

Fish use of intertidal mangrove creeks at Qeshm Island, Iran

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ABSTRACT: Habitat use by fish in intertidal mangrove creeks is relatively unstudied in the Persian Gulf. We investigated the role of temporal variations and creek elevation in shaping fish community structure in intertidal mangrove creeks in the Strait of Hormuz, Qeshm Island, Iran (western Indian Ocean). Block net sampling was carried out to examine the influence of 3 types of temporal dynamics on patterns of fish diversity and biomass. Tides, diel day/night variations, and season all proved important for fish dynamics. The fish assemblage of 29 species was dominated by Mugilidae, which constituted 62% of biomass and 41% by abundance. Although the most abundant species occurred in all creeks and months, the number of species, community biomass and abundance of individuals were significantly influenced by tide and day/night cycles, with highest values during nighttime spring tides and lowest values during daytime neap tides. Gut content studies showed that fish accessing marsh surfaces on nighttime spring tides generally had 75–100% full guts, indicating trophic use of mangrove areas. The findings from this meso-tidal arid area generally agree with previous studies of mangrove creeks from wetter tropical sites, but there were some exceptions. Notably, fish community abundance and biomass in February winter conditions were highest during nighttime neap tide conditions, instead of during nighttime spring tide conditions. This neap tide maximum was associated with a relatively greater dominance of resident fish species during winter, but may also indicate some temperature-related differences in fish use of mangroves that are at the northernmost regional limit of their distributions at Qeshm Island.

KEY WORDS: Intertidal mangrove creeks · Fish community · Tidal cycle · Persian Gulf · Western Indian Ocean

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INTRODUCTION

Mangrove ecosystems are important habitat for fish worldwide (Robertson & Duke 1990, Sasekumar et al. 1992, Nagelkerken 2009). However, the importance of mangroves to fish populations varies among systems according to several environmental conditions (Blaber & Blaber 1980, Blaber 2000, Faunce & Serafy 2006). This study investigated mangroves of the Persian Gulf that occur under extreme conditions of aridity and large (>20°C) seasonal variations in temperatures, at the northern edge of mangrove distributions in the Indian Ocean. This harsh environ-

mental setting involves high salinities and restricts mangrove diversity to 2 species (*Avicennia marina* and *Rhizophora mucronata*) in this arid region (Al-Khayat & Jones 1999, Sheppard et al. 2010). This study assessed the fish use of mangrove creeks in this environment.

There are many regular features of intertidal mangrove forests. Mangrove forests are alternately inundated and exposed by tides, and fish have to cope with variations in tidal habitat availability (Quinn & Kojis 1987, Rooker & Dennis 1991, Sheaves 2005). The regular changes in water level may cause significant changes in mangrove-associated fish fauna on

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meso-tidal and macro-tidal coasts (Davis 1988, Wilson & Sheaves 2001, Krumme 2009). Tidal- and diel-related patterns of fish assemblages are well documented for humid mangroves, e.g., in Brazil and Thailand (Krumme et al. 2004, Krumme & Saint-Paul 2010, Krumme et al. 2015). In the western Indian Ocean, only a few studies have examined how mangrove fish assemblages are affected by the influence of tides (Laroche et al. 1997, Weis et al. 2009). Strong diel components involved in fish use of mangroves were also found in Madagascar (Laroche et al. 1997). This study examined the tidal and day/night dynamics that help shape intertidal fish assemblages of arid mangroves.

In addition to tide and day/night factors, temperature may also be important for fish use of mangrove habitats. Tidal influences of fish assemblages have been mostly studied in regions with stable temperatures (Vance et al. 1996, Rönnbäck et al. 1999). This study included winter and summer sampling to examine the effects of a $>20^{\circ}\text{C}$ seasonal temperature variation on fish use of mangroves.

The elevation of tidal creeks was also studied as a factor possibly influencing fish distributions (Kneib & Wagner 1994, Allen et al. 2007). Along the Iranian coast of the Persian Gulf, intertidal mangrove creeks are generally flooded during high tide and become completely exposed at low tide. However, intertidal creeks can be located at differing elevations, which affects the timing and depth of inundation during high water. Intertidal creek use by fish can be influenced by creek drainage characteristics (Kneib 1997). Fish use of the intertidal salt marsh creeks of South Africa and California has been reported previously (Paterson & Whitfield 2003, Allen et al. 2007), but there are few reports concerning creek drainage effects on the dynamics of intertidal mangrove fish assemblages (Lugendo et al. 2007a). Thus, it was important to understand the role of creek elevation on fish habitat use in the mesotidal regimes of Qeshm Island.

This factorial-design study examined temporal patterns of intertidal mangrove fish assemblage structure along the southern Iranian coast, addressing: (1) the taxonomic composition of intertidal mangrove fish fauna, and (2) tide, diel, and monthly related patterns of fish use of mangrove creeks that were located at different elevations. The number of fish species and their abundance and biomass were expected to differ in accordance with tides, day/night cycles, seasons, and interactions between these factors in mangrove creeks of different elevations.

MATERIALS AND METHODS

Sampling sites

The study was carried out at Qeshm Island, on the Iranian coast of the Persian Gulf (26.8°N , 55.75°E) (Fig. 1). Details of the study area can be found in Shahraki et al. (2014). Four mangrove-lined creeks, flowing into a main channel, were chosen as sampling sites to test the fish use of creeks relative to tidal cycles. Creeks 2 and 3 were situated at a lower elevation and were larger in size (low-lying creeks) than the high-lying Creeks 1 and 4 (Fig. S1 in the supplement at www.int-res.com/articles/suppl/m542p153_supp.pdf). High-lying creeks were smaller and had a lower flooding frequency than low-lying creeks; this resulted in less time available for fish to use these high-lying creeks. Tides were semidiurnal, with 2 highs and 2 lows per day, and tidal amplitude averaged 2.5 m. Tides selected for study were night tides that fell during the later part of the night, reaching low tide at dawn, and day tides that fell during the afternoon, reaching low tide at dusk. Corresponding fish sampling was at dawn for the night tides and at dusk for the day tides.

