

Fish Community Structure and Food Web
Dynamics in Low Rainfall Mangrove and
Non-mangrove Ecosystems
(Persian Gulf)



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**Fish Community Structure and Food Web Dynamics in
Low Rainfall Mangrove and Non-mangrove
Ecosystems (Persian Gulf)**

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ABSTRACT

Mangroves are considered as an important source of nutrition to aquatic consumers, which, in return, sustain the fish population. However, there is still controversy about the importance of mangroves to fish communities, and furthermore, not all mangroves fulfill every function ascribed to them. The Persian Gulf presents the northernmost mangroves in the Indo-Pacific region, thriving under extreme environmental conditions such as very low rainfall and high salinities. Very few studies have addressed fish distribution patterns of mangroves in this arid region.

The main objective of this study is to describe and compare the fish community structure and food web dynamics of mangrove and non-mangrove intertidal creeks in a low-rainfall system in Qeshm Island, Persian Gulf, Northern Indian Ocean (26.8°N, 55.75°E). Therefore, this thesis addresses temporal changes in mangrove fish assemblages related to the tidal and diel cycles in the meso-tidal mangrove of Qeshm Island. Also, the food web's dynamics were studied to determine the role of mangroves in fish food webs. Moreover, due to the arid climate along the northern Indian Ocean, many neighboring creeks are devoid of mangroves but still provide habitat for fish. This provided the necessary conditions for a natural experiment to compare fish assemblage structures and trophic diversity between creeks that are mangrove lined, and creeks without mangroves across seasons. For that, fish were collected with respect to the different combinations of tidal amplitude (and lunar phase) and day light conditions as well as seasons (winter, summer). Also, various potential food sources were collected for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ measurements from both habitats across seasons.

The findings show the impact of environmental variables (e.g. tide and temperature) in structuring fish assemblages in Qeshm intertidal creeks. The interaction between tide and time of day emerged as an important factor in organizing mangrove fish assemblages in this meso-tidal arid region. The highest fish biomass, abundance, and diversity were observed during spring tide night. High inundation during spring tides coinciding with the darkness provided the most favorable conditions for fish. When mangrove fish communities were compared with the non-mangroves, seasonality appeared as a more important factor than habitat. Extreme summer water temperatures ($>33^\circ\text{C}$) likely limit the fish abundances and biomass. Fish assemblages of mangrove and non-mangrove intertidal creeks were equally diverse and dominated by the same fish families (e.g. Mugilidae). Small-sized fish dominated

catches in both habitats. Also, there were no consistent differences in fish abundance and biomass for mangrove vs. non-mangrove fish collections. Community trophic diversity, measured with size-corrected standard ellipse areas (SEA_c), also showed no significant difference across habitats. Instead, strong seasonal patterns were observed for the food sources and fish communities isotopic niche sizes. These findings demonstrate that the structuring effect of seasonality is more important than habitat in determining the fish distribution patterns in this region.

Mangrove-derived organic matter contributed to a maximum of 36% to the fish tissue, whereas organic matter produced by microphytobenthos and plankton plays a major role in the diets of the most abundant fish species, with contributions of 64 - 100%. Thus, the fish food web's support of mangrove and non-mangrove intertidal creeks seems to be energetically driven by pelagic and benthic food pathways in this study area. Furthermore, the dominance of detritivores in both mangrove and non-mangrove intertidal creeks suggests the importance of benthic food webs in the intertidal creeks at Qeshm Island.

The outcomes of this dissertation contribute to the global understanding of the importance of mangrove and non-mangrove intertidal creeks for fish food webs and fisheries support in a low-rainfall coastal ecosystem. The findings imply some potentially interesting consequences on habitat conservation and indicate that the abundance of small fish is not always higher in complex vegetation. Like mangrove creeks, the bare creeks are utilized by a wide variety of fish, suggesting greater attention should be drawn to these habitats.

Keywords Fish community structure, rainfall, tidal and diel cycles, food webs, trophic diversity, isotopic niche size, mangrove, non-mangrove, intertidal creeks, Qeshm Island, Persian Gulf, Western Indian Ocean

ZUSAMMENFASSUNG

Mangroven werden als wichtige Nahrungsquellen für aquatische Konsumenten angesehen, welche ihrerseits als Nahrungsgrundlage für Fischpopulationen dienen. Die Bedeutung von Mangroven für Fischpopulationen ist jedoch noch nicht abschließend geklärt, und nicht jedes Mangrovensystem erfüllt alle Funktionen die ihm zugeschrieben werden. Entlang der Küstengebiete des Persischen Golfes findet man die am weitesten im Norden gelegenen Mangrovensysteme des Indo-Pazifiks, die dort unter z.T. extremen Umweltbedingungen, wie z.B. geringem Niederschlag und hohem Salzgehalt, gedeihen. Gerade für diese Gebiete mangelt es an Untersuchungen zur Bedeutung von Mangrovensystemen für die lokalen Fischpopulationen.

Das Ziel dieser Arbeit ist die Beschreibung der Struktur und Dynamik von Fischgemeinschaften und der lokalen Nahrungsnetze in Gezeitenpriele mit und ohne Mangrovenbewuchs der durch ein arides Klima geprägten Insel Qeshm, Persischer Golf, Nördlicher Indischer Ozean (26.8°N, 55.75°E). Ihr Fokus liegt auf der Untersuchung der Einflüsse von Gezeiten- und Tag-Nacht-Zyklen auf die Zusammensetzung von estuarinen Fischgemeinschaften. Des Weiteren wurde die Dynamik lokaler Nahrungsnetze untersucht, um die Rolle von Mangroven in Nahrungsnetzen der Fische besser deuten zu können. Durch das aride Klima sind viele der Gezeitenpriele ohne Vegetation, fungieren aber dennoch als Habitat für verschiedene Fischarten. Das Vorkommen von Gezeitenpriele mit und ohne Mangrovenbewuchs ermöglichte die Durchführung eines natürlichen Experimentes, um den Einfluß der Vegetation auf die Struktur der Fischgemeinschaften und die trophische Diversität während verschiedener Jahreszeiten zu untersuchen. Die Probenahmen für $\delta^{13}\text{C}$ - und $\delta^{15}\text{N}$ -Messungen der Fische und ihrer potentiellen Nahrungsquellen berücksichtigten mögliche Einflussfaktoren wie Gezeiten und Tidenhub (und Mondphasen) sowie Tageslichtbedingungen und Jahreszeiten (Winter, Sommer). Die Proben wurden aus den bewachsenen und unbewachsenen Habitaten während der Winter- und Sommermonate genommen, um anschließend Nahrungsnetze mittels der stabilen Isotopenverhältnisse zu ermitteln.

Die Ergebnisse der vorliegenden Studie zeigen den Einfluss von Umweltfaktoren (z.B. Tide und Temperatur) auf die Strukturierung von Fischgemeinschaften in Gezeitenpriele der Insel Qeshm. Insbesondere die Wechselwirkung zwischen Tide und Tageszeitpunkt erwies sich als wichtiger Faktor für die Zusammensetzung der mangrovenbewohnenden Fischgemeinschaften in dieser

meso-tidalen, ariden Region. Die höchsten Werte an Biomasse, Abundanz und Diversität von Fischen wurden während nächtlicher Springtiden festgestellt. Beim Vergleich der Fischgemeinschaften erwies sich die Saisonalität als stärkerer Einflussfaktor als die Unterscheidung der Gezeitenpriele mit und ohne Mangrovenbewuchs. Extreme Wassertemperaturen im Sommer ($> 33^\circ$) sind wahrscheinlich ein limitierender Faktor für die Fischabundanz und -biomasse. Die Artenvielfalt der Fischgemeinschaften war ähnlich in Gezeitenpriele mit und ohne Mangrovenbewuchs und es dominierten jeweils Arten aus denselben taxonomischen Familien (z.B. Mugilidae). Fische mit kleinen Körpergrößen dominierten die Fänge in beiden Habitattypen. Auch bezüglich Fischabundanz und -biomasse zeigten sich keine deutlichen Unterschiede zwischen beiden Habitaten. Die trophische Diversität der Gemeinschaften, welche mittels größenkorrigierten Standardellipsenflächen ("standard ellipse areas", SEAc) ermittelt wurde, unterschied sich nicht signifikant zwischen beiden Habitattypen. Allerdings wurden ausgeprägte saisonale Muster für Fischgemeinschaften und Nahrungsquellen in ihren trophischen Nischen, basierend auf Isotopenmessungen, sichtbar. Dies verdeutlicht, dass für die Strukturierung der Fischgemeinschaften in dieser Region die Saisonalität der entscheidende Einfluss ist und nicht die Unterscheidung der Habitate.

Organisches Material mit Ursprung aus Mangrovensystemen machte bis zu 36 % des Fischgewebes aus. Deutlich größer war jedoch der Anteil von organischem Material, das sich auf Mikrophytobenthos und Plankton zurückführen ließ (64-100 % des Gewebes). Die Nahrungsnetze beider Habitattypen (mit und ohne Mangroven) erscheinen somit energetisch durch pelagische und benthische Pfade bestimmt. Die Dominanz detritivorer Fische in bewachsenen wie unbewachsenen Gezeitenpriele unterstreicht die Wichtigkeit benthischer Nahrungsnetze in den Gezeitenpriele entlang der Insel Qeshm.

Die Ergebnisse der vorliegenden Dissertation tragen zum globalen Verständnis der Bedeutung mangrovenbewachsener und -unbewachsener Gezeitenpriele für Fischgemeinschaften und ihre Nahrungsnetze in regenarmen küstennahen Ökosystemen bei. Die Resultate lassen Rückschlüsse auf potentiell interessante Konsequenzen in Bezug auf den Schutz natürlicher Lebensräume zu und zeigen auf, dass die Abundanz kleiner Fische in Habitaten mit komplexer Vegetation nicht zwangsläufig höher ist. Priele mit Mangrovenbeständen werden ebenso wie Priele ohne Mangrovenbestände von einer Vielzahl verschiedener Fische genutzt. Dies legt

nahe, dass letztgenannte Habitate verstärkt in den Fokus wissenschaftlicher Untersuchungen gerückt werden sollten.

Stichwörter Struktur von Fischgemeinschaften, Niederschlag, Tidenzyklen, Tagesgang, Nahrungsnetze, trophische Diversität, isotopische Nischengröße, Mangroven, Gezeitenpriele, Insel Qeshm, Persischer Golf, westlicher Indischer Ozean

CHAPTER I

General Introduction



Mangroves function and distribution

Mangrove forests are predominantly intertidal habitats that occur along sheltered and shallow water coastlines in the tropics and subtropics (FAO 2007), comprising a worldwide area of 137,760 km² in the year 2000 (Giri et al. 2011). Mangroves fulfill important socio-economic and ecological functions such as aquaculture and protection against shoreline erosion (Hogarth 1999; Walters et al. 2008). Mangroves are considered to be highly productive ecosystems with high rate of primary production, harboring high species diversity and thus complex food webs (Manson et al. 2005; Nagelkerken et al. 2008; Alongi 2014). Observation of high abundances of juvenile fish in mangrove have supported the idea that they are a valuable nursery habitat (Robertson and Duke 1987; Laegdsgaard and Johnson 1995; Nagelkerken 2009). Structural complexity, reduced predation pressures and abundant food have been hypothesized to explain the high abundances of the fish in mangroves (Robertson and Blaber 1992; Blaber 2000; Laegdsgaard and Johnson 2001). 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 remain under threat for the same reasons (Alongi 2002).

Mangrove species and forest structure vary with location and climate, ranging from the extremely arid coast of the Persian Gulf to the cool-temperate coast of southern Australia, to the wet equatorial coast of Asia, Africa and Latin America (Robertson and Alongi 1992; Sheaves 2005). Mangroves are divided into two global hemispheres: the Indo-West Pacific (IWP), with highest species diversity, and the Atlantic East Pacific (AEP) with four times less mangrove species diversity compared to IWP (Fig. 1) (Duke et al. 1998).

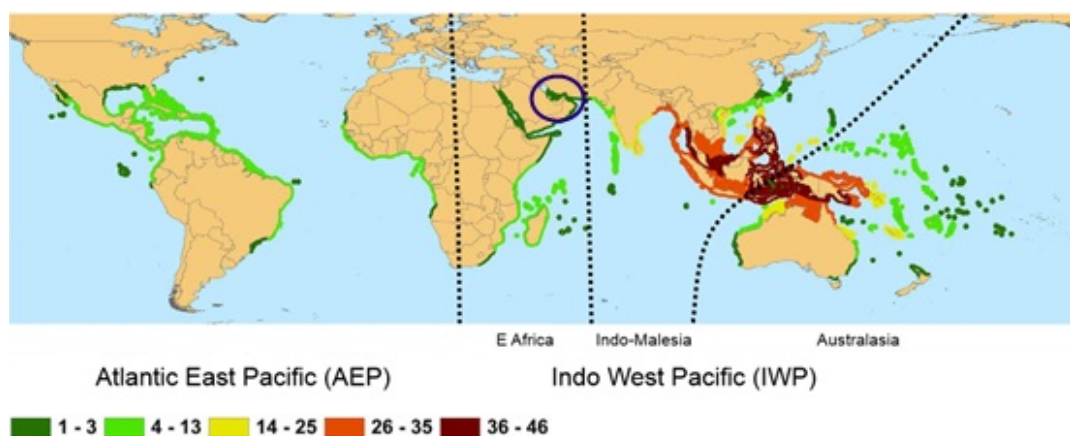


Figure 1 Distributions of mangrove forest (species); Modified from Duke et al. (1998) and Polidoro et al. (2010). Mangroves in the Persian Gulf are shown in circle.

