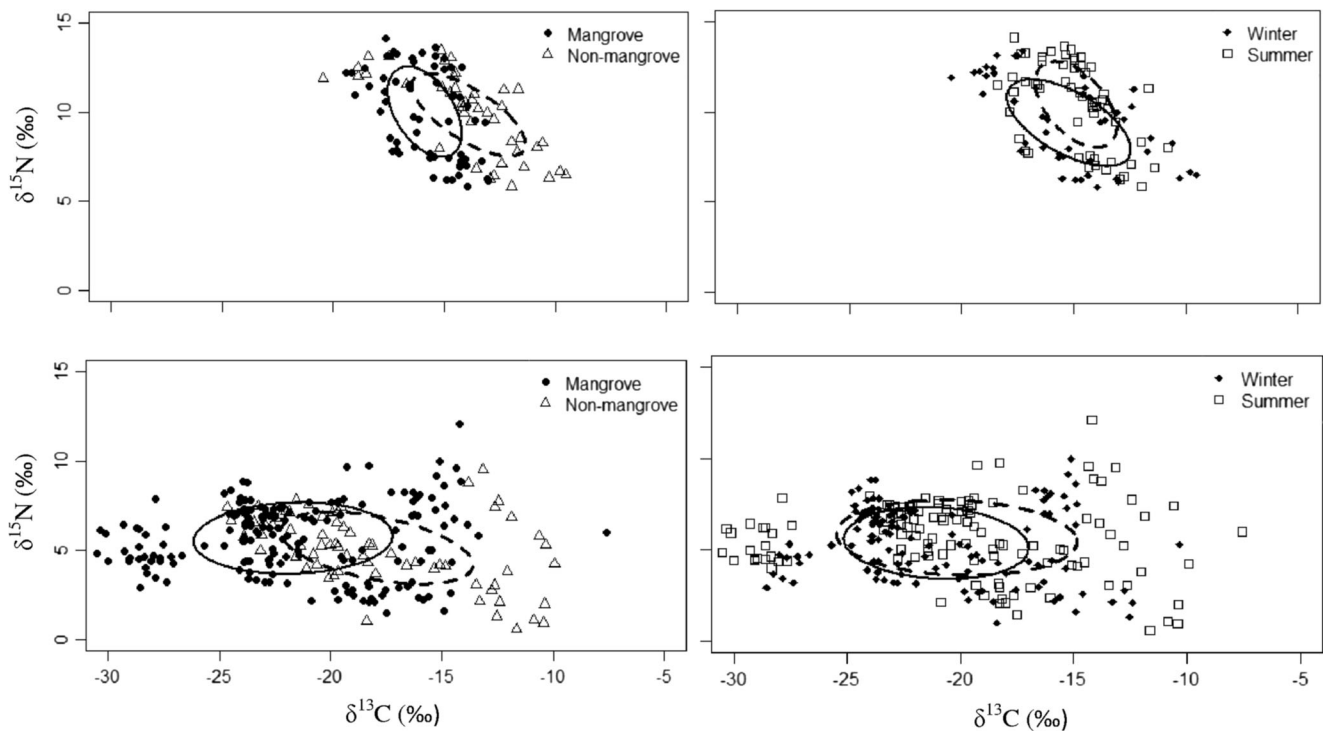


Fig. 5 Standard ellipses areas (SEA) based on carbon and nitrogen stable isotope compositions of fish and food sources from different sites (*left panels*) and seasons (*right panels*); *upper panels* show data for fish, *lower*

panels show data for potential foods. *Solid and dashed lines* enclose the standard ellipses area (SEA_c) that contain ca. 40 % of the data and show the isotopic niche of communities and sources at each habitat and season

We used the fish and food SEA values of Table 3 to calculate $(SEA_c\text{-fish})/(SEA_c\text{-food})$ ratios, finding a convergence towards similar results of no difference for mangrove vs. non-mangrove fish (ratios of 0.4 and 0.5 respectively; Table 3) but more pronounced differences for winter vs. summer (respective ratios of 0.7 vs. 0.3). These ratio calculations of larger niche diversity in winter matched winter increases in fish abundance and biomass, so that this winter increase in the community feeding niche appeared relatively robust. Also, much less seasonality was observed in these ratios at the mangrove sites (0.4 and 0.3 for winter and summer, respectively) versus at non-mangrove sites (0.8 and 0.4 for winter and summer, respectively).