Sampling design

Fish were sampled from the 4 intertidal creeks with block nets (15–25 m in length, 4 m high; 12 mm stretched mesh size) lifted at slack high water during 3 lunar cycles in December 2011–January 2012, February–March 2012 and August–September 2012. The nets were deployed 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. Net lengths were adjusted to stretch across the entire widths of the tidal creeks. At high tide, the tops of the nets were lifted onto wooden stakes. During the following low tide, when the creeks were almost empty, the fish were collected (Shahraki & Fry 2015). The block net method is commonly used for fish collection in mangrove studies (e.g. Thayer et al. 1987, Barletta et al. 2003), and this method is regarded as highly efficient in capturing fish that use intertidal habitats (Bozeman & Dean 1980). Block net sampling is usually considered an area-based method, but results are reported here both on a per sample and per area (m^{-2}) basis. The per sample results are given mostly for comparison with other studies (see 'Discussion').

Overall 96 block net samples were taken (4 intertidal mangrove creeks \times 3 lunar cycles \times 4 lunar phases \times 2 times of day). Sampling targeted the 4 most important combinations of tidal amplitude (and lunar phase) and daylight conditions: spring tide–night (SN; new moon/full moon night), spring tide–day (SD; new moon/full moon day), neap tide–night (NN; wax/wane moon night) and neap tide–day (ND; wax/wane moon day). Lunar phases were considered as replicates for spring and neap tide. SN and NN sampling took place in the early morning, when fish had entered the creeks during the nightly flood tide and were leaving on the morning ebb tide. SD and ND sampling were carried out in the evening, when fish had entered with

the afternoon flood tide and were leaving during the first part of the night. The time of each sampling was chosen according to the tide tables for the area (Qeshm Meteorological Station, data received as personal communication).

Fish were collected during low tide and transported on ice to the laboratory. The high-lying creeks dried out at each tide. However, the low-lying creeks still contained water at neap low tide. In this instance, a small hand net was used to collect all the fish behind the block nets. Collected fishes were identified to the lowest possible taxonomic level (Fischer & Bianchi 1984, Kuronuma & Abe 1986, As-sadi et al. 1997), counted, and weighed (wet weight;

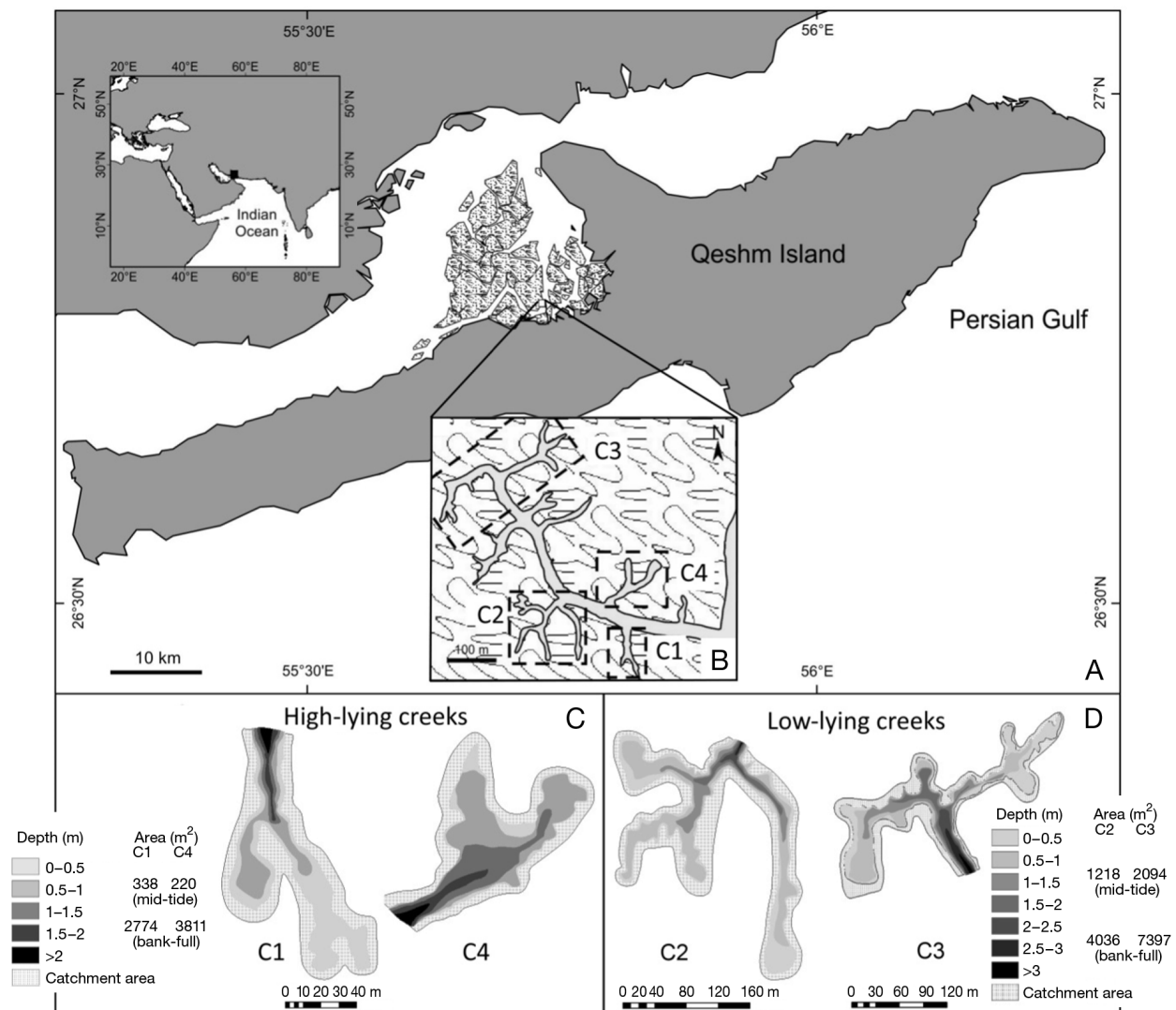


Fig. 1. (A) Location of the study area at Qeshm Island, Strait of Hormuz, Iran. (B, inset) Mangroves in light gray with the main channel and the 4 intertidal creeks (C1–C4, dashed rectangles). Bathymetric maps of (C) high-lying Creeks 1 and 4 and (D) low-lying Creeks 2 and 3. The total inundation areas of the creeks are indicated at mid-tide (beyond 1 and 1.5 m depths for the high- and low-lying creeks, respectively) and at full bank (beyond 2 and 3 m depths for the high- and low-lying creeks, respectively)

$g \pm 0.1$). Fish species were assigned to resident or transient categories based on available literature (Day 1989, Elliott et al. 2007, Froese & Pauly 2012). Given the fact that the residency status of only a few species collected in this study was available in the literature, we categorized the fish residency based on information from the same family and genus and considered personal expert consultations (M. Elliott pers. comm.) and also data from Ley et al. (1999) and Ley & Halliday (2007).