The ecological role of mangroves is varied among regions and is constrained by environmental variables, thereby not all mangrove types fulfill every function ascribed to them (Ewel et al. 1998; Twilley and Day 1999; Faunce and Serafy 2006). Existing knowledge on mangrove fish is mostly from Australia, North and Latin America and South Asia and to a lesser extent from Africa (Faunce and Serafy 2006; Sheaves 2012; Blaber 2013). IWP mangroves are a subset of three regions, highly variable in climate, comprising East Africa, Indo-Malesia and Australasia (Duke et al. 1998). The Persian Gulf region is located in the East African region (Fig. 1). It is the northern edge of mangrove distribution in the Indian Ocean. Mangroves in the Gulf region are subject to extreme conditions such as very low rainfall and high salinities (Al-Khayat and Jones 1999) which restrict the mangrove species in this area to one species, *Avicennia marina*, although possibly one or two more species occur in some locations (Sheppard et al. 2010). The harsh environment may influence the functionality of mangroves as a fish habitat in this region. To date, little is known about mangrove habitat use by fish in the meso-tidal coast of the Persian Gulf. There is scarcity of knowledge in this area in terms of variables controlling for fish distribution patterns and food webs support in mangrove ecosystems, indicating that there is a need to study the dynamics of fish communities in relation to environmental variables and food sources in this low-rainfall system at Qeshm Island, Iranian coast of the Persian Gulf (26.8°N, 55.75°E).

Drivers of structural changes in fish communities

Variations in fish communities in mangrove habitats have been shown to be dynamic on a variety of temporal scales. Many variables such as abiotic parameters, prey availability, and predation avoidance have been suggested to determine the structural changes in fish assemblages (Blaber 2000; Laegdsgaard and Johnson 2001). However, the importance of these factors to the fish population is variable among systems (Blaber and Blaber 1980; Faunce and Serafy 2006).

On tidal coasts, fish have to deal with variations in habitat availability due to tidal fluctuations (Quinn and Kojis 1987; Rooker and Dennis 1991). Mangrove fish of tidal coasts regularly move between high water level foraging and low water level resting sites and the interaction between tide and diel cycle may cause significant changes in fish assemblage composition (Krumme 2009). In the Caribbean, where tidal ranges are small, only a few fish species respond to changes in water level (Ellis and Bell 2008) and the diel cycle is the major rhythm driving short-term changes in

mangrove fish assemblages (Nagelkerken et al. 2000). In Indo-Pacific mangroves, where the tidal range is greater than the Caribbean, fish assemblages are affected by the interactive influence of the tidal and diel cycle (Laroche et al. 1997; Wilson and Sheaves 2001). While tidal variations cause structural alteration in the fish assemblages in the tidally-influenced mangroves, other environmental variables such as salinity and rainfall (Sheaves 1998; Barletta et al. 2005) and water temperature (Lin and Shao 1999) have been also documented as main drivers structuring fish assemblages in different ecoregions. Salinity might have less deterministic influence on organizing fish assemblages in the African mangroves, except during the rainy season, compared to the Brazilian mangroves (Lugendo et al. 2007; Barletta and Saint-Paul 2010). Also, a combination of salinity and water temperature have been viewed as a main factor affecting mangrove fish assemblages in the Indo-Pacific region (Lin and Shao 1999). Arid mangroves of the Persian Gulf are influenced by meso-tides, and are characterized by a high seasonal water temperature fluctuation (Sheppard et al. 2010). Therefore, tidal changes in the water level may influence fish distribution patterns in the intertidal creeks in the Persian Gulf. In addition, the extreme seasonal temperature difference might organize the dynamics of the fish community in this region (Chapters II and IV).

Habitat types and food availability are also known to partially shape the structure of fish assemblages (Hajisamae et al. 2003; Akin and Winemiller 2006). High fish abundance in mangroves has been attributed to the diversity and availability of food sources in this habitat (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). The use of mangrove litter has been observed to be minor compared to other primary producers by invertebrates and fish communities, e.g. in African mangroves (Nyunja et al. 2009; Igulu et al. 2013), suggesting that mangrove derived resources are not important to these intertidal communities. This might affect the dynamics of the fish community and the mangrove-associated fisheries. Therefore, a combination of community descriptors and isotopic niche estimates represents a more holistic approach to determine the habitat use and function of mangroves for fisheries in the arid coast of Persian Gulf (Chapter IV).

Food web dynamics in mangrove ecosystems

Studying food webs is important to determine the feeding relationships among organisms in aquatic ecosystem and the influence of community structure and trophic interactions on ecosystem functioning. Early food web studies used conventional techniques such as gut content analysis, which provide relatively high resolution of prey items ingested by a consumer but only reveal a snapshot of the consumer's diet within the last few hours (Hyslop 1980). Over the last decades, stable isotope analysis has emerged as an useful tool to investigate food web connections (Peterson and Fry 1987; Fry 2006), with the aim to describe animal diet and identify the main sources of energy for the consumers (Nyunja et al. 2009; Vaslet et al. 2012) and to track the source of organic matter through the ecosystem (Bouillon et al. 2000; Bouillon et al. 2009). Carbon and nitrogen stable isotope analyses provide insights into the food sources assimilated by a consumer in the preceding weeks to months (Gearing 1991), although it cannot offer the taxonomic resolution. Carbon isotopes offer insights into the sources of organic matter for consumers, whereas nitrogen isotopes can indicate trophic levels (Pinnegar and Polunin 1999; McCutchan et al. 2003; Melville and Connolly 2003). Enrichment of stable isotopes occurs with trophic transfers and is about 0 to 1.3‰ for carbon and 2.0 to 3.5‰ for nitrogen (DeNiro and Epstein 1978; Fry and Sherr 1984; Post 2002). However, these values have shown high variability with regard to taxonomic classes, specific tissues, habitat, protein quality of the diet, life-history level and other factors (e.g., Caut et al. 2009; Robbins et al. 2010; Boecklen et al. 2011), and recent stable isotope studies suggest ^{13}C fractionations maybe higher than commonly assumed (Herbon and Nordhaus 2013; Bui and Lee 2014).

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. There have been several attempts to compare interlinked mangrove, seagrass, and mudflat food webs through stable isotope analysis that have highlighted the low importance of mangrove litter as food source for fish (Marguillier et al. 1997; Kruitwagen et al. 2010; Igulu et al. 2013). Also, in a low-rainfall system of Gulf region, mangroves were an insignificant source of nutrition for benthic and epi benthic invertebrates and only one endemic shrimp species relies on mangrove leaves throughout its post settlement life cycle (Al-Maslamani et al. 2012; Al-Maslamani et

al. 2013), but fish food web dynamics has not been studied in the Iranian mangroves (Chapter III).

Objectives and structure of thesis

The specific implementation of the content of this dissertation was developed by Maryam Shahraki, with advice and scientific guidance by Professor Saint-Paul. The overall objective of this thesis is to describe fish community structure and food web dynamics in two different ecosystems (mangrove and non-mangrove intertidal creeks), of the Persian Gulf, Iran. Thus, this study is aimed at better understanding of the role of environmental variables and food sources in the dynamics of the fish community and food web fisheries support in low-rainfall coastal ecosystems by addressing the following questions:

1. What is the fish assemblage composition found in the intertidal mangrove and non-mangrove creeks of Qeshm Island?
2. How do the interaction of tide (spring-neap) with the diel cycle affect the structure of the intertidal mangrove fish assemblage?
3. Do food sources in the two habitat types (mangrove vs. non-mangrove) differ in isotopic compositions?
4. Do fish rely on different food sources in winter and summer?
5. What are the main food pathways for fish in mangrove vs. non-mangrove sites?
6. What is the importance of mangroves in supporting fish food webs?
7. Is the fish assemblage structure similar across habitats (mangrove vs. non-mangrove) and seasons?
8. Do the fish have similar isotopic niche size across habitats and seasons?

Hence, three studies were designed and implemented, corresponding to the three data chapters of this thesis. **Chapter II** was focused on temporal changes in mangrove fish assemblages related to tidal and diel cycle in a meso-tidal mangrove area of Qeshm Island. In **Chapter III**, carbon and nitrogen compositions of a wide range of food sources and fish were analyzed across habitats and seasons to determine the main food pathways for fish and to identify the importance of mangroves in supporting fish food webs. Also, identifying trophic pathways based on stable isotope analyses can sometimes be problematic, i.e., when multiple sources exist (as is the common case), there is usually no unique solution indicated from the tracer information. Therefore, in this chapter, a well-recognized way to evaluate

underdetermined systems was used by focusing on minimum and maximum estimates rather than on means, medians or other parameters or model-generated distributions of solutions. **Chapter IV** showed whether mangroves enhance fisheries in the low-rainfall system by comparing the community-level fish diversity, abundance, biomass and trophic diversity across habitats and seasons.

Also two new concepts are profiled in this thesis:

1- The fish abundance and biomass comparisons are made on both a per m² basis and on a per sample basis, with the per m² comparisons more appropriate when fish are resident, and the per sample comparisons more appropriate when fish are transient. We consider comparisons ecologically robust when significant differences are found in parallel and significant for both ways of expressing the data (e.g., results are considered ecologically robust when abundance is higher both on a per m² basis and also on a per sample basis). Alternatively, if abundance (or biomass) results are not parallel and significant when expressed on a m² and a per sample basis, results are not considered ecologically robust (Chapters II & IV).

2- Fish and food standard ellipse areas (SEA) values are calculated from isotope values to describe food use and availability. Higher SEA values for fish communities indicate a broader use of foods, and higher SEA values for foods indicate a wide diversity in food values. A ratio of these fish/food SEA isotope values is used to test whether fish communities expand in isotope space just following food isotopes, or whether there is genuine expansion of food use by fish, once changes in food isotopes are taken into account. This approach seems to be a valuable first approach reinforcing the conclusions reach on the basis of fish-only SEA estimates (Chapter IV).

List of manuscripts and contribution of authors

Manuscript I

Shahraki, M., Saint-Paul, U. (submitted) Tidal induced changes in intertidal mangrove fish assemblages (Qeshm Island, Persian Gulf).

Conceived and designed the experiments: MS and USP. Performed the experiments: MS. Analyzed the data: MS. Wrote the paper: MS. Provided feedback on different versions of the manuscript: USP.

Manuscript II

Shahraki, M., Fry, B., Krumme, U., Rixen, T., 2014. Microphytobenthos sustain fish food webs in intertidal arid habitats: A comparison between mangrove-lined and un-vegetated creeks in the Persian Gulf. *Estuarine, Coastal and Shelf Science* 149, 203-212.

Conceived and designed the experiments: MS and TR. Performed the experiments: MS. Analyzed the data: MS, BF. Wrote the paper: MS. All the coauthors read the different versions of the draft.

Manuscript III

Shahraki, M., Fry, B. (submitted) Seasonal fisheries changes in low-rainfall mangrove ecosystems.

Conceived and designed the experiments: MS. Performed the experiments: MS. Analyzed the data: MS and BF. Wrote the paper: MS and BF.

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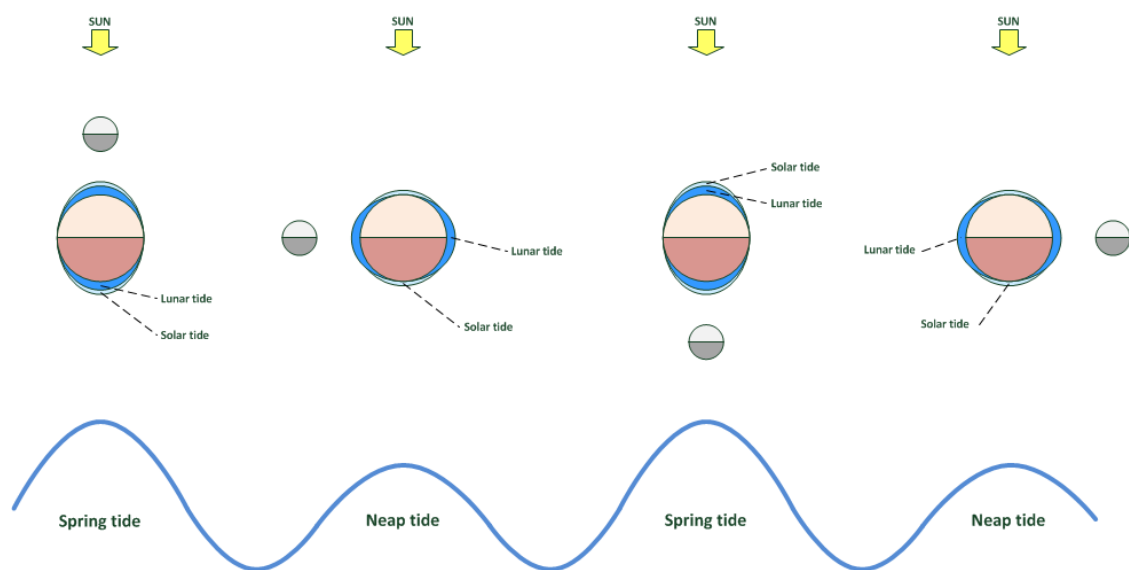
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CHAPTER II

Tidal Induced Changes in Intertidal Mangrove Fish Assemblages (Qeshm Island - Persian Gulf)



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ABSTRACT

Fish distribution patterns in relation to the tidal cycle is relatively unstudied in the Persian Gulf. We investigated the role of temporal variations and creek topography 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 tide-time of day combinations and month in intertidal fish assemblage structure. The fish assemblage (29 species) was dominated by Mugilidae (catch mass: 62%, abundance: 41%). The number of species was significantly influenced by tide-time of day interactions and was highest during nightly spring tide inundations, although the most abundant species occurred in all creeks and months. Temporal variations in fish abundance and biomass were a function of specific tide and time of day combinations, and high fish abundance and biomass were observed during spring tide night. However, inconsistent monthly and creek-level patterns in fish abundance and biomass per sample and per m² were not considered ecologically robust. Combined results from PERMANOVA and CAP confirmed that tide-time of day drove changes in the structure of intertidal fish assemblage. Variations in fish assemblage structure were closely related to changes in water temperature and high water level. High inundation during spring tide coinciding with the darkness and cool water temperature provided favorable condition for fish. These findings emphasize the importance of tidal and diel cycle for fish habitat use in mesotidal mangroves in this low-rainfall ecosystem, and highlight that spring tides provide fish with greater accessibility to intertidal habitats.