Discussion

Season emerged as the most important and significant factor in our analyses of fish communities of Qeshm Island. Fish were less abundant in summer than in winter. Very low precipitation and lack of fresh water inputs in the region result in year-round hyper-saline conditions, and summer water temperatures are often high $>32^\circ\text{C}$ (Shahraki et al. 2014). Our findings on seasonality are not unexpected and agree with other studies that have shown that fish abundance and biomass in tropical mangrove habitats can be related to the environmental parameters such as salinity (Wright 1986), rainfall (Robertson and Duke 1990; Rooker and Dennis 1991), and

Table 3 Small size-corrected standard ellipse areas (SEA_c) for food sources and fish

Groups	Food sources			Fish			Ratios
	SEA_c (‰^2)	SEA_B non-mangrove $< SEA_B$ mangrove	SEA_B winter $< SEA_B$ summer	SEA_c (‰^2)	SEA_B mangrove $> SEA_B$ non-mangrove	SEA_B winter $> SEA_B$ summer	
Mangrove	28.0	0.12	–	11.6	0.30	–	0.4
Non-mangrove	24.0	–	–	13.1	–	–	0.5
Winter	25.0	–	<i>0.99</i>	16.5	–	<i>0.96</i>	0.7
Summer	34.3	–	–	11.6	–	–	0.3

Probability that the SEA of food sources and fish from one group is smaller than the other group (habitats and seasons) is indicated based on Bayesian standard ellipse areas (SEA_B). The SEA_c ratios (SEA_c fish)/(SEA_c food sources) are shown for different habitats and seasons. Italic numbers indicate the high probability of significant differences in SEA

turbidity (Little et al. 1988). Fish seasonal patterns in abundance occur against a wider biogeographic variation in fish diversity, with relatively low diversity characteristic of the study region (Wright 1989; Blaber 1997; Blaber 2000).

In contrast to the clear seasonal differences in fish communities, habitat differences were much weaker, so that creeks with and without mangroves seemed more similar than different in terms of fish diversity and biomass. For example, the most abundant species were common in both mangrove and non-mangrove creeks (Table 1), and a single species *L. klunzingeri* made up almost more than 50 % of the biomass of all fish sampled in both habitats. The strongest difference we observed between mangrove and non-mangrove habitats was in the rarer species, so that non-mangrove creeks seemed to offer fewer unique characteristics than the mangrove creeks. This is consistent with the idea that higher complexity and shelter of mangroves may attract more fish species due to abundant food, increased microhabitat availability and shelter from predation (Blaber and Blaber 1980; Laegdsgaard and Johnson 2001; Nanjo et al. 2014b). Also, presence of mangrove snapper and a commercial shrimp only in mangroves may be significant for fisheries (Vance et al. 1996; Rönnbäck 1999).

Not enough survey has been done in our study region to make good comparative estimates of the nursery function of creeks versus more offshore habitats. But most (96 %) of the fish collected in the study were small juveniles so that the creeks should be considered in future surveys of nursery areas.

Our estimates of fish abundance and biomass varied depending on whether results were expressed on a per sample basis or a per m² basis, with mangrove creeks supporting a less fish biomass and abundance per sample, but more biomass and abundance per m². This may seem somewhat contradictory, but reflects a real dichotomy in results observed in other studies where it also has been observed that fish can be either more or less abundant than in mangroves than in other nearby habitats. For example, studies that have observed higher biomass (abundance) of fish per area include those from south Florida (Thayer et al. 1987), the Caribbean (Nagelkerken and Velde 2002), and Japan (Nanjo et al. 2014a). Structural complexity and reduced predation pressures in mangrove habitats have been hypothesized to help explain the relatively high fish densities found in these habitats (Blaber 2007; Nagelkerken et al. 2008). On the other hand, a study in the Barwon River Estuary in Australia reported less fish biomass per area in mangrove habitats than in other microtidal habitats (Smith and Hindell 2005). Also a study that made per sample comparisons found that the vegetated areas of mangroves had lower fish abundances compared to nearby treeless mudflats and creeks (Wang et al. 2009). Lack of uniform methods and sampling strategies among the various studies make it difficult at this time to generally assess mangrove importance for fish abundances and densities. Also,

block net studies show varying fish abundance and biomass in mangroves with different environmental settings, limiting direct comparisons to this study. Future surveys may need to consider fish residency status more explicitly when reporting fisheries use of mangrove vs. non-mangrove habitats. Block net studies usually express results on a per m² basis, but some thought and further investigation may be needed as to whether the appropriate basis reporting results is per sample, per m² or per m³.