Stomach fullness of 4 species (*Acanthopagrus latus*, *Pomadourys kaakan*, *Liza klunzingeri*, *Lutjanus johnii*) was determined to assess whether fish feeding was related to tides and time. For that analysis, a total of 304 stomachs (~20 individuals from different tide-time of days from each species) were selected. Stomach fullness was visually assigned to 1 of 4 fullness categories: empty or nearly empty, 0–25% (1), 25–50% (2), 50–75% (3), or nearly or completely full, 75–100% (4).

For each sampling event, surface water temperature was measured (WTW Multi 3430), and tidal height was recorded at the mouth of the creeks at high water (tidal gauge). Mean pH values (\pm SD) were 8.1 ± 0.2 , and salinity averaged 38.3 ± 0.5 throughout the sampling period (Shahraki et al. 2014). The transparency of the water measured by Secchi disk was 52 ± 2 cm. Additionally, a HOBO water data level logger (U20-001-01-Ti) was used to assess the interaction between water level changes and water temperature in the main mangrove channel in August (the HOBO did not operate in December or February). This device measured water level (water level accuracy: ± 0.5 cm) and water temperature (temperature accuracy: $\pm 0.44^\circ\text{C}$) every 15 min, resulting in information about changes in the water height and temperature over several spring and neap tide cycles.

Creek attributes

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. The survey included measuring water levels at horizontal transects for each creek and drawing approximate inundation areas on a grid map in the field using a tape measure, GPS, and a compass. This information was used with GIS software to produce a bathymetric map of each creek (Fig. 1). The map was sourced using the GNU Lesser General Public License. Intertidal creek depth points were added using GPS waypoints from the drainage areas.

A topographic height was assigned to each depth polygon in attribute tables. All depth polygons were transformed to raster data to calculate water surface area and volume for each creek with high-resolution 3-dimensional models. Relationships between high water level and inundated area and volume were established (Fig. S2 in the supplement). Abundance and biomass for each species per sample were converted to abundance and biomass per square meter by dividing by the respective inundation area for each creek.

Qeshm mangrove forests are flooded only during spring tides. The low-lying creeks were characterized by having greater water depths (mean \pm SD; 0.37 ± 0.2 m) in relation to mean sea level and greater time of inundation during high-water periods when compared to the high-lying creeks. GIS-generated estimates indicated that the relationship between surface area, volume, and intertidal water level increased slowly until an approximately 1–1.5 m water level rise at the mouth of the creeks and inundation was still restricted to the creek network. At this water stage, mean drainage areas were 338, 815, 2937, and 1281 m² for Creeks 1, 2, 3, and 4, respectively. Beyond 2–3 m water level rise, the water left the creek network and the mangrove creeks became flooded (Fig. S2). Mean drainage areas were then 2774, 6481, 11460, and 3811 m² for Creeks 1, 2, 3, and 4, respectively.

Data analysis

EstimateS software was used to produce rarefaction curves and estimates of species richness for each creek (Colwell 2009). Species richness between the factors month and tide-time of day combination (SN, SD, NN, ND) and also the stomach fullness difference between SN, SD, NN, and ND were analyzed with Kruskal-Wallis 1-way analysis of variance on ranks (for each factor), followed by a Tukey test in SigmaPlot 12.5. The Shapiro-Wilk test was used to test for normality.

The effect of water conditions on intertidal fish abundances or biomass was assessed with 4-way permutational multivariate analysis of variance (PERMANOVA) model. Factors included: location (fixed, 2 levels: high-lying and low-lying creeks), creek nested in location (random, 4 levels: 1, 2, 3, 4), tide-time of day combination (fixed, 4 levels: SN, SD, NN, ND) and month (fixed, 3 levels: December, February, August). Additionally, differences among fixed factors were analyzed with pairwise comparisons,

and, in the case of location, Monte-Carlo generated p-values were used because there were inadequate unique permutations possible to determine permutational p-values (Anderson et al. 2008). Canonical analysis of principal coordinates (CAP) was applied as a constrained ordination procedure to visualize patterns revealed by PERMANOVA. CAP finds axes through multivariate data clouds to maximize the differences among *a priori* groups (Anderson et al. 2008). The species most responsible for differences were identified based on relatively high correlation ($|r| > 0.4$) with the CAP axes (Anderson & Willis 2003, Willis & Anderson 2003). Analyses were performed on square-root-transformed data and based on Bray-Curtis distances.

Pearson correlation tests were used in Statistica 11 to test whether high water level and surface water temperature correlated with intertidal fish abundance and biomass per sample.

RESULTS

Species composition and richness

A total of 5954 individuals from 29 fish species and 22 families were caught in 96 block net samples. Half of the species (15 of 29 species) were abundant with 10 or more individuals. The most speciose families were Clupeidae (4 species), Haemulidae, Sparidae, Lutjanidae, and Gobiidae (2 species each). The most abundant species were *Liza klunzingeri* (41%, Mugilidae), *Leiognathus daura* (18%, Leiognathidae), *Pentaprion longimanus* (10%, Gerreidae), and *Thryssa vitrirostris* (8%, Engraulidae). All other species accounted for the remaining 20% of the total abundance, each with <5%. In terms of catch biomass, *L. klunzingeri* (62%), *T. vitrirostris* (8%), and *Acanthopagrus latus* (5%, Sparidae) made up 75% of the catch (Table 1). Transient species represented 82% of the species and >85% of total abundance and biomass (Table 1).

The most abundant species (relative abundance of >1%) occurred in all creeks (Table 1). Also, the observed number of species was similar at 13–16 species when 500 individuals were considered for comparisons between creeks (Fig. 2).

Species richness differed between tide-time of day (Kruskal-Wallis (KW) test, $H = 32.7$, $p < 0.001$; Tukey's test, SN > ND) and between months (KW test, $H = 6.06$, $p < 0.05$). Significantly more species were captured at SN, while ND had the lowest species numbers (Fig. 3). The median number of species at

SN was 7 (the 25th and 75th percentiles were 6 & 8), while for the other tide and time combinations the median ranged between 4 and 5 (Fig. 3). The median numbers of species were 4, 5 and 6 for December, February and August, respectively, but these median values were not significantly different (Fig. 3). However, detailed species data did show significant presence/absence differences among months and tidal and diel cycles. For example, *Sardinella longiceps* was not found at SN and *Pomadys kaakan* did not occur at NN. Also, some rare species with a relative abundance of <1% occurred mostly at SN, e.g. *Upeneus sulphureus*, *Hemiramphus archipelagicus*, and *Pseudosynanceia melanostigma* (Table 1). Five species (*L. klunzingeri*, *T. vitrirostris*, *A. latus*, *P. kaakan*, and *Lutjanus johnii*) made up 85% of the catch biomass at SN. Some resident species, *Sardinella longiceps* and *Sardinella gibbosa* (Clupeidae), were absent in August, whereas these species were more abundant in February (Table 1). The NN/SN ratios of biomass for the resident species were 2.4 in February and 0.2 and 0.5 in December and August, respectively.