Key words Intertidal mangrove creeks, fish community, tidal cycle, Persian Gulf, Western Indian Ocean

INTRODUCTION

Mangroves in the Persian Gulf are at the northern edge of mangrove distribution in the Indian Ocean. They thrive under extreme conditions and are subjected to very low rainfall and high salinities (Al-Khayat and Jones 1999). This harsh environment restricts mangrove diversity to two species in this arid region (Duke et al. 1998). Worldwide, mangroves are considered important habitat for fish (Robertson and Duke 1990; Sasekumar et al. 1992). However, change in environmental variables causes structural alteration in the dynamics of fish assemblages and consequently the importance of the mangroves to fish population among systems. Despite the socio-economic importance of mangrove forests in terms of associated fisheries, little is known about the dynamics of fish assemblages in relation to the environmental variables in the mesotidal coast of the Persian Gulf.

Many variables such as environmental attributes, prey availability and predation avoidance have been suggested to determine fish habitat use of intertidal mangrove creeks (Blaber 2000; Laegdsgaard and Johnson 2001). But the relative importance of different environmental factors is variable among the biogeographical regions (Blaber and Blaber 1980; Blaber 2002). Mangroves in meso/macro tidal coasts are inundated and exposed by the alternating tidal cycle, and fish have to cope with variations in habitat availability (Quinn and Kojis 1987; Rooker and Dennis 1991). In the Caribbean, where tidal ranges are small, only few fish species respond to changes in water level (Ellis and Bell 2008) and the diel cycle is the dominant rhythm driving short-term changes in mangrove fish assemblages (Nagelkerken et al. 2000). Indo-West Pacific mangroves, where the tidal range is large, fish accessibility to mangroves is limited to periods of intertidal inundation (Wilson and Sheaves 2001; Weis et al. 2009). On coasts with larger tidal ranges, fish exploit temporarily accessible habitats via tidal movements (Gibson 2003). Given the fact that the coasts of Persian Gulf are subjected to mesotides, the regular changes in the water level may cause significant variance in mangrove associated fish fauna as is known from other tidally-influenced shallow water habitats of Kuwait Bay (e.g. Abou-Seedo et al. 1990; Wright et al. 1990). High-frequency trawls on a non-estuarine mud flat in Kuwait Bay showed the strong influence of tidal condition on fish assemblage (Wright et al. 1990). In the western Indo-Pacific, only few studies have examined how non-estuarine mangrove fish assemblages are affected by the interactive influence of the tidal cycle. Laroche et al. (1997) found strong lunar, tidal and diel interactions in a fish assemblage in a

semiarid mangrove in Madagascar (Laroche et al. 1997). How mesotides affect intertidal mangrove fish assemblage structure, however, are still lacking for Gulf mangroves communities.

Water height and flooding frequency are important factors that influence fish composition and abundance in mangroves that are drained at low tide (Davis 1988; Laegdsgaard and Johnson 1995). Along the Iranian coast of the Persian Gulf, generally intertidal mangrove creeks are flooded during the high tide and become completely exposed at low tide. However, intertidal creeks can be located on differing topographic levels in a coastal plateau which affect the time of inundation during high water. Thus, it is important to understand the role of the attributes of a creek, i.e. relative height in the coastal plain, on fish habitat use in this region.

Mangroves in the Persian Gulf have been neglected with respect to studies of fish population dynamics, and there is a need to assess the role of the mangrove habitat for fisheries in this arid system. This study aimed to examine, for the first time, temporal patterns of mangrove creek fish assemblage structure in the mesotidal coast of Qeshm Island, Iran. Therefore, this paper addressed: (i) the taxonomic composition of the intertidal mangrove fish fauna in this arid region, (ii) tidal and diel related patterns on the structure of fish assemblages considering the relative height of the creek in the coastal plain. Therefore, this study compliments a previous study in the area assessing resource use, by contributing to the understanding of fish community patterns in relation to changes in the abiotic variables. Furthermore, we hypothesized that number of fish species, abundance and biomass differ in accordance with the interaction of tide and time-of-day in mangrove intertidal creeks.

MATERIALS AND METHODS

Sampling sites

The study was carried out at Qeshm Island, Iranian coast of 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 creek use in relation to the tidal cycle. Creeks 2 and 3 were situated at a lower topographic level and were larger in size (low-lying creeks) than Creeks 1 and 4. Creeks 1 and 4 were located at a slightly higher topographical level of the intertidal plateau and were smaller and shorter (high-lying creeks) (Fig. 1 and Fig. S1). High-

lying creeks were smaller and have a lower flooding frequency resulting in a reduced time allowance for intertidal visitors than low-lying creeks.

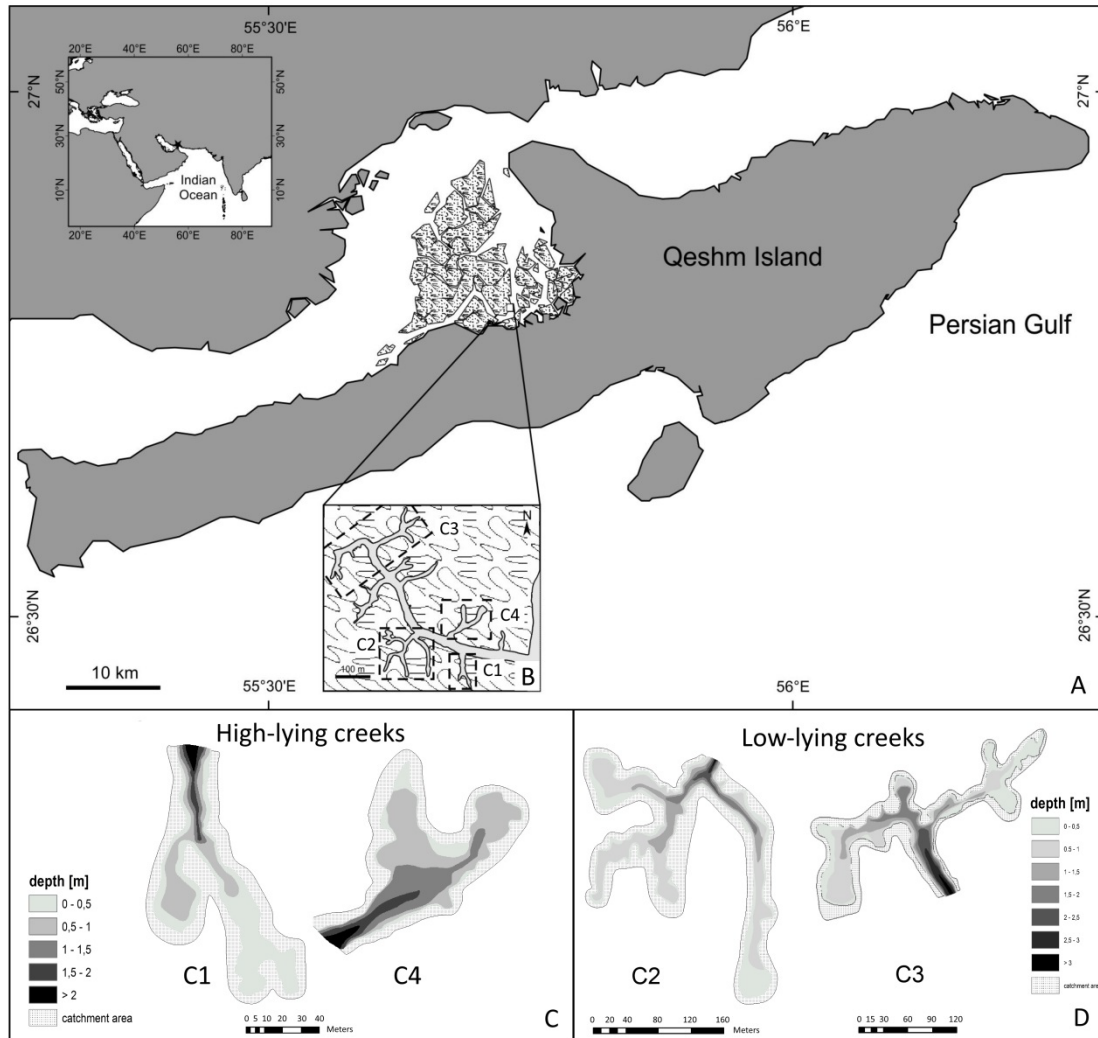


Figure 1 Location of the study area in Qeshm Island, Strait of Hormuz, Iran (A); mangroves in light gray with the main channel and the 4 intertidal creeks (numbered dashed rectangles in B) (upper figure). Bathymetric map of high-lying creeks 1 and 4 (C), and low-lying creeks 2 and 3 (D).

Sampling design

Fish were sampled from the four intertidal creeks with four block nets (15 - 25 m in length, 4 m high; 12 mm stretched mesh size) lifted simultaneously at slack high water during three lunar cycles in December 2011 - January 2012, February - March 2012 and August- September 2012. The block net method is commonly used for fish collection in mangroves studies e.g. in South Florida and Brazil (Thayer et al. 1987;

Barletta et al. 2003); and this method is regarded as highly efficient in capturing the identity of fish fauna using intertidal habitats (Bozeman and Dean 1980).

Overall 96 block net samples were taken (4 intertidal mangrove creeks x 3 lunar cycles x 4 lunar phases x 2 times of day). Fish sampling accounted for the four 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 fishes had entered the creeks during the nightly flood tide and were leaving in the morning ebb tide. SD and ND sampling were carried out in the evening when fishes had entered with the afternoon flood tide and were leaving in the first part of the night. The time of each sampling were chosen according to the tide tables for the area (<http://217.218.133.169/hydrography/DrawChart.aspx>).

Fish were collected during low tide and transported on ice to the laboratory. The high-lying creeks were dried out at each tide. However, the low-lying creeks were inundated at neap low tide. In this instance, a small hand net was used to collect all the fishes behind the block nets. Collected fishes were identified to the lowest possible taxonomic level (Fischer and Bianchi 1984; Kuronuma and Abe 1986; Assadi et al. 1997), counted and wet-weighed ($g \pm 0.1$). Fish total length was analyzed in class intervals of 2.5 cm, except for six large-sized species (see species name with asterisks, Table 1) where a 10 cm class interval was used.

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). pH values were 8.1 ± 0.2 and salinity averaged 38.3 ± 0.5 throughout the sampling period, suggesting a stable non-estuarine mangrove environment (Table S1). The visibility 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 (HOBO did not operate in December and February). This device measured water pressure (± 0.6 KPa) and temperature ($\pm 0.44^\circ\text{C}$) every 15 minutes resulting in information about changes in the approximate water height and temperature over several spring and neap tide cycles.

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. This information was introduced to GIS software to produce a bathymetric map of each creek (Fig. 1). Relationships between high water level and inundated area and volume were established to standardise catch numbers and weights to density and biomass, respectively. Abundance and biomass for each species per sample were converted to abundance and biomass per m² by dividing total values by respective inundation area for each creek.

Creek attributes

The area was characterized by a plateau mangrove where the mangrove forest is flooded only during spring tides. Average tidal range is ~ 2.5 m in the study area. The low-lying creeks were characterized by having greater water depths ($0.37 \text{ m} \pm 0.2 \text{ SD}$) and greater time of inundation during high water periods when compared to the high-lying creeks. GIS generated water surface and volume indicated that the relationship between surface area, volume and intertidal water level increased slowly until approximately 1 -1.5 m water level rise at the mouth of the creeks and inundation was still restricted to the creek network. Beyond 2 m water level rise, the water left the creek network and the mangrove plateau became flooded (Fig. S2).

Data analysis

We used the EstimateS software to produce the 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) were analyzed with Kruskal-Wallis One 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 four-way permutational multivariate analysis of variance (PERMANOVA) model. Factors included: location (fixed, two levels: high-lying and low-lying creeks), creek nested in location (random, four levels: 1, 2, 3, 4), tide-time of day combination (fixed, four levels: SN, SD, NN, ND) and month (fixed, three levels: December, February, August). Additionally, differences among factors were analyzed

with pairwise comparisons and in the case of factor 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. The 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 and based on Bray-Curtis distances. It should be noted that the abundance and biomass comparisons were made on both a per m² basis and on a per sample basis, with the per m² comparisons more appropriate if fish were resident, and the per sample comparisons more appropriate if fish were 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 m² basis and also on a per sample basis). Alternatively, if abundance (or biomass) results were not parallel and significant when expressed on a per m² and a per sample basis, results were not considered ecologically robust.