It is possible that food may contribute to these often conflicting patterns of fish abundance and biomass. Greater food availability has been suggested as a factor responsible for greater fish numbers in mangroves compared to other habitats (Robertson and Blaber 1992; Laegdsgaard and Johnson 2001). But in our study area, there is a low estimated role of mangrove detritus and a likely shared dependence on mudflat algal food resources (Shahraki et al. 2014). Thus, similarity in the food resources may partially account for similarities in fish communities in the mangrove and non-mangrove creeks of Qeshm Island.

The SEA_c analyses showed that fish communities had similar isotopic niche sizes in both mangrove and non-mangrove habitats. This might reflect the similarity in fish compositions among sites and a common reliance on algal food resources in both habitats (Shahraki et al. 2014). Also, fish movement between habitats could lead to connectivity of food webs across habitats (Layman 2007; Hammerschlag-Peyer and Layman 2010). However, there was a broader trophic diversity among fish in winter. The presence/absence of some species largely accounted for this seasonal variation in the isotopic niche size. Especially, the zooplanktivores *L. daura* and *S. longiceps* were present at high abundances in winter. Their presence increased the isotopic niche size because they had high $\delta^{15}\text{N}$ values. Similar high $\delta^{15}\text{N}$ values have been reported for zooplanktivores in other food webs studies (Abrantes and Sheaves 2009; Vaslet et al. 2012). If these zooplanktivores were removed from our SEA analysis, seasonal differences in SEA were no longer significant as indicated by lower (15 %) probability of difference based on SEA_B.

Our summer fish isotope diversity results are similar in some respects to those of Layman et al. (2007) who found less isotopic diversity in stressed ecosystems (Layman et al. 2007). High water temperature in summer may decrease fisheries productivity by increasing energy costs in juvenile fishes (Wuenschel et al. 2004; Wuenschel et al. 2005). However, our results contrast to those of Abrantes et al. (2014) who found trophic diversity increased with increased food isotope diversity following wet season flooding. In our study, we found the opposite pattern, namely that fish trophic diversity decreased in summer at a time when food isotope diversity increased. Because of these similarities and differences across studies, further research about isotope

niche sizes and isotope trophic diversity seems warranted. Some caution must be used in these studies because the isotope values are usually (as in this study) measured for many potential foods rather than just the actual important foods, and because isotope diversity in foods does not necessarily equate to an increased availability of foods themselves (Matthews and Mazumder 2004; Newsome et al. 2007). Future studies should probably be conducted in concert with gut content studies to better identify important foods and the relationship of fish isotope diversity to the diversity of those important foods. However, seasonal changes in fish/food isotope niche ratios agreed with and magnified the seasonal patterns observed in fish isotope diversity in this study, so that our coarse-level view of food isotope diversity based on all potential foods, not just important foods, seemed to be a reasonable first approach.

Our findings emphasized that fish communities had different niche sizes across the seasons in Qeshm Island. The lower seasonality observed in the fish/food isotope niche ratios at the mangrove sites may indicate more consistent food web dynamics at the mangrove sites. Fish communities at both mangrove and non-mangrove sites had similar isotopic niche sizes, and both habitats appeared to support juvenile fish. Our findings indicate that the abundance and biomass of small fish is not always higher in mangrove areas. Like mangrove creeks, the non-mangrove creeks are utilized by a wide variety of fish suggesting greater attention should be given to these habitats.

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Ethics Statement All research activities were allowed by the Iranian fisheries organization (Qeshm fisheries office) in strict accordance with the law of protection and exploitation of fisheries resources of Islamic Republic of Iran. All sampling procedures and experimental manipulations were reviewed by the Qeshm fisheries office as part of the field permit. The vertebrate work was approved by the animal ethics committee of Iranian Veterinary Organization.

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