The monthly variations in species richness were mostly related to the seasonally transient species. In detail, *Scomberoides lysan*, *H. archipelagicus*, and *U. sulphureus* only occurred in August; *Pseudorhombus elevatus*, *Eleutheronema tetradactylum*, *Strongylura strongylura*, *Abalistes stellatus*, and *Acanthopagrus cuvieri* were only found in February, and *P. melanostigma* only in December. The most abundant species changed rank between months (Fig. S3 in the supplement).

Spatio-temporal patterns

PERMANOVA results for the effect of month were highly significant (Table 2), with significant differences between February and August (February > August, $p < 0.05$; Fig. 4). Highest abundance and biomass per sample and per square meter were observed at SN (Fig. 5). Also, tidal and diel variations were highly significant ($p < 0.001$) in PERMANOVA results (Table 2). The pairwise comparisons for abundance and biomass per sample and per square meter showed higher values at SN compared with ND ($t > 3.1$, $p < 0.05$). While the tide-time of day combination had a strong effect on the fish assemblage composition, the effect was not constant between months (Fig. S4 in the supplement). For instance, unlike other NN conditions, high biomass per sample and per square meter and abundance per square meter

Table 1. Fish species composition from 4 intertidal mangrove creeks (C1–C4) of Qeshm Island collected during 3 lunar cycles in December 2011–January 2012, February–March 2012, and August–September 2012, accounting for the 4 tidal and diel combinations of spring–day (SD), spring–night (SN), neap–day (ND), and neap–night (NN). Fish species (sorted by total number of individuals [N]). Res: estuarine residents; Tran: transient juvenile migrants and marine stragglers; RA%: relative abundance, RB%: relative biomass

Species	Residency	N	RA%	RB%	Tide-time of day				Biomass per sample						
					SN	SD	NN	ND	Dec	Feb	Aug	Creek			
<i>Liza klunzingeri</i> (Mugilidae)	Tran	2443	41	62	64248	9631	9079	9954	67140	13501	12270	10571	29464	48099	4777
<i>Leiognathus daura</i> (Leiognathidae)	Tran	1057	18	3	2704	1081	3487	22.5	857	2475	979	366.9	1665	1445	833.9
<i>Pentaptrion longimanus</i> (Gerreidae)	Tran	577	10	4	1373.5	3214	964.5	754	2316	1506	2025	1160	3003	745.5	937.5
<i>Thryssa vitirostris</i> (Engraulidae)	Tran	468	8	8	7757.7	167	773	472	565.5	4397	6921	844.7	2994	6225	1820
<i>Scatophagus argus</i> (Scatophagidae)	Res	302	5	2	1000.6	266.5	505.5	683	876.5	170	1428	158.5	1109	964.2	243.1
<i>Acanthopagrus latus</i> (Sparidae)	Tran	257	4	5	4097.8	2802	286	69.5	3937	1235	2761	1686	2119	2132	1997
<i>Anodontostoma chacunda</i> (Clupeidae)	Res	188	3	2	859	1696	504	361	922	1566	454	122	461	2214	145
<i>Sardinella longiceps</i> (Clupeidae)	Res	166	3	1	0	327	26	1567	7	1915	0	27	1228	0	667
<i>Pomadasygys kaakan</i> (Haemulidae)	Tran	161	3	3	3632.5	565	0	13.5	3193	318	986	1615	805.2	1239	837.6
<i>Sardinella gibbosa</i> (Clupeidae)	Res	120	2	1	220	777	524.8	35	5	1027	0	35	232	20	745
<i>Lutjanus johnii</i> (Lutjanidae)	Tran	73	1	4	5488	65.5	28	11	4354	820	1164	315	2640	2682	701
<i>Ilisha melastoma</i> (Clupeidae)	Res	53	1	0	77.5	287	0	3	67	288	17.5	22.5	78	247	25
<i>Sillago sihama</i> (Sillaginidae)	Tran	18	0	0	192	205	600	0	276	216	132	101	294	89	140
<i>Pseudorhombus elevatus</i> (Paralichthyidae)	Tran	15	0	0	120	0	0	215	0	335	0	0	15	320	0
<i>Plectorhynchus pictus</i> (Haemulidae)	Tran	13	0	0	253	74	227	0	30	0	397	158	84	30	155
<i>Scartelaos tenuis</i> (Gobiidae)	Res	8	0	0	31	0	100	47.5	17	39	82.5	30.5	69	24	15
<i>Lutjanus russelli</i> (Lutjanidae)	Tran	6	0	0	0	7.5	0	0	0	80	7.5	0	87.5	0	0
<i>Platycephalus indicus</i> (Platycephalidae)	Tran	5	0	2	1200	0	5	1650	2300	0	550	0	250	2300	300
<i>Bathygobius fuscus</i> (Gobiidae)	Tran	5	0	0	24	0	0	67	53	38	0	0	31	0	60
<i>Scomberoides lysan</i> (Carangidae)	Tran	5	0	0	0	18	60	49.5	0	0	67.5	0	21.5	46	0
<i>Eleutheronema tetradactylum</i> (Polynemidae)	Tran	3	0	0	7	0	0	7	0	59	0	0	20	0	39
<i>Sphyaena putnamiae</i> (Sphyraenidae)	Tran	2	0	1	38.8	0	0	600	600	0	638.8	600	0	638.8	0
<i>Epinephelus coioides</i> (Serranidae)	Tran	2	0	1	1400	0	0	200	1400	0	200	1600	0	0	0
<i>Strongylura strongylura</i> (Belontiidae)	Tran	2	0	0	130	0	80	0	0	130	0	0	0	130	0
<i>Pseudosynanceia melanostigma</i> (Synanceiidae)	Tran	1	0	0	395	0	0	0	395	0	0	0	261	40	94
<i>Abalites stellatus</i> (Balistidae)	Tran	1	0	0	16	0	45	0	0	16	0	16	0	0	0
<i>Acanthopagrus cuvieri</i> (Sparidae)	Tran	1	0	0	2	109	0	0	0	4	107	0	47	4	60
<i>Hemiramphus archipelagicus</i> (Hemiramphidae)	Tran	1	0	0	55	0	0	0	0	0	55	0	55	0	0
<i>Upeneus sulphureus</i> (Mullidae)	Tran	1	0	0	2.5	0	0	0	0	0	2.5	0	0	0	2.5