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

RESULTS

Species composition and richness

A total of 5954 individuals from 29 fish species and 22 families were caught by 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). Most abundant species were *Liza klunzingeri* (Mugilidae) (41%), *Leiognathus daura* (Leiognathidae) (18%), *Pentaprion longimanus* (Gerreidae) (10%), *Thryssa vitrirostris* (Engraulidae) (8%), and all other species accounted for the remaining 20% of the total abundance, each with less than 5%. In terms of catch mass, *L. klunzingeri* (62%), *T. vitrirostris* (8%) and *Acanthopagrus latus* (Sparidae) (5%) made up 75% of the catch (Table 1). The most abundant species (relative abundance of > 0.1) occurred in all creeks (Table 1). Also, a general similarity in the diversity patterns was indicated in the spatial comparisons of

Figure 2 because the observed number of species was similar at 16-20 species when 800 individuals were considered for comparisons between creeks.

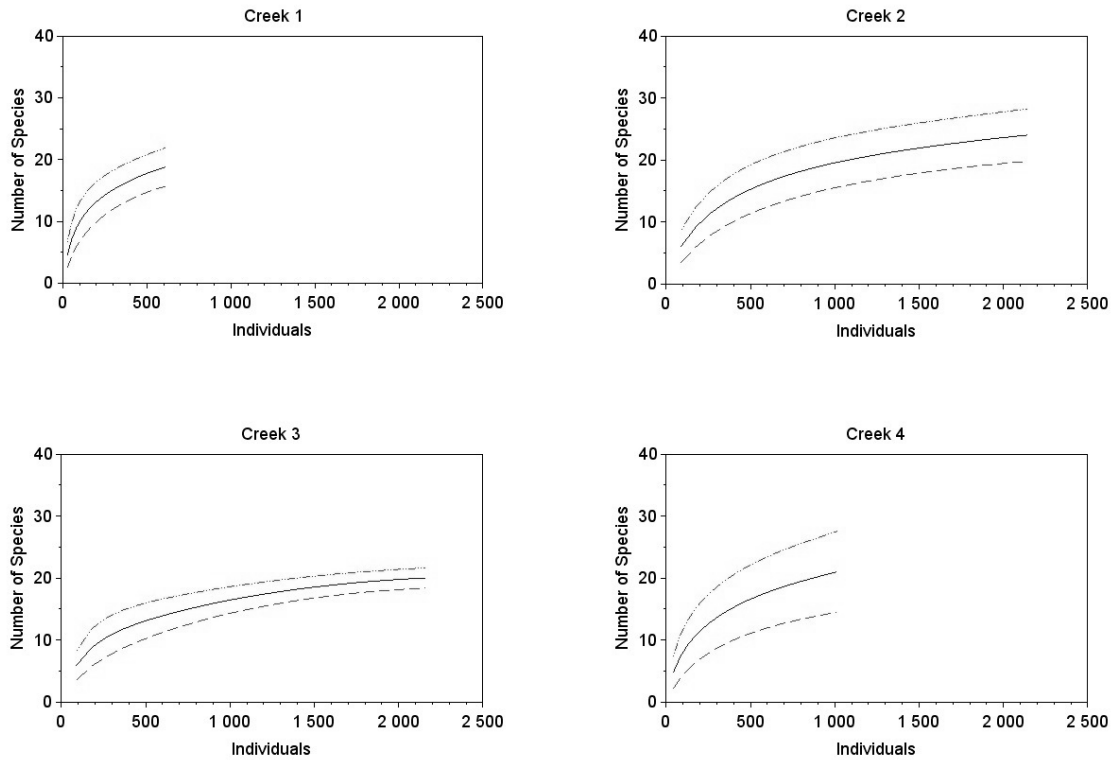


Figure 2 Individual-based rarefaction curves of fish species caught in four mangrove-lined creeks sampled at different combinations of the tidal and diel cycle during 3 months (December 2011, February and August 2012) in Qeshm Island, Iran. Dashed lines indicate 95% confidence intervals.

Table 1 Fish species composition from 4 intertidal mangrove creeks of Qeshm Island collected during three lunar cycles in December 2011-January 2012, February-March 2012 and August-September 2012, accounting for the four tidal and diel combinations of spring-day (SD), spring-night (SN), neap-day (ND), and neap-night (NN). Fish species sorted decreasing by total number of individuals (N). Relative abundance (RA), relative biomass (RB) and biomass per sample is shown for tide-time of the day, month and creek. Asterisks symbols indicate large-sized species.

Species	Size	N	RA%	RB %	Tide-time of day				Month			Creek			
					SN	SD	NN	ND	Dec.	Feb.	Aug.	C1	C2	C3	C4
<i>Liza klunzingeri</i> (Mugilidae)	5-20	2443	41	62	64248	9631	9079	9954	67140	13501	12270	1057 1	2946 4	4809 9	4777
<i>Leiognathus daura</i> (Leiognathidae)	5-12.5	1057	18	3	2704	1081	3487	22.5	857	2475	979	366. 9	1665	1445	833. 9
<i>Pentaprion longimanus</i> (Gerreidae)	5-12.5	577	10	4	1373.5	3214	964.5	754	2316	1506	2025	1160	3003	745.5	937. 5
<i>Thryssa vitrirostris</i> (Engraulidae)	10-15	468	8	8	7757.7	167	773	472	565.5	4397	6921	844. 7	2994	6225	1820
<i>Scatophagus argus</i> (Scatophagidae)	2.5-10	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)	5-15	257	4	5	4097.8	2802	286	69.5	3937	1235	2761	1686	2119	2132	1997
<i>Anodontostoma chacunda</i> (Clupeidae)	5-10	188	3	2	859	1696	504	361	922	1566	454	122	461	2214	145
<i>Sarinella longiceps</i> (Clupeidae)	5-10	166	3	1	0	327	26	1567	7	1915	0	27	1228	0	667
<i>Pomadasyys kaakan</i> (Haemulidae)	5-10	161	3	3	3632.5	565	0	13.5	3193	318	986	1615	805.2	1239	837. 6
<i>Sardinella gibbosa</i> (Clupeidae)	5-10	120	2	1	220	777	524.8	35	5	1027	0	35	232	20	745
<i>Lutjanus johni</i> (Lutjanidae)	5-15	73	1	4	5488	65.5	28	11	4354	820	1164	315	2640	2682	701
<i>Ilisha melastoma</i> (Clupeidae)	5-10	53	1	0	77.5	287	0	3	67	288	17.5	22.5	78	247	25
<i>Sillago sihama</i> (Sillaginidae)	10- 17.5	18	0	0	192	205	600	0	276	216	132	101	294	89	140
<i>Pseudorhombus elevatus</i> (Paralichthyidae)	10-15	15	0	0	120	0	0	215	0	335	0	0	15	320	0
<i>Plectorhinchus pictus</i> (Haemulidae)	5-15	13	0	0	253	74	227	0	30	0	397	158	84	30	155
<i>Scartelaos tenuis</i> (Gobiidae)	5-10	8	0	0	31	0	100	47.5	17	39	82.5	30.5	69	24	15

Tidal Induced Changes in Intertidal Mangrove Fish Assemblages

Species	Size	N	RA%	RB %	Tide-time of day				Month			Creek			
					SN	SD	NN	ND	Dec.	Feb.	Aug.	C1	C2	C3	C4
<i>Lutjanus russelli</i> (Lutjanidae)	10-15	6	0	0	0	7.5	0	0	0	80	7.5	0	87.5	0	0
<i>Platycephalus indicus</i> (Platycephalidae)*	20-30	5	0	2	1200	0	5	1650	2300	0	550	0	250	2300	300
<i>Bathygobius fuscus</i> (Gobiidae)	5-10	5	0	0	24	0	0	67	53	38	0	0	31	0	60
<i>Scomberoides lysan</i> (Carangidae)	5-10	5	0	0	0	18	60	49.5	0	0	67.5	0	21.5	46	0
<i>Eleutheronema tetradactylum</i> (Polynemidae)*	20-30	3	0	0	7	0	0	7	0	59	0	0	20	0	39
<i>Sphyraena putnamiae</i> (Sphyraenidae)*	20-30	2	0	1	38.8	0	0	600	600	0	638.8	600	0	638.8	0
<i>Epinephelus coioides</i> (Serranidae)*	30-40	2	0	1	1400	0	0	200	1400	0	200	1600	0	0	0
<i>Strongylura stronglura</i> (Belontiidae)	10-15	2	0	0	130	0	80	0	0	130	0	0	0	130	0
<i>Pseudosynanceia melanostigma</i> (Synanceiidae)*	20-30	1	0	0	395	0	0	0	395	0	0	0	261	40	94
<i>Abalistes stellatus</i> (Balistidae)*	20-30	1	0	0	16	0	45	0	0	16	0	16	0	0	0
<i>Acanthopagrus cuvieri</i> (Sparidae)	15-20	1	0	0	2	109	0	0	0	4	107	0	47	4	60
<i>Hemiramphus archipelagicus</i> (Hemiramphidae)	12.5-15	1	0	0	55	0	0	0	0	0	55	0	55	0	0
<i>Upeneus sulphureus</i> (Mullidae)	10-15	1	0	0	2.5	0	0	0	0	0	2.5	0	0	0	2.5

Asterisks indicate large-sized species.

Species richness differed between tide-time of day (KW- $H=32.7$, $P<0.001$; Tukey's test, $SN > NN$ and ND) and between months (KW- $H=6.06$, $P=0.04$; Tukey's test; $Aug > Dec$). Significantly more species were captured at SN, and ND was responsible for the lowest species numbers (Fig. 3). The median number of species at SN was 7 (the 25th and 75th percentiles was 6-8), while for the other tide and time combinations the median ranged between 4-5 (Fig. 3).

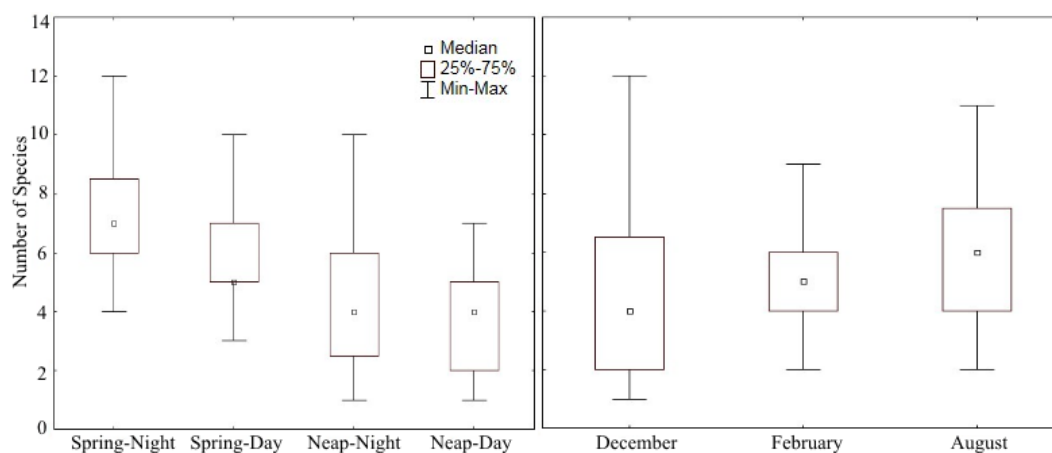


Figure 3 Median number of fish species captured at spring tide night, spring tide-day, neap tide-night and neap tide-day and three months (December 2011, February and August 2012) in intertidal mangrove creeks at high water ($n=96$ samples). The 25 to 75% quartiles and minimum and maximum values are shown.

The median numbers of species were 4, 5 and 6 for the Dec, Feb and Aug, respectively (Fig. 3). Detailed species data showed the presence/absence differences among months and tidal and diel cycle. For example, *S. longiceps* was not found at SN. *P. kaakan* and *I. Melastoma* did not occur at NN. Also, some rare species with the relative abundance of <0.1 , e.g. *U. sulphureus*, *H. archipelagicus* and *P. melanostigma* occurred mostly at SN (Table 1). Five species were caught in high biomass during spring tide night: *L. klunzingeri*, *T. vitrirostris*, *A. latus*, *P. kaakan* and *L. johni*. *S. longiceps* and *S. gibbosa* (Clupeidae) were absent in August. However, the monthly variations in species richness were mostly related to the occasional migrant, e.g. *S. lysan*, *H. archipelagicus* and *U. sulphureus* only occurred in August, *P. elevatus*, *E. tetradactylum*, *S. stronglura*, *A. stellatus*, *A. cuvieri* found in Feb and *P. melanostigma* in December. The most abundant species changed rank between months (Fig. S3).

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 m². Difference were considered to be significant when P < 0.05 (bold values).