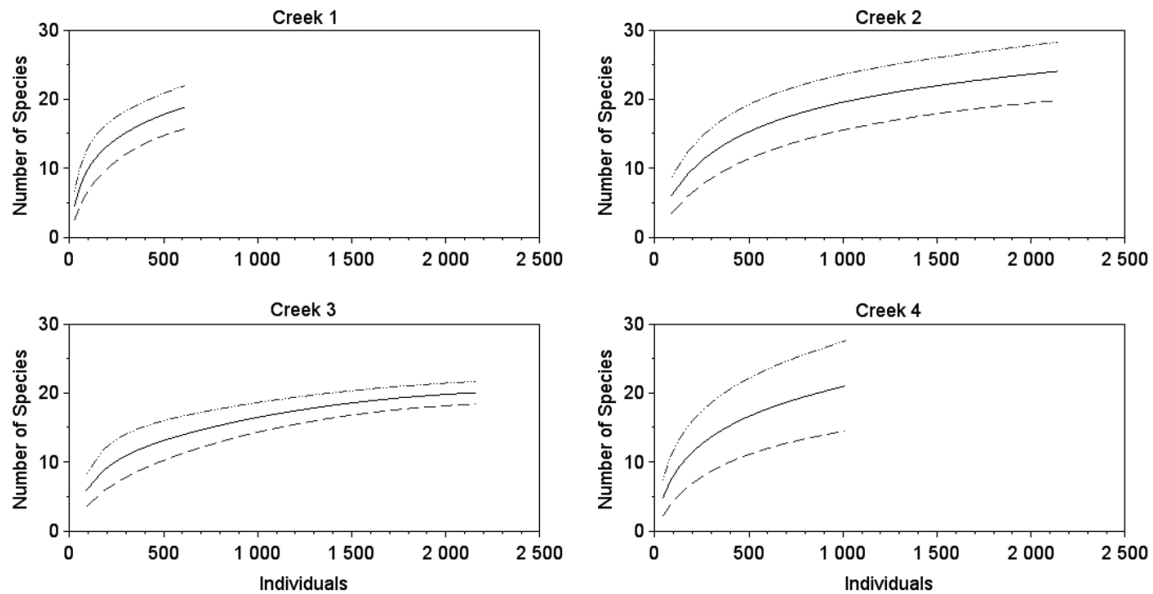


Fig. 2. Individual-based rarefaction curves of fish species caught in 4 mangrove-lined creeks sampled in different combinations of tidal and diel cycles during 3 months (December 2011, February and August 2012) at Qeshm Island, Iran. Dashed lines indicate 95% confidence intervals

occurred at NN in February. Also, resident species were more abundant in February than in other months (Table 1). The interactions between months and tides were also significant ($p < 0.05$) in all cases (per sample and per area) in PERMANOVA (Table 2).

Creek-level variations (nested in location) were significant in PERMANOVA results at the 0.006–0.03 p-level in 3 of 4 cases (Table 2). Mean abundance and biomass per sample were higher at Creeks 2 and 3, but inconsistent patterns were observed when the biomass and abundance were expressed per square meter (Fig. S5 in the supplement). This indicates that

low-lying creeks do not support more fish abundance and biomass per square meter. Statistical tests showed no significant interactions between creeks and tides or between creeks and months (Table 2). Overall, creeks and associated interactions showed fewer significant differences than the time-related factors that included tides, day/night, and season (Table 2).

Further examination of the significant abundance and biomass factors in PERMANOVA, with the CAP routine, indicated low overall allocation success for the factor month (Table S1 in the supplement). CAP only allocated the samples according to the factor tide and time of the day (Fig. 6). *A. latus*, *L. daura*, and *T. vitrirostris* were positively correlated with the high water level (spring tide samples), as indicated by the correlation coefficients of 0.4, 0.5, and 0.5, respectively, whereas *P. longimanus* was negatively correlated (-0.5) with the high water level.

Total abundance and biomass were significantly positively related to the high water level ($r = 0.4$ and 0.2 , $n = 96$, $p < 0.05$) and negatively correlated to the surface water temperature ($r = -0.09$ and -0.1 , $n = 96$, $p < 0.05$). Spring tide was indicated by higher water levels in all months (Fig. S6a in the supplement), and the lowest water temperatures were detected at SN and NN in all months (Fig. S6b).

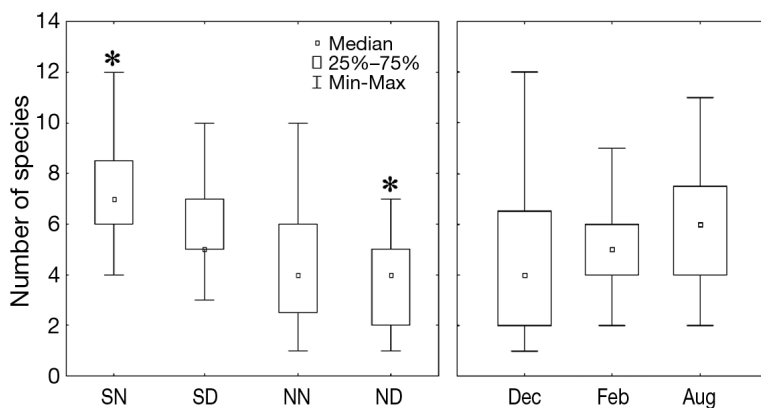


Fig. 3. Median number of fish species captured at spring tide–night (SN), spring tide–day (SD), neap tide–night (NN), and neap tide–day (ND) and in 3 months (December 2011, February and August 2012) in intertidal mangrove creeks ($n = 96$ samples). The 25 to 75% quartiles and minimum and maximum values are shown. Asterisks indicate significant differences between groups (SN > ND, $p < 0.05$)