Abund. per m²	df	SS	MS	Pseudo-F	P(perm)	perms	P(MC)	Biomass per m²	df	SS	MS	Pseudo-F	P(perm)	perms	P(MC)
Location	1	2538.4	2538.4	0.4883	1	3	0.853	Location	1	2008.9	2008.9	0.4784	1	3	0.862
Month	2	22397	11199	6.249	0.008	998		Month	2	18768	9384.1	5.4654	0.003	995	
Tide	3	32421	10807	5.9633	0.001	999		Tide	3	35670	11890	6.3456	0.001	999	
Creek (Location)	2	10397	5198.5	2.7903	0.001	999		Creek (Location)	2	8398.2	4199.1	2.1301	0.006	997	
LocationxMonth	2	4422.6	2211.3	1.2339	0.358	999		LocationxMonth	2	3577.8	1788.9	1.0419	0.458	999	
LocationxTide	3	4365.5	1455.2	0.80295	0.68	998		LocationxTide	3	4276.8	1425.6	0.76082	0.748	997	
MonthxTide	6	23034	3839	2.6898	0.001	996		MonthxTide	6	26027	4337.8	2.9852	0.001	998	
Creek(Location)xMonth	4	7168.3	1792.1	0.9619	0.535	998		Creek(Location)xMonth	4	6868	1717	0.87097	0.654	997	
Creek(Location)xTide	6	10874	1812.3	0.97274	0.514	997		Creek(Location)xTide	6	11243	1873.8	0.95049	0.583	997	
LocationMonthxTide	6	7861.4	1310.2	0.918	0.584	999		LocationMonthxTide	6	8350.5	1391.7	0.95777	0.546	999	
Creek(Location)xMonthxTide	12	17127	1427.3	0.76609	0.92	997		Creek(Location)xMonthxTide	12	17437	1453.1	0.73711	0.969	997	
Residual	48	89427	1863.1					Residual	48	94625	1971.4				
Total	95	232030						Total	95	237250					
Abund. per sample	df	SS	MS	Pseudo-F	P(perm)	perms	P(MC)	Biomass per sample	df	SS	MS	Pseudo-F	P(perm)	perms	P(MC)
Location	1	4423.8	4423.8	1.3206	0.346	3	0.293	Location	1	4384.5	4384.5	1.497	0.335	3	0.219
Month	2	21330	10665	6.2234	0.004	999		Month	2	17265	8632.5	5.0643	0.01	997	
Tide	3	33799	11266	6.031	0.001	998		Tide	3	34244	11415	6.2851	0.001	999	
Creek (Location)	2	6699.7	3349.9	1.8168	0.036	998		Creek (Location)	2	5857.6	2928.8	1.4733	0.093	999	
LocationxMonth	2	4749.1	2374.5	1.3856	0.251	999		LocationxMonth	2	4081.9	2040.9	1.1973	0.347	997	
LocationxTide	3	5196.3	1732.1	0.92722	0.575	999		LocationxTide	3	5354.2	1784.7	0.9827	0.506	999	
MonthxTide	6	22529	3754.8	2.62	0.001	997		MonthxTide	6	26243	4373.8	2.9337	0.001	995	
Creek(Location)xMonth	4	6854.7	1713.7	0.92943	0.561	999		Creek(Location)xMonth	4	6818.3	1704.6	0.85747	0.728	995	
Creek(Location)xTide	6	11208	1868.1	1.0132	0.446	998		Creek(Location)xTide	6	10897	1816.1	0.9136	0.64	999	
LocationMonthxTide	6	8882.7	1480.5	1.033	0.467	998		LocationMonthxTide	6	9739.9	1623.3	1.0888	0.354	998	
Creek(Location)xMonthxTide	12	17198	1433.1	0.77728	0.934	996		Creek(Location)xMonthxTide	12	17891	1490.9	0.74998	0.965	996	
Residual	48	88502	1843.8					Residual	48	95419	1987.9				
Total	95	231370						Total	95	238200					

Spatio-Temporal patterns

PERMANOVA results for the effect of month were highly significant (Table 2). But the pairwise tests were non-significant in all monthly comparisons ($t < 4.3$, $P < 0.05$). Also, inconsistent patterns in abundance and biomass per sample and per m^2 indicated that month cannot be considered as significant factor (Fig. 4).

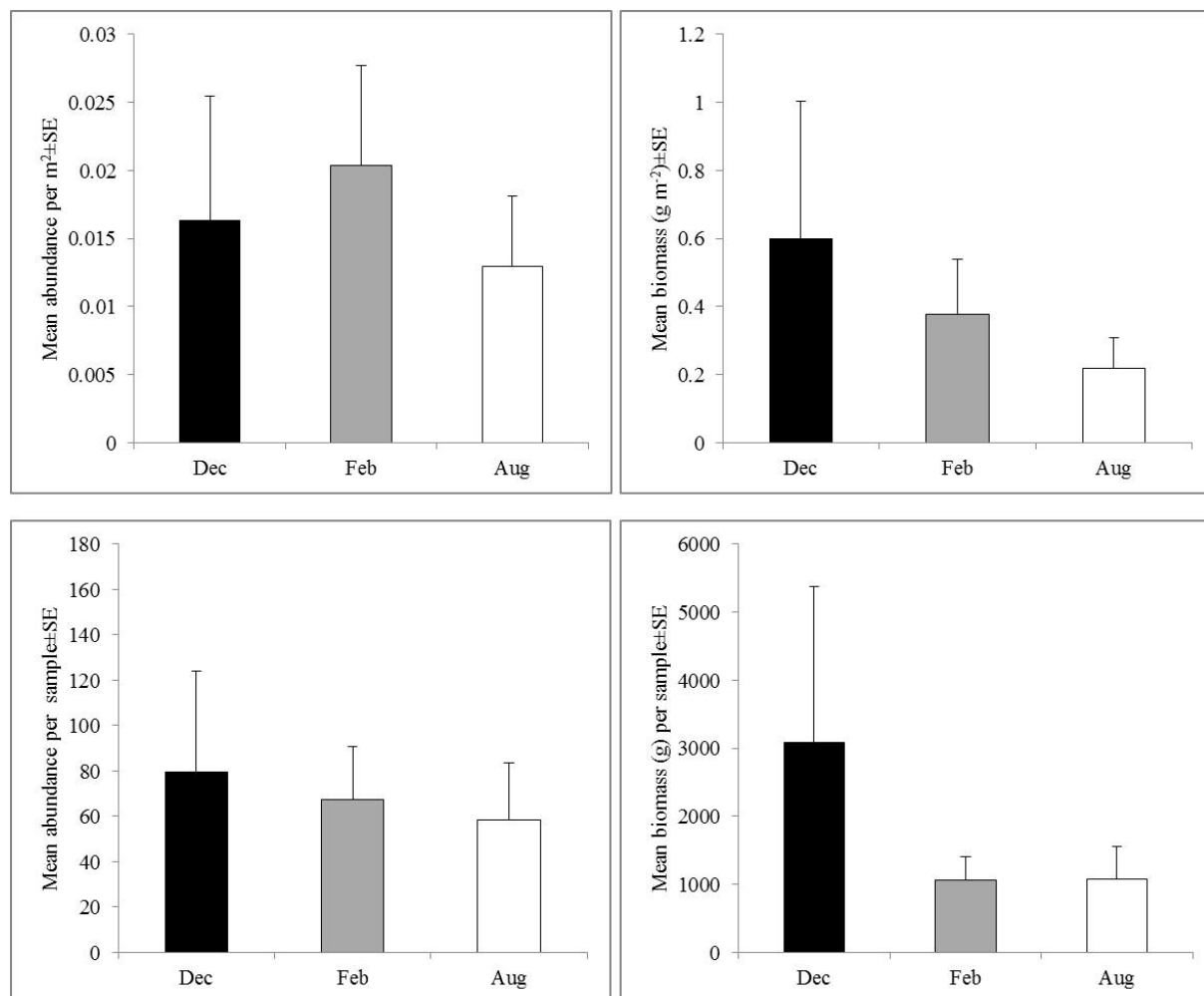


Figure 4 Mean abundance and biomass per sample and per $m^2 \pm 1SE$ of fishes during different months: December 2011, February and August 2012 from intertidal mangrove-lined creeks in Qeshm Island, Iran.

Highest abundance and biomass per sample and per m^2 were observed at SN (Fig. 5). Also, tidal and diel variations were strong in PERMANOVA results with $P < 0.001$ (Table 2). The pairwise comparisons for abundance and biomass per sample and per m^2 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). For instance, unlike other NN conditions, high biomass per sample and per m^2 and abundance per m^2 occurred at NN in February. However, this pattern was not observed

for abundance per sample. Thus, the interaction between months and tides cannot be considered ecologically robust, despite being significant in the PERMANOVA (Table 2).

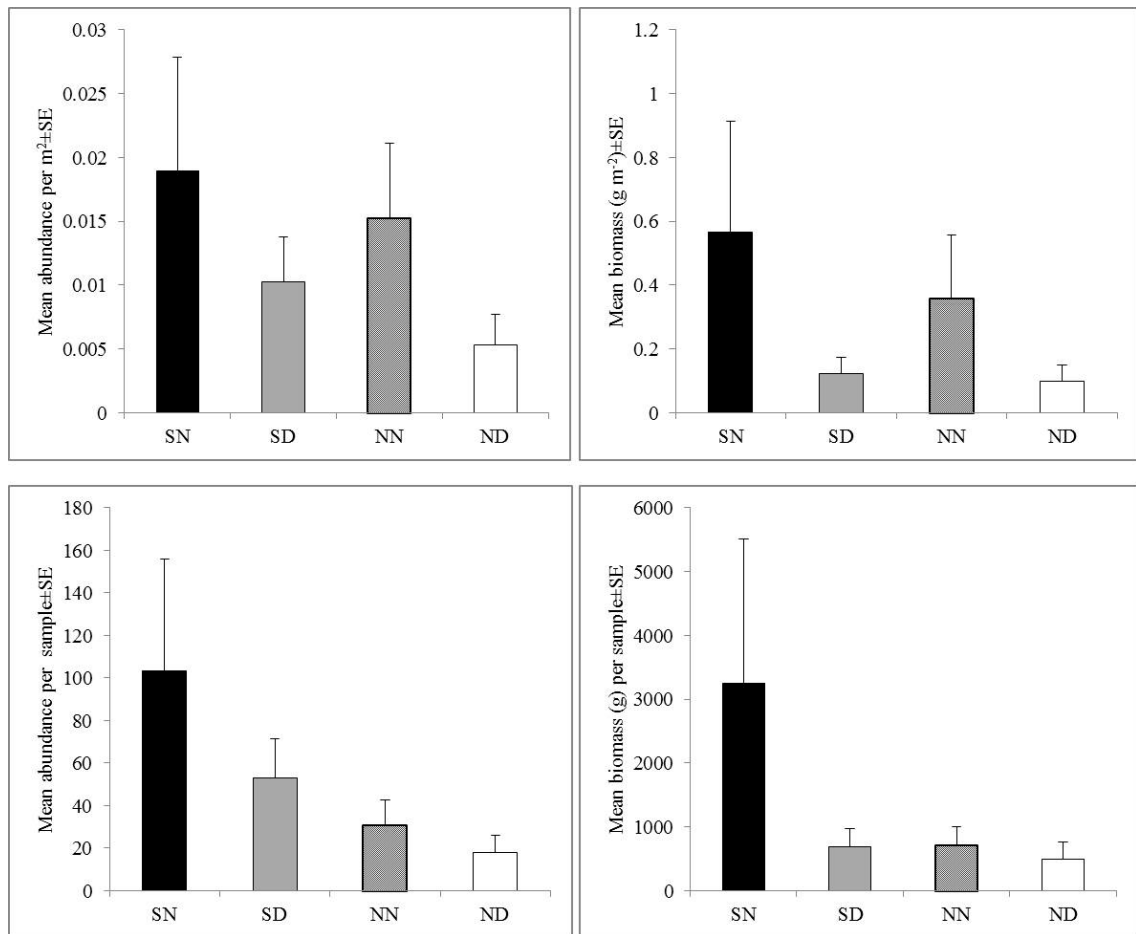


Figure 5 Mean abundance and biomass per sample and per m² ± 1 SE of fishes at different combinations of the tidal-diel cycle: spring tide-night (SN), spring tide-day (SD), neap tide-night (NN), neap tide-day (ND) from intertidal mangrove-lined creeks in Qeshm Island, Iran.

Mean abundance and biomass per sample were higher at the low-lying creeks (2, 3) but inconsistent patterns were observed when the biomass and abundance referred to m². PERMANOVA tests showed that all the location differences were insignificant (Monte-Carlo p values > 0.05). Creek-level (nested in location) variations were significant in PERMANOVA results at the 0.006-0.03 level in three of four cases (Table 2). But the creek level variations did not consider ecologically robust because the pattern was not consistent between creeks (Fig. S5).

Further examination of the significant factors in the PERMANOVA test (for the factors that were significant in all four cases (abundance and biomass per sample and per m²), with the CAP routine, indicated smaller canonical correlation coefficients for the factor month

(Table S2); CAP only allocated the samples according to the factor tide and time of the day (Fig. 6). The CAP plot showed that *A. latus*, *L. daura* and *T. vitrirostris* were correlated with the spring tide. *P. longimanus* was correlated with the neap tide (Fig. 6).

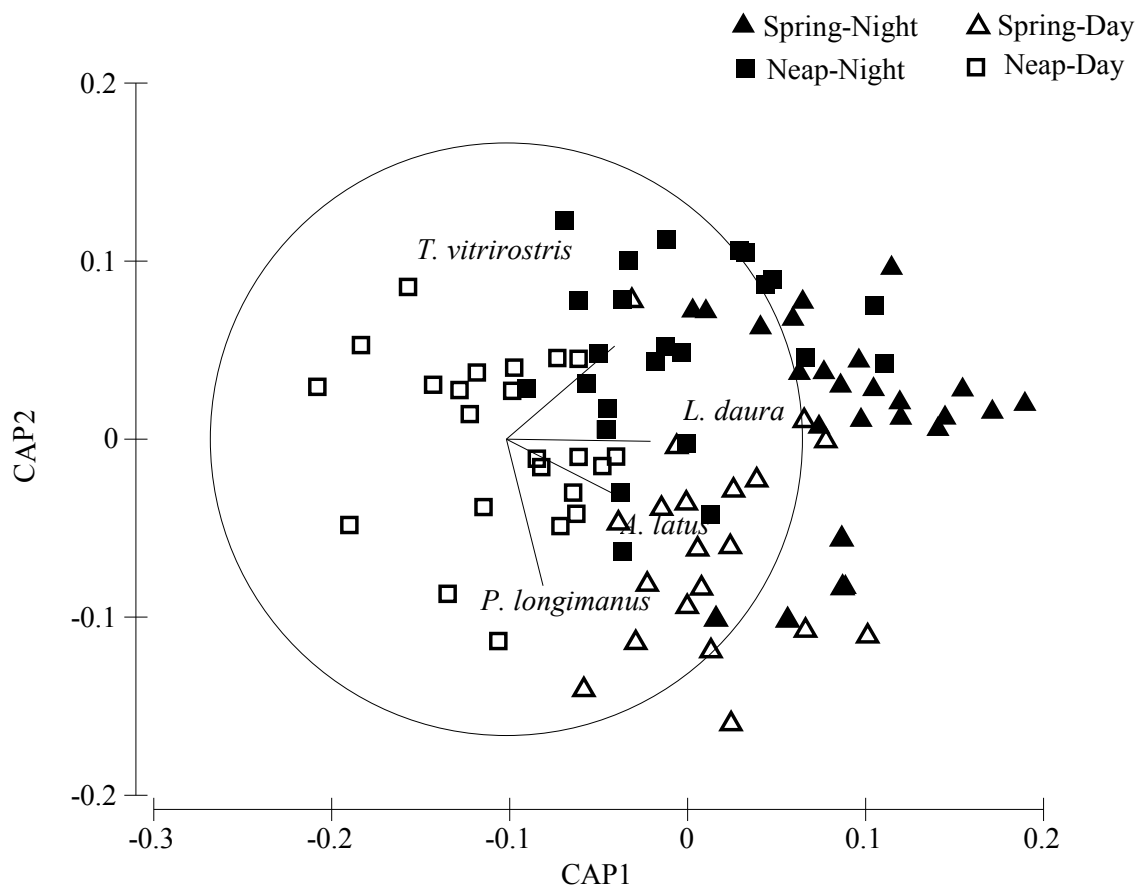


Figure 6 Canonical analysis (CAP) yielded two axes regarding factor tide-time, with squared canonical correlations of $\delta_1^2=0.68$ and $\delta_2^2=0.40$. Symbols represent individual biomass per sample and vectors show individual species correlations with the 2 CAP axes where $|r|>0.4$. See Table 1 for full species names.

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 , $N=96$, $P<0.05$).

DISCUSSION

Fish assemblage structure of Qeshm mangrove was characterized by low diversity. This could be explained by low habitat diversity and lack of other near shore habitats e.g. seagrass beds and coral reef in the vicinity of the mangroves (Pittman et al. 2004; Blaber 2007). Relatively high salinities and temperatures that prevail much of the year at the study area might also

influence species richness. The number of fish species in the mangrove intertidal creeks in Qeshm Island was lower than in other comparable intertidal shallow water habitats in the Western Indian Ocean (Table 3), despite covering the major short and mid-term time scales in this study. For example, intertidal fish communities were represented by 50 species in non-estuarine Sulaibikhat Bay, in Kuwait (Wright 1989). Also, 60 and 44 species were reported from the mangrove creeks in Madagascar and Zanzibar, respectively (Laroche et al. 1997; Lugendo et al. 2007). In contrast, high species diversity has been viewed from the Kenyan mangrove where the seagrass bed occurred in close vicinity of mangroves (Kimani et al. 1996). However, differing sampling methods and efforts hinder direct comparisons. At a global scale, the low species diversity in the study area agrees with the standard species gradient from the center of shallow water species richness in the coral triangle (Blaber 2000; Carpenter and Springer 2005).

Table 3 Comparison of the number of species and families from different intertidal shallow water habitats in the Western Indian Ocean; studies sorted according to marine biogeographical regions and descending by the year of study.

Western Indian Ocean	Sampling method	Habitat type	Species (Families)	Abundant fish families
East Africa				
Gazi Bay, Kenya ¹	beach seine	Mangrove & seagrass	128 (50)	Atherinidae, Clupeidae and Gerreidae
Sarodrano mangrove, Madagaascar ²	Gillnet	Mangrove creek	60 (35)	Gerreidae and Teraponidae
Chwaka Bay, Zanzibar ³	seine net	Mangrove creeks and chanles	Mangrove creek (44) Mangrove chabnnel (62)	Ambassidae, Apogonidae and Gerreidae
Gulf Region				
Sulaikhat Bay, Kuwait ⁴	Otter trawl	Intertidal & subtidal	46(28)	Mugilidae and Haemulidae
Sulaikhat Bay, Kuwait ⁵	Otter trawl	Intertidal & subtidal	50 (30)	Mugilidae, Haemulidae and Leiognathidae
Kuwait Bay ⁶	Otter trawl	Intertidal & subtidal	Period 1: 37 (29) Period 2: 38 (29)	Leiognathidae, Ariidae and Soleidae
Kuwait Bay ⁷	Trawl & Seine	Mud flat and sandy beaches	37 (22)	Engraulidae and Gobiidae
Qeshm Island, Iran (persent study)	Block net	Mangrove	29 (21)	Mugilidae and Leignathidae

1-Kimani et al (1996); 2-Laroche et al (1997); 3-Lugendo et al (2007); 4-Wright (1988); 5-Wright (1989); 6-Wright et al (1990); 7-Abou-Seedo et al (1990)

In this study area, Mugilidae, Leiognathidae and Engraulidae dominated in terms of abundance. Mugilidae were also an abundant family along the coast of Gulf region (Wright 1988), suggesting that mullets are dominant in shallow-water intertidal habitats in the Gulf region (Table 3). Also, the dominant species made up more than 75% of the total abundance and biomass. Similarly, other mangrove fish studies showed that many fish visited the mangrove but few species are dominant (Bell et al. 1984; Little et al. 1988; Chong et al. 1990) this supporting a general notion that higher complexity and shelter of mangroves attract more fish species.

Species richness differed between months in the low-rainfall mangroves of Qeshm Island, but differences were mostly related to the seasonally vagrant species while the highly abundant species were found during all months. This could be linked to very low precipitation and lack of fresh water input resulting in year-round hyper saline conditions with low allochthonous nutrient input. Conversely, in other semiarid and arid mangroves in Madagascar and Mexican Pacific coast, high species richness was reported in the warm and rainy season (Laroche et al. 1997; González-Acosta et al. 2005). Also, high food availability in the wet season explained as a reason for high species richness from the humid mangroves (Ikejima et al. 2003). This suggests that rainfall regime may play a determinant role in low species diversity in this study area.

Tide emerged as an important and significant factor in the analyses of fish communities. The results demonstrated that the numbers of species, abundance and biomass were highest at nightly spring tide inundations. However, species did not avoid low tide and most abundant species were found in both spring and neap tides, except *S. longiceps* that correlated strongly with the neap tide. Qeshm Island presents mangroves where much larger intertidal areas are inundated at spring than at neap tides. Higher number of species during the night spring tide could be driven by higher water level and inundation time that may attract more species in the intertidal mangrove creeks. It has been observed that most fish using the tidal creeks at high tide move into main tidal channel during low tide to avoid exposure to air (Barletta and Saint-Paul 2010). Moreover, the high water could facilitate the movement of fish into the creeks, thus the fish may rely on the tide for transport (Davis 1988).

Tide-diel related changes in fish assemblages also correlated with different water temperature dynamics in the creeks during spring and neap tides. This could be explained by different combination of high and low water level and time (day and night) that influenced SD, SN, NN and ND water temperature. But the inter-correction

of these factors (water height and water temperature) is not justifiable with the statistics. The results of the HOBO water level logger, operated in August, showed that the water temperature cooled during the nightly low water and heated during the daytime low water period, with higher daytime values at spring (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. S6). Therefore, smaller water temperature ranges during SN provided better conditions because of the converging of a high level of intertidal inundation and low water temperatures.

Similarly, in meso/macro tidal coasts of Australia, more fish use the intertidal area during spring tide rather than neap tide (Laegdsgaard and Johnson 1995; Wilson and Sheaves 2001). Likewise, in the macrotidal mangrove in northern Brazil, catch weight of fish entering intertidal mangrove creeks were highest during spring tides (Krumme et al. 2004; Krumme and Saint-Paul 2010). But in the microtidal coast of Curaçao and Florida, the mangrove habitats are continuously available for fish resulting in a lack of pattern in fish community structure according to tidal cycle (Ley and Halliday 1999; Nagelkerken et al. 2001). The diel cycle is the major rhythm driving short-term changes in mangrove fish assemblages in non-estuarine system of Caribbean Sea (Nagelkerken et al. 2000). Also, catches were greater during the night on the falling tide than the rising tide while the day catches were greater on the falling tide than the rising tide in intertidal mudflat in the Gulf region (Abou-Seedo et al. 1990). Also, tidal and diel patterns on species diversity were mostly species-specific in Qeshm mangroves. Lutjanidae (*L. johni*) was mainly caught at SN yet this family was largely absent during the day. It is assumed that Lutjanidae are nocturnal so to reduce risk of predation, and also because of higher activity of their potential prey (i.e. crustaceans) (Hobson 1965).

Lastly, fish habitat use was greater in the low-lying creeks (C2 and C3) with regard to the biomass and abundance per sample. The longer inundations in the low-lying creeks may provide greater habitat accessibility and consequently lead to longer foraging periods for the fish. But the disproportional increases in the water surface and the volume of water of low-lying creeks indicated inconsistency in fish biomass and abundance per sample and per m². Nevertheless, the findings indicate that interaction of tide (spring and neap) with day-night cycles can explain the organization of fish assemblages using intertidal mangroves creeks in mesotidal coasts of Qeshm Island. Greater habitat use by fishes during spring tide night could be related to the cooler

water temperature at night and also spring tide provides longer foraging time for fishes. Thus, tides can be considered as a determinant of fish habitat use in the mesotidal coast of the Persian Gulf.

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Supplementary data is given in Annex I

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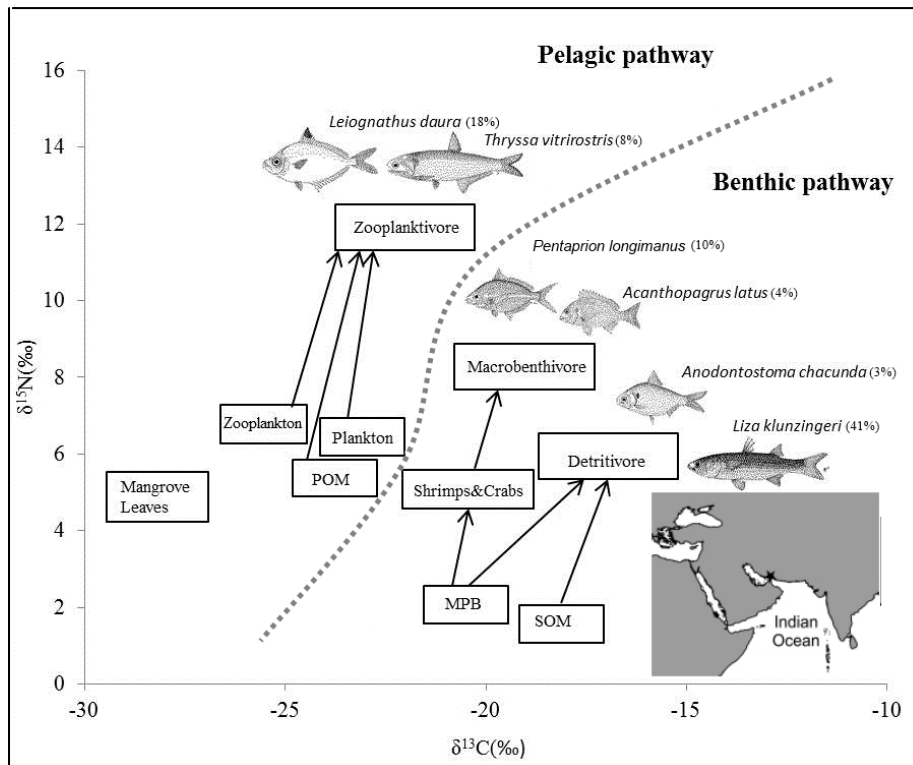
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CHAPTER III

Microphytobenthos Sustain Fish Food Webs in Intertidal Arid Habitats: A Comparison between Mangrove-lined and Un-vegetated Creeks in the Persian Gulf



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ABSTRACT

The dietary importance of mangroves for fish production often seems to be minor. However, robust comparisons of fish food webs at mangrove vs. non-mangrove sites are largely lacking. We analyzed stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope values of dominant fishes (in terms of number) and their potential food sources in summer and winter from arid mangrove-lined and un-vegetated intertidal creeks in Qeshm Island, Persian Gulf, Northern Indian Ocean (26.8°N, 55.75°E). Detritivorous *Liza klunzingeri* (47%) and *Anodontostoma chacunda* (34%) dominated the abundance at the un-vegetated site; at the mangrove site *L. klunzingeri* (41%) also dominated, while the zooplanktivores *Leiognathus daura* (18%), *Thryssa vitrirostris* (8%) and macrobenthivores *Pentaprion longimanus* (10%), *Acanthopagrus latus* (4%) also contributed. Our findings showed high dietary reliance by fish on food items associated with non-mangrove sources as indicated by 2 source mixing models. Mangrove-derived organic matter contributed a maximum of 36% to the fish tissue whereas organic matter produced by microphytobenthos and plankton played a major role in the diet of the most abundant fish species with contributions of 64 - 100%. Two trophic pathways, a pelagic pathway and a benthic pathway, were present in the fish food webs at both sites. The pelagic and benthic food sources of the un-vegetated site were ^{13}C -enriched, consistent with stronger contributions of abundant benthic cyanobacteria found within that food web. Spatial $\delta^{13}\text{C}$ variation of microphytobenthos and plankton was also reflected in the $\delta^{13}\text{C}$ values of the feeding guilds and some fish species, suggesting that fish were relatively resident at each site. The isotope values of most food sources and fish did not differ significantly between seasons. Overall, regardless of habitat type and season, microphytobenthos and plankton largely sustained fishes in this region while mangroves, where present, were of minor importance. Our results suggest both mangrove and un-vegetated sites act as feeding grounds for fishes via pelagic and benthic food pathways in this arid region.