Table 2. Results of 4-way PERMANOVA testing the effects of location (high and low-lying creeks), creeks (Creek 1, 2, 3, 4) nested in location, tide-time of day combination (spring tide-day, spring tide-night, neap tide-day, neap tide-night), and month (December, February, August) on biomass and abundance per sample and per square meter. Difference was considered to be significant when $p < 0.05$ (bold values)

	df	SS	MS	Pseudo-F	p (perm)	perms	p (MC)	df	SS	MS	Pseudo-F	P (perm)	perms	p (MC)
Abundance (m⁻²)														
Location	1	2538.4	2538.4	0.4883	1	3	0.853	1	2008.9	2008.9	0.4784	1	3	0.862
Month	2	22397	11199	6.249	0.008	998		2	18768	9384.1	5.4654	0.003	995	
Tide	3	32421	10807	5.9633	0.001	999		3	35670	11890	6.3456	0.001	999	
Creek (Location)	2	10397	5198.5	2.7903	0.001	999		2	8398.2	4199.1	2.1301	0.006	997	
Location × Month	2	4422.6	2211.3	1.2339	0.358	999		2	3577.8	1788.9	1.0419	0.458	999	
Location × Tide	3	4365.5	1455.2	0.80295	0.68	998		3	4276.8	1425.6	0.76082	0.748	997	
Month × Tide	6	23034	3839	2.6898	0.001	996		6	26027	4337.8	2.9852	0.001	998	
Creek (Location) × Month	4	7168.3	1792.1	0.9619	0.535	998		4	6868	1717	0.87097	0.654	997	
Creek (Location) × Tide	6	10874	1812.3	0.97274	0.514	997		6	11243	1873.8	0.95049	0.583	997	
Location × Month × Tide	6	7861.4	1310.2	0.918	0.584	999		6	8350.5	1391.7	0.95777	0.546	999	
Creek (Location) × Month × Tide	12	17127	1427.3	0.76609	0.92	997		12	17437	1453.1	0.73711	0.969	997	
Residual	48	89427	1863.1					48	94625	1971.4				
Total	95	232030						95	237250					
Abundance (sample⁻¹)														
Location	1	4423.8	4423.8	1.3206	0.346	3	0.293	1	4384.5	4384.5	1.497	0.335	3	0.219
Month	2	21330	10665	6.2234	0.004	999		2	17265	8632.5	5.0643	0.01	997	
Tide	3	33799	11266	6.031	0.001	998		3	34244	11415	6.2851	0.001	999	
Creek (Location)	2	6699.7	3349.9	1.8168	0.036	998		2	5857.6	2928.8	1.4733	0.093	999	
Location × Month	2	4749.1	2374.5	1.3856	0.251	999		2	4081.9	2040.9	1.1973	0.347	997	
Location × Tide	3	5196.3	1732.1	0.92722	0.575	999		3	5354.2	1784.7	0.9827	0.506	999	
Month × Tide	6	22529	3754.8	2.62	0.001	997		6	26243	4373.8	2.9337	0.001	995	
Creek (Location) × Month	4	6854.7	1713.7	0.92943	0.561	999		4	6818.3	1704.6	0.85747	0.728	995	
Creek (Location) × Tide	6	11208	1868.1	1.0132	0.446	998		6	10897	1816.1	0.9136	0.64	999	
Location × Month × Tide	6	8882.7	1480.5	1.033	0.467	998		6	9739.9	1623.3	1.0888	0.354	998	
Creek (Location) × Month × Tide	12	17198	1433.1	0.77728	0.934	996		12	17891	1490.9	0.74998	0.965	996	
Residual	48	88502	1843.8					48	95419	1987.9				
Total	95	231370						95	238200					

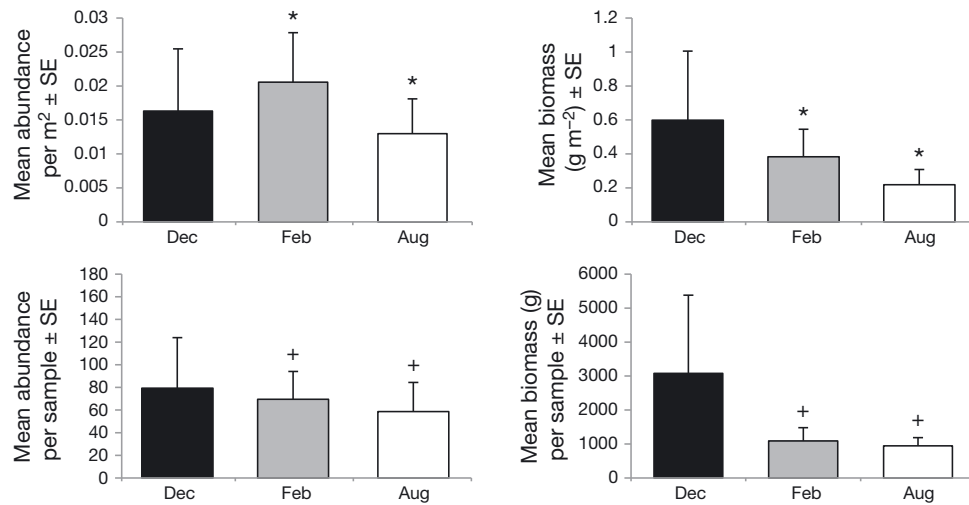


Fig. 4. Mean fish abundance and biomass per sample and per square metre (\pm SE) during different months (December 2011, February and August 2012) from intertidal mangrove creeks at Qeshm Island, Iran. Asterisks indicate significant differences between groups (February > August, $p < 0.05$). Plus symbols indicate differences existed at $p = 0.07$

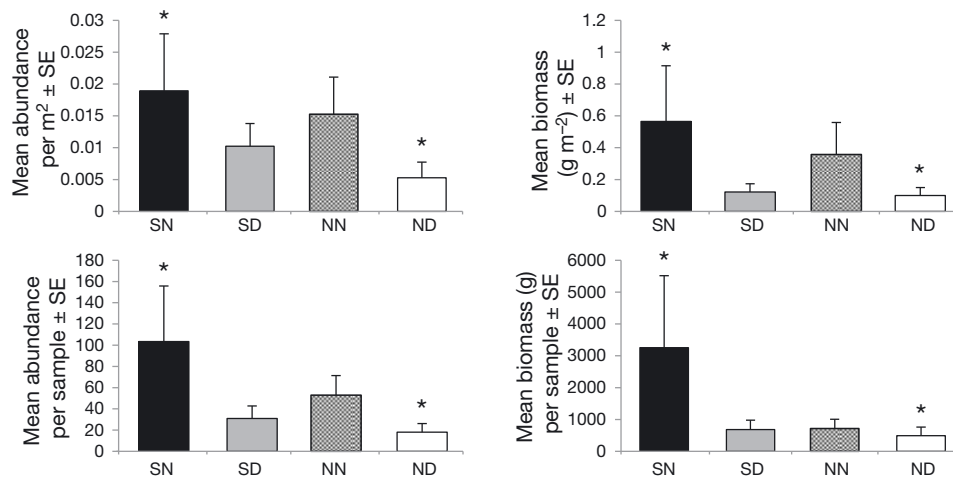


Fig. 5. Mean fish abundance and biomass per sample and per square meter (\pm SE) at different combinations of tidal-diel cycles: spring tide-night (SN), spring tide-day (SD), neap tide-night (NN), and neap tide-day (ND) from intertidal mangrove creeks at Qeshm Island, Iran. Asterisks indicate significant differences between groups (SN > ND, $p < 0.05$)

The results of the HOBO water level logger, operated in August, showed that the water temperature cooled during nightly low water and heated during the daytime low-water period, with higher daytime values at spring tide (up to 36°C) than at neap tide (33.5°C). Lowest water temperatures were measured during nightly neap tide low water (31°C; Fig. S7 in the supplement).

Stomachs of all 4 common fish species selected for study were generally 75 to 100% full on spring tide nights. Stomachs were fuller at night than during the day ($p < 0.05$). Stomachs at SN were fuller than at SD,

ND, and NN ($p < 0.05$). This indicates more successful feeding at night and also at spring tide. Stomach contents of *A. latus*, *P. kaakan*, and *L. johnii* consisted mostly of crabs, while the stomachs of *L. klunzingeri* were filled by sediment and algae (M. Shahraki unpubl. data).

DISCUSSION

Fish assemblages occupying Qeshm intertidal mangrove creeks are characterized by low species

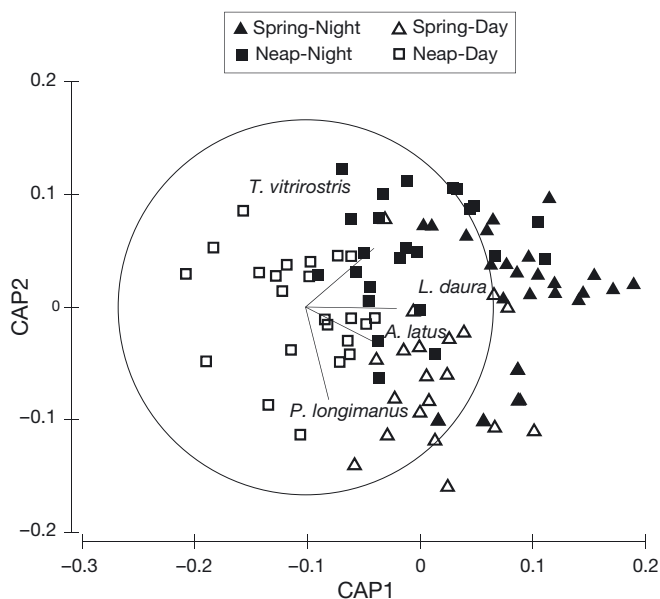


Fig. 6. Canonical analysis of principal coordinates (CAP) of Qeshm mangrove fish assemblages (biomass m⁻²) yielded 2 axes regarding the factor tide-time, with squared canonical correlations of $\delta_1^2 = 0.68$ and $\delta_2^2 = 0.40$. Symbols represent individual biomass values (g m⁻²), and vectors show individual species' correlations with the 2 CAP axes where $|r| > 0.4$. See Table 1 for full species names

diversity. The number of fish species in the mangrove intertidal creeks of Qeshm Island is lower than that in other comparable intertidal shallow water habitats of the Indo-Pacific (Table 3). In the Indo-Pacific, fish species richness varies from 29 in Iranian mangroves to 136 species in Malaysian and Thai mangroves

Table 3. Comparison of the number of species and families from mangroves in the Indo-West Pacific divided into 3 regions according to Duke et al. (1998): East Africa, Indo-Malesia and Australasia; studies sorted by descending year of study. NA: not available

Indo-West Pacific	Species	Species/ Family	Source
East Africa			
Tudor creek, Kenya	83	2.1	Little et al. (1988)
Tulear Lagoon, Madagaascar	60	1.7	Laroche et al. (1997)
Chwaka Bay, Zanzibar	44	1.6	Lugendo et al. (2007b)
Qeshm Island, Iran	29	1.3	Present study
Indo-Malesia			
Selangor, Malaysia	119	NA	Chong et al. (1990)
Luzon, Philippines	37	1.7	Rönnbäck et al. (1999)
Sikao Creek, Trang Province, Thailand	135	3.1	Tongnunui et al. (2002)
Sikao Creek, Trang Province, Thailand	89	2.9	Ikejima et al. (2003)
Australasia			
Solomon Islands	136	3.2	Blaber & Milton (1990)
Alligator Creek, Australia	128	2.9	Robertson & Duke (1990)
Embley River, Australia	55	1.8	Vance et al. (1996)

(Table 3 and references therein). The ratios of species to families also show the low diversity within families in the Persian Gulf and African mangroves (Table 3). In contrast, these values are high in the humid region Malaysian and Thailand mangroves. Overall the diversity of fish may be closely linked to the environmental conditions, e.g., the lack of fresh water and rainfall in the Persian Gulf as compared to the high precipitation in Southeast Asia. In Qeshm mangroves, the Mugilidae, Leiognathidae, and Engraulidae fish families dominate in terms of abundance. Mugilidae are also an abundant family in the shallow water intertidal habitats of Kuwait (Wright 1988, Wright 1989), indicating that mullets are dominant along the coast of the Gulf region. The dominance of Mugilidae is likely linked to the benthic algae and sediment-based food webs in this arid region (Shahraki et al. 2014).

Of the fish species found, 6 were resident and 23 were transient, so that most fish used Qeshm mangroves as a temporary habitat. In contrast, a study in Florida reported that residents may account for >90% of the species in mangroves (Ley et al. 1999). Ley et al. (1999) observed more resident species in winter when the water temperature was low. Therefore, the high water temperatures that prevail most of the year in this region might explain the low fish residency in Qeshm mangroves. Additionally, studies in the Indo-Pacific and western Atlantic have highlighted the effects of salinity in fish distributions and residency (Barletta & Blaber 2007). For example, in the Embley estuary in North Australia, where salinities are uniform and relatively high, marine immigrants (transients) dominate fish guilds. In contrast, most species are categorized as estuarine species (fresh water and marine stragglers) in the Caeté estuary in North Brazil, where a wide range in salinity gradients exists (Barletta & Blaber 2007, Barletta et al. 2008, Barletta & Saint-Paul 2010). In particular, these studies reported higher numbers of resident species during the wet season, when the salinity was very low. Thus, the environmental parameters salinity and temperature are among the main factors influencing fish residency and diversity in mangrove areas, reflecting the arid region of this study.