Keywords Intertidal mangrove creeks, Un-vegetated habitat, Intertidal fishes, Stable isotopes, Food web structure, Western Indian Ocean

INTRODUCTION

Mangroves forests are known to be highly productive ecosystems with high rates of primary production (Alongi, 2014). However, according to the outwelling hypothesis, large amounts of mangrove leaves, detritus, and particulate or dissolved organic matter are exported to adjacent habitats and are thus thought to be important in local food webs (Lee, 1995; Bouillon et al., 2000). Also, mangrove ecosystems contribute to local fisheries by providing food and shelter (Manson et al., 2005; Chong, 2007) and thus act as important nursery grounds for many fish species (Robertson and Duke, 1987; Nagelkerken, 2009). The specific function of mangroves as feeding and nursery ground for fishes can vary depending on environmental factors (i.e. precipitation, temperature, tidal regime), and on geomorphological features such as the tidal creek structure within a mangrove forest (Twilley et al., 1999; Fry and Ewel, 2003; Lugendo et al., 2007). In the Indo-Pacific where tides are large, fish show little reliance on organic carbon produced by mangroves trees (Marguillier et al., 1997; Nyunja et al., 2009). These results are also supported by studies in the Caribbean where mangroves are often permanently inundated, and primary producers such as microphytobenthos, algae, seagrass and phytoplankton have been identified as important food sources for many fishes in mangrove ecosystem (Nagelkerken and Velde, 2004; Nagelkerken et al., 2008). On the other hand, some studies in high-rainfall areas of the central Indo-Pacific conclude that organic carbon produced by mangroves trees plays important role as food source in fish food webs (Rodelli et al., 1984; Zagars et al., 2013). Furthermore, food sources of different origins can be seasonally important for consumers in each particular habitat and fishes can change their food habits as a consequence of prey availability (Vizzini and Mazzola, 2003; Olin et al., 2012). Given these divergent findings, it seems possible that environmental variables could determine use of mangrove litter in coastal food webs.

Mangroves in the Persian Gulf thrive under extreme conditions and are subjected to very low rainfall and high salinities (Al-Khayat and Jones, 1999) which may influence the functionality of mangroves in this region. So far, there are only a few studies of mangroves in the Gulf region, mainly from the southern Arabic coast. These studies focus on the role of different habitats including natural and planted mangroves on the diet of benthic invertebrates. At the east coast of Qatar, stomach content analysis and stable isotope approaches indicated that endemic shrimp species (*Palaemon khori*) relies on mangrove leaves throughout its post settlement life cycle,

while other shrimps such as *Penaeus semisulcatus* and *Metapeneus ensis* mostly feed on seagrass and microbial mat foods (Al-Maslamani et al., 2012; Al-Maslamani et al., 2013). In the Sulaibikhat Bay also microphytobenthos (microbial mats) are a major food sources supporting benthic and pelagic macro faunal species (mostly invertebrate and few subtidal fish species) and the minor role of mangroves trees has been highlighted as food source for these organisms (Al-Zaidan et al., 2006).

Stable carbon and nitrogen isotopes are often used to compare interlinked mangrove, seagrass and mudflat food webs. These studies have highlighted the limited role of mangrove as primary sources of carbon to higher trophic levels (Kruitwagen et al., 2010; Igulu et al., 2013). However, direct comparisons between mangrove-lined creeks and similar creeks lacking mangroves have not been previously reported. Here we use stable carbon and nitrogen isotopes to examine the food pathways in mangrove-lined and un-vegetated creeks at the arid coast of Qeshm Island, Iran during winter and summer. More specifically we address the following questions: 1) Do food sources in the two habitat types (mangrove vs. un-vegetated) differ in isotopic compositions? 2) What are the main food pathways for fishes in mangrove vs. non-mangrove sites? 3) Does fish rely on different food sources in winter and summer? 4) What is the importance of mangroves in supporting fish food webs?

To address these questions, carbon and nitrogen isotope values of food sources and fishes were considered from two sites each sampled in summer and winter. Stable isotope analyses provide information on the long-term feeding habits of fish and the relative contributions of different primary sources to fish nutrition (Peterson and Fry, 1987; Layman, 2007). Two-source mixing models were used to set upper maximum and lower minimum limits on the mangrove contributions to the fish food webs at the mangrove site.

MATERIALS AND METHODS

Study sites

The study was carried out at Qeshm Island, Iranian coast of the Persian Gulf, a protected biosphere reserve at the northern edge of mangrove distribution in the Indian Ocean (26.8°N, 55.75°E)(Fig. 1). The northwest of Qeshm Island has the largest mangrove area of Iran, composed exclusively of *Avicennia marina*, growing in the high intertidal area, with tree heights of 3 to 6 m (Spalding et al., 2010). The area is characterized by a plateau mangrove where the mangrove floor is flooded only during

spring tides. The mangroves extend 5-50m inland as a fringe along the creek banks. During neap tides, inundation is restricted to the creek networks. Thus, the mangrove forests proper is directly accessible for fishes approximately <10% of the time. The tide is semidiurnal, with tidal ranges from 1 - 3 m at neap tides and 3 - 4 m at spring tides (Reynolds, 2002). This tidal regime produces relatively strong flushing of the mangrove creek systems. The region is arid with an annual precipitation below 200 mm (Reynolds, 2002). High temperatures in summer and dry winds in winter can cause 1 – 2 m of evaporation per year creating salinities >39, typical for most Gulf waters (Sheppard et al., 2010). The daily air temperatures fluctuated between 12 and 24 °C in winter, and between 30 and 45 °C in summer; humidity was 75 % in both seasons; no precipitation was recorded during the entire sampling period (Qeshm Meteorological Station, data received as personal communication).

Two sites on Qeshm Island were chosen as sampling sites: site A with 4 mangrove-lined creeks and site B with 2 un-vegetated creeks. Although multiple creeks were sampled at each site, creeks were along the same main channels and so could not be considered true replicates; for this reason results have been aggregated into just the two sites A and B. The distance between the sites was ca. 4 km (Fig. 1). Site A was located in an extensive mangrove forest which was virtually devoid of human influence and pollution. Site B is located at the border of a small artisanal harbor. There are no reefs, seagrass or macroalgae beds in the vicinity of the two sites.

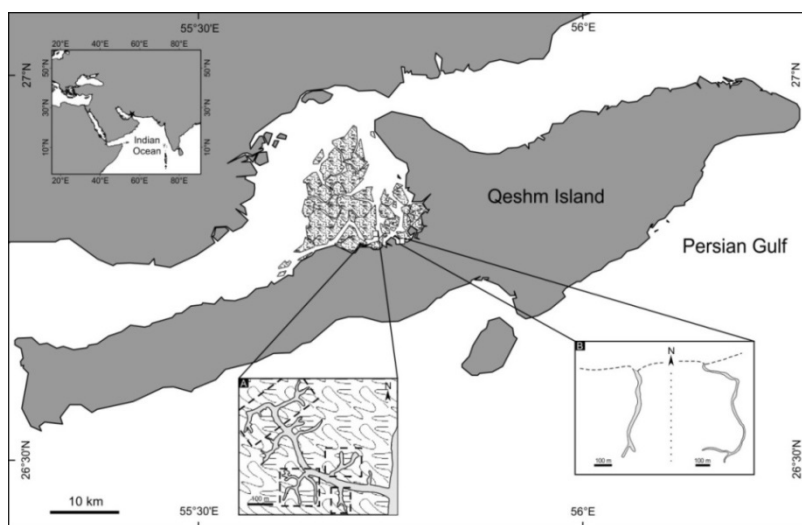


Figure 1 Sampling location in Qeshm Island, Strait of Hormuz, Iran. ★: Location of study area in the region; Mangroves in light gray; A: Mangrove-lined site with 4 intertidal creeks, B: Un-vegetated site (2 bare intertidal creeks).

Sample collection

Various potential food sources (mangrove leaves, microphytobenthos (MPB), plankton, particulate organic matter (POM), sediment organic matter (SOM)), macrobenthos (shrimps & crabs) and fishes were collected for carbon and nitrogen isotopic analysis at both sites in December 2011 and February 2012 (cool, dry period) and in August 2012 (hot, dry period).

Samples of fresh (green) *A. marina* leaves were hand-picked. Decomposing mangrove leaves (yellow) were also collected from the bottoms of the creeks and combined for the analysis. MPB was collected at low tide by gently scraping off the visible mats from the sediment surface. SOM was collected from the top layer of the sediment with a spoon. POM was collected during ebb tide and plankton was sampled at high water after sunset by filtering 10 l of water through plankton nets (10 μm mesh size for phytoplankton, 200 μm for zooplankton). Since it was not possible to obtain phytoplankton samples free of zooplankton, phytoplankton samples were a mixture of phyto- and zooplankton. Plankton and POM samples were filtered on pre-combusted (4 h, 450°C) Whatmann GF/F glass fiber filters. Each filter was sun-dried and stored in a clean glass vial. Benthic invertebrates (shrimps & crabs) were collected with a hand net. Fish were collected with block nets (20 x 5 m x 12 mm mesh size) set at slack high water at spring and neap tides in both habitat types and seasons (M. Shahraki Unpubl. data) and assigned to 4 trophic guilds (detritivores (DV), zooplanktivores (ZP), macrobenthivores (MB), omnivores (OV)) based on findings from previous studies (Woodland, 1984; Yamashita et al., 1987; Gandhi, 2002; Kiso and Mahyam, 2003; Elliott et al., 2007; Hajisamae and Ibrahim, 2008; Tse et al., 2008; Chew et al., 2012; Froese and Pauly, 2012; Uddin et al., 2012).

For the fish samples, white muscle tissue (1 - 2 g) was taken from below the anterior end of the dorsal fin. For shrimps and crabs shell or exoskeleton were removed and soft tissues were extracted for analysis. All samples were dried at 60 °C for 48 h. Fish and benthic invertebrate white muscle tissue was used because it is less variable in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ than other tissue types (Pinnegar and Polunin, 1999) and because it reflects the food assimilated over a longer time period of several weeks (Gearing, 1991). Tissue lipid content is known to affect bulk $\delta^{13}\text{C}$ because lipids are depleted in $\delta^{13}\text{C}$ relative to proteins and carbohydrates (DeNiro and Epstein, 1978; McConnaughey and McRoy, 1979). To account for lipids, Following (Post et al., 2007), prior to statistical analysis, carbon isotopic values of fish and invertebrates were

normalized for lipid content following the mathematical normalization technique of Post et al. (2007). Correction factor for $\delta^{13}\text{C}$ was used based on C:N values (i.e. C:N ratios >3.5 for lipid-rich tissue). This normalization changed isotope values by an average of 0.2‰.

For $\delta^{13}\text{C}$ -DIC (dissolved inorganic carbon), 20 ml amber-colored glass bottles were filled with water samples and preserved with a mercury chloride solution. All samples were sealed and stored cool until analysis at the Leibniz Center for Tropical Marine Ecology (ZMT), Bremen, Germany.

For microphytobenthos community composition, samples from daytime spring high tides were taken, fixed with 4% formaldehyde and in the lab, 5 samples were analyzed for each site. A sub-sample from each of the original mat samples was removed using a scalpel. Each sub-sample was placed in 100 ml of filtered seawater. A 1 ml sub-sample was extracted from the suspension and equally divided into 3 glass slides. The number of cells on each slide was counted to give the number of algal cells per ml using Axioskop (Zeiss) and followed by taxonomical determination to genera level using (Al-Hasan and Jones, 1989).

In addition, water parameters (water temperature and salinity) were regularly measured (WTW Multisonde 3430) in both mangrove and un-vegetated sites at slack high water.