Seasonal variations in species richness were mostly due to the presence of more minor transient species, al-

though resident species from the family of Clupeidae were largely absent in summer. Most highly abundant species were found during all months. Overall, these seasonal patterns indicate the highest fish abundance and biomass in the cold winter months. The results contrast those of mangrove studies in the western Pacific Ocean (e.g. Australia and Taiwan), which found higher fish abundance in warmer seasons (Laegdsgaard & Johnson 1995) and higher fish diversity with increases in water temperature (Lin & Shao 1999). Because of the diverse results across regions, further research is needed regarding the seasonal patterns of mangrove fish distribution.

The numbers of species, abundance, and biomass were highest during nighttime spring tide inundations in Qeshm mangroves, even though lower numbers of all the top 12 species (relative abundance of >1%) were also present during the day. Especially the Mugilidae (*Liza klunzingeri*), Leiognathidae (*Leiognathus daura*), Engraulidae (*Thryssa vitirostris*), Haemulidae (*Pomadasys kaakan*), and Lutjanidae (*Lutjanus johnii*) dominated spring nighttime samples. The high nighttime dominance of these species might be related to the feeding strategy of some of these fish, as reported by Nagelkerken et al. (2000) and Ley & Halliday (2007). In Australia, diel variations in subtidal mangrove fish assemblages are related to the nocturnal activities of benthic fauna, which, in turn, attract nocturnal fish (Ley & Halliday 2007). The diel cycle is the major rhythm associated with short-term changes in nocturnal Haemulidae and Lutjanidae in non-estuarine systems of the Caribbean Sea (Nagelkerken et al. 2000). Moreover, the temporary nature of most species combined with the stomach fullness index of selected species indicates that the fish migrate to Qeshm Island mangroves to feed under nighttime high-water conditions. Qeshm Island presents mangroves where much larger intertidal areas are inundated at spring than at neap tides. Larger inundation areas during spring tides enable fish to access intertidal forest rich in prey resources that are not available during inundations at neap tides. Other studies also reported that fish from adjacent habitats, such as mud flats and seagrass beds, migrate into the mangroves during high tides to feed (Vance et al. 1996, Sheaves & Molony 2000). Also, for those transient species with a relative abundance of <1% that migrate to mangroves on nighttime spring tides, the higher water level might facilitate the movements of these species to the creeks, with fish relying on tides for transport (Davis 1988). Overall, however, nighttime rather than tide level (spring vs. neap) seemed more important for fish use of man-

groves, because even though daytime inundations were deeper and longer lasting than nighttime inundations in Qeshm mangroves (Fig. S6a), fish abundances were almost always lower during the day. These seasonal and diel observations may indicate causal relationships between temperature and fish assemblage structure, and would need further physiological study and modeling for a better understanding of temperature effects on fish use of mangroves.

This work provides the first evidence of the influential role of month on patterns in fish distributions from a low-rainfall mangrove system. The fact that the distributions were not consistent between months further emphasizes the importance of water temperature in the structuring of mangrove fish assemblages at Qeshm Island (Shahraki & Fry 2015). Similarly, fish habitat use of the intertidal area of Australian mangroves is a function of both month and tidal cycle (Wilson & Sheaves 2001). Tides are an important factor structuring fish assemblages in many mangroves worldwide (e.g. Vance et al. 1996, Laroche et al. 1997, Ellis & Bell 2008). These studies show significant separation of spring and neap tide effects on fish assemblages, either per sample or per area basis. For example, greater fish abundance per sample was detected during spring tides in mangroves in Madagascar (Laroche et al. 1997). Likewise, in the macrotidal mangroves in northern Brazil, catch weight of fish (per sample) entering intertidal mangrove creeks was highest during spring tides (Krumme et al. 2004). On the other hand, a study reported more biomass per area of the shrimp *Penaeus merguensis* at high tide in northern Australian mangroves (Vance et al. 1996), and Ellis & Bell (2008) found higher mean numbers of fish at high water per minute in video recordings in mangroves in Florida. Most of these observations were made in mangroves exposed to high precipitation, and there are only few studies of tidally influenced shallow water habitats in low-rainfall systems (Abou-Seedo et al. 1990, Wright et al. 1990). High-frequency trawls on a non-estuarine mud flat in Kuwait Bay showed the significant influence of tidal stage on fish assemblages (Wright et al. 1990). Also, catches were greater during both day and night on falling tides than on rising tides for the intertidal mudflat of the Gulf region (Abou-Seedo et al. 1990). Our results also emphasized the role of tide and diel cycles in shaping the distributions of intertidal mangrove fish assemblages in the low-rainfall system of the Persian Gulf.

Lastly, results showed no spatial differences in fish distribution patterns with respect to creek elevation and size. Fish habitat use was equal across all creeks

on a per area basis, with the larger Creeks 2 and 3 having more fish because of their larger areas. Also, there was little species difference that could be attributed to creek size; only some resident species (*S. gibbosa* and *S. argus*) were more dominant in Creeks 2 and 3. These results contrast those of Desmond et al. (2000), who found that the smallest intertidal creeks were dominated by resident gobiids and cyprinodontids in the salt marshes of southern California (Desmond et al. 2000). Also, a study in salt marshes revealed that broader creeks, with long-lasting inundation, supported the greatest use by fish (Allen et al. 2007). Because of these similarities and differences across studies, further research is needed to understand the habitat use of resident species of particular creeks.

CONCLUSIONS

The study generally agreed with previous work, showing greater fish use of intertidal mangrove habitats during nighttime spring tides when temperatures were cooler and foraging success was high. However, there were 2 unexpected findings in this study of arid Iranian mangrove systems. First, most fish species were transient rather than resident. This may be due in part to the stressful environmental conditions of the relatively high summer temperatures at this northern edge of the mangrove distribution in the western Indian Ocean. Secondly, in the February winter samples, relatively low fish biomass was observed in all samples and the highest numbers of fish occurred during nighttime neap rather than during nighttime spring tides. This high occurred when the fish assemblage was most resident, so that future studies should probably carefully separate resident and transient species when evaluating mangrove creeks as fish habitat.

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