Sample analysis

Samples for stable isotope analysis were ground to powder with a mortar and pestle. For samples rich in carbonates such as SOM and filters of POM and plankton, sub-samples were prepared for $\delta^{13}\text{C}$ analysis by treatment with dilute hydrochloric acid, followed by rinsing with deionized water and drying. Remaining untreated sub-samples were used for $\delta^{15}\text{N}$ analysis as acid has been reported to affect $\delta^{15}\text{N}$ values (Goering et al., 1990; Bunn et al., 1995). Elemental values for C and N were determined with an Euro EA3000 Elemental Analyzer. Samples for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were analyzed with a Delta Plus isotope ratio mass spectrometer connected to the Carlo Erba Flash EA elemental analyzer via a Finnigan ConFloII interface.

The carbon and nitrogen analysis are expressed in conventional delta (δ) notation as parts per mil (‰), where the isotopic ratio of $^{15}\text{N}/^{14}\text{N}$ is expressed relative to air and $^{13}\text{C}/^{12}\text{C}$ relative to the international PDB standard, as defined by the equation:

$$\delta X(\text{‰}) = [(R_{\text{sample}} - R_{\text{standard}}) / (R_{\text{standard}})] \times 1000$$

where X is ^{13}C or ^{15}N , and R represents the ratios $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. The analytical precision of the measurement was $<0.06\text{‰}$ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Samples with higher $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values are “heavier” or enriched in the heavy ^{13}C or ^{15}N isotope, while samples with lower values are “lighter” and depleted in ^{13}C or ^{15}N .

Carbon isotopes in DIC were measured with a GasBench II, coupled with a MAT 253, both from Thermo Scientific. The reference gas used in measurements was calibrated with NBS19 and with Solenhofener Plattenkalk (SPK) was routinely run as a control along with samples.

Data analysis

Shapiro-Wilk test were used to test the normality of stable isotope data. Independent samples t-tests (Equal Variance Test (EV), and Mann-Whitney Rank Sum Test (MWR) in case the data were not normally distributed) were used to assess site and seasonal differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of food sources and fishes belonging to the same species collected from mangrove-lined and un-vegetated sites. Since we did not detect any seasonal differences in the carbon and nitrogen stable isotope values of the same fish species, the isotopic values of fish species were pooled by season. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ among different feeding guilds were also tested with independent t-tests.

Two-way ANOVAs (TA) followed by Tukey tests were used to test for the effects of site and season on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of main food groups and feeding guilds (DV, ZP, MB). Food sources were grouped into mangrove leaves (green and yellow), pelagic sources (phytoplankton, zooplankton and POM), benthic sources (MPB, SOM) and macrobenthos (crabs). The shared species belonging to the same feeding guilds in two sites were considered for two-way ANOVA. Species and feeding guilds were grouped as LK and AC (detritivores); LD and TV (zooplanktivores) and PL, PK and AL (macrobenthivores). All statistical tests were performed using SigmaPlot 12.3.

Potential minimum and maximum mangrove contributions to fish diets were calculated from $\delta^{13}\text{C}$ data within a framework of two-source mixing models (Fry, 2013a, b). There were several mixtures of plant food sources (mangroves, phytoplankton, and microphytobenthos) that could explain isotope results for fish, and unfortunately no source mixture was uniquely indicated. In this situation of underdetermined isotope solutions, it is still possible to calculate minimum and

maximum potential contributions of plants to fish diets, and we used conventional two-source mixing models in these calculations (Fry, 2006). These models require end-member sources which we characterized from measured data and literature estimates. Green and yellow mangrove leaves measured in this study averaged -28.3‰ and a recent study (Bui and Lee, 2014) indicates that macrofaunal consumers of mangroves average 5.2‰ enriched in $\delta^{13}\text{C}$ when fed mangroves, so that in our system, a value of -23.1‰ was expected for fish that were 100% reliant on mangroves. For fish that were 0% reliant on mangroves at our sites, we used average isotope values for fish species or groups from our non-mangrove sites. Values between the two source values for 0% and 100% reliance on mangroves (sources 1 and 2, respectively) indicated possible maximum mangrove contributions for a fish sample of interest according to two-source mixing:

$$\text{Maximum Mangrove Contribution (\%)} = 100 * (\delta_{\text{SAMPLE}} - \delta_{\text{SOURCE1}}) / (\delta_{\text{SOURCE2}} - \delta_{\text{SOURCE1}})$$

Samples were fish averages at the whole community level, at the level of fish functional groups, and at the species level for seven species where several individuals were caught at both the mangrove and non-mangrove sites. Errors associated with the two-source calculations were evaluated using the IsoError programming (Phillips and Gregg, 2001). The inputs for IsoError were the $\delta^{13}\text{C}$ values of mean, standard deviation, and number of samples measured for mangrove and no-mangrove sources. The output generated by the set of IsoError equations provides estimate contributions for each source (0-100%), standard errors for these contribution estimates, and approximate 95% confidence intervals for source contributions, considering error propagation.

In our study system, we generally found that "aggregated basal plant sources" (phytoplankton and MPB) could be substituted for mangroves into the 2-source model above and also explain the observed fish isotope values without any involvement of mangroves. Thus, the minimum required mangrove contributions were always zero. Stated another way, the above two-source calculation represents a theoretical possible or maximum mangrove contribution, but a contribution that could also be zero based on measured data. Overall, the minimum and maximum mangrove contributions ranged between respectively 0% and 36% for the various fish groups and species tested in this study. Other food sources were aggregated in the 2-source model as

various types of “algae”, and “algal” contributions to the various fish groups ranged from a minimum of 64% to a maximum of 100%.

RESULTS & DISCUSSION

Isotopic composition of potential food sources

Four groups of potential sources were considered 1) mangrove leaves (G and Y), 2) benthic sources (MPB and SOM), 3) pelagic sources (plankton (phyto- and zooplankton) and POM), 4) macrobenthos (shrimps & crabs).

In mangrove-lined creeks, mangrove leaves were isotopically distinct from plankton and MPB (Fig. 2), with the most ^{13}C -depleted values for mangroves ($-28.2\pm 1.1\text{‰}$), intermediate values for plankton ($-22.8\pm 1.5\text{‰}$) and enriched values for MPB ($-17.8\pm 2.1\text{‰}$) (Table 2). In the un-vegetated site, plankton was the most ^{13}C -depleted ($-21.8\pm 1.7\text{‰}$), whereas MPB was even more ^{13}C -enriched ($-13.8\pm 3\text{‰}$) (Table 2). Tracing the origin of POM and SOM can be complex due to the many potential sources (Wu et al., 2003). However, the isotopic composition of POM in both sites was similar to plankton, suggesting a high contribution of phyto- and zooplankton to POM, while $\delta^{13}\text{C}$ values of SOM were closely linked to MPB (Fig. 2).

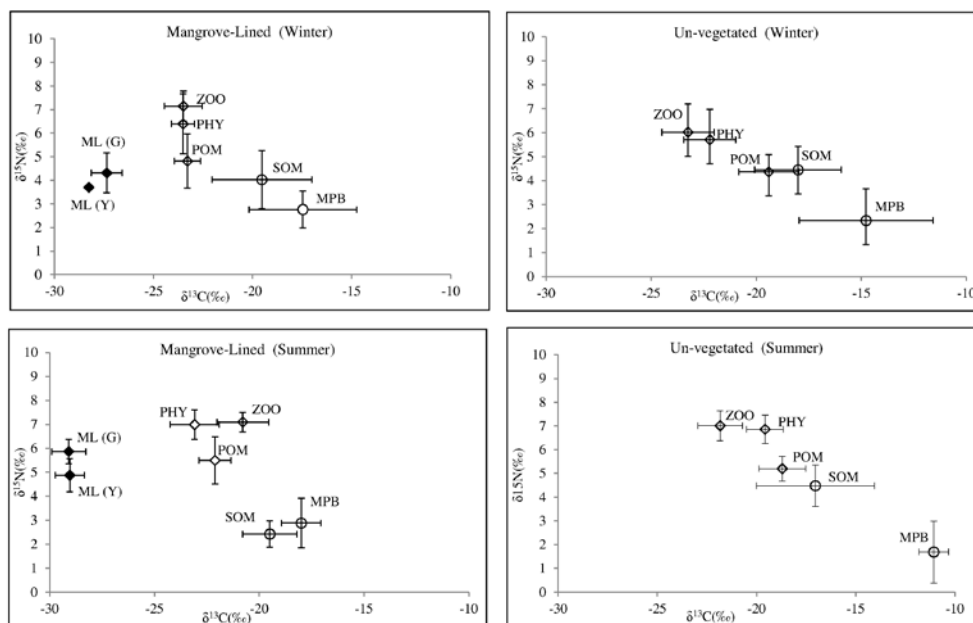


Figure 2 Plot of mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (\pm SD) of different food sources from the mangrove-lined and un-vegetated sites in winter and summer, Qeshm Island, Iran. Black and white dots represent mangrove and non-mangrove sources, respectively. Green and yellow mangrove leaves (ML-G and ML-Y); phytoplankton (PHY), zooplankton (ZOO), particulate organic matter (POM), sediment (SOM), microphytobenthos (MPB).

The mangrove leaves had a mean $\delta^{13}\text{C}$ value of -28.2‰ , which is in the range calculated for mangroves (median = -28.1‰ ; the 25th and 75th percentiles -29.4‰ to -27.0‰) (Bouillon et al., 2008), and falls well within the ranges found for mangroves around the globe (Marguillier et al., 1997; Abrantes and Sheaves, 2008; Giarrizzo et al., 2011). In this study, MPB had $\delta^{13}\text{C}$ range from -17‰ to -13‰ and fall in the most ^{13}C -enriched part of the spectrum for carbon sources in aquatic environment reported by (Bouillon et al., 2008). In relation to plankton that ranged from -23‰ to -21‰ , MPB was enriched in $\delta^{13}\text{C}$ in both sites due to cyanobacteria which is known to be enriched in $\delta^{13}\text{C}$ owing CO_2 -concentrating-mechanism (CCM) (Price et al., 2008). Benthic microalgae in marine waters are known to be more ^{13}C -enriched (by an average of $\sim 5\text{‰}$) relative to phytoplankton due to the thicker boundary layer experienced by benthic algae (France, 1995; MacLeod and Barton, 1998).

The mean $\delta^{13}\text{C}$ values of MPB and POM food sources in the mangrove-lined site were 4-5‰ more depleted than in the un-vegetated site. In the presence of mangroves, aquatic primary producers can have lower than expected $\delta^{13}\text{C}$ due to the incorporation of ^{13}C -depleted DIC of mangrove origin (Bouillon et al., 2008). In our study, however, the $\delta^{13}\text{C}$ DIC values were very similar at -0.6‰ and -0.9‰ for mangrove and un-vegetated sites, respectively. $\delta^{13}\text{C}$ DIC measurements in the oligotrophic surface waters of the Arabian Sea close the Strait of Hormuz show values of 1.5‰ (Rixen et al., 2011). These values are in line with those of Bouillon et al. (2008), indicating that the respiration of organic matter affects the $\delta^{13}\text{C}$ DIC value in our sites of study. The reasons for the ^{13}C depletion in MPB and POM at the mangrove site remain unknown at this time, but may be related to differences in the MPB community itself, a community that can contribute to POM when tides resuspend sediments. Cyanobacteria dominated the MPB community at the un-vegetated site, while diatoms dominated the MPB community at the mangrove site. (see Table S1 in the Supplement). Cyanobacteria typically show the most enriched $\delta^{13}\text{C}$ values among aquatic autotrophs (e.g., Al-Zaidan et al., 2006). Higher $\delta^{13}\text{C}$ values of plankton could be also partly explained by the slightly more saline condition in the un-vegetated site. Higher $\delta^{13}\text{C}$ values of zooplankton and POM were partly related to increased salinities in estuarine mangroves in India (Bouillon et al., 2000).

$\delta^{15}\text{N}$ values of food sources did not differ between sites (EV, $p > 0.05$). $\delta^{15}\text{N}$ values averaged 3.2‰ and 2.0‰ for MPB at the mangrove and un-vegetated sites, respectively, and to 7‰ and 6.5‰ for zooplankton (Table 2). The mean $\delta^{15}\text{N}$ values of

mangrove leaves were 4.6‰ and 5.2‰ for green and yellow leaves, respectively. Low $\delta^{15}\text{N}$ values of MPB would be consistent with presence of benthic nitrogen-fixing cyanobacteria in both sites. Low $\delta^{15}\text{N}$ values are related to a large contribution of fixed nitrogen from the atmosphere, as the $\delta^{15}\text{N}$ value of atmospheric N_2 is defined as 0‰ (Yamamuro et al., 1995; France et al., 1998). High $\delta^{15}\text{N}$ values of phytoplankton (6.2‰) may reflect some contribution from zooplankton (6.5‰; Table 2).

Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of macrobenthos did not show significant difference between sites (EV; $p > 0.05$). $\delta^{13}\text{C}$ values of macrobenthos were very close to the values of MPB, suggesting that macrobenthos relied on MPB. In other mangroves, e.g. along the southeast coast of India and Tanzania, $\delta^{13}\text{C}$ values of benthic invertebrates were very close to the $\delta^{13}\text{C}$ values of benthic algae (Bouillon et al., 2002; Kruitwagen et al., 2010). Similarly in another study in the Caribbean, the mean value of $\delta^{13}\text{C}$ of invertebrate spanned in the range of algae (Kieckbusch et al., 2004).

Abundant feeding guilds

The fish communities were dominated by 12 and 8 species (with relative abundance >1%) from the mangrove and un-vegetated sites, respectively. These species were selected for the carbon and nitrogen isotope analysis because of their high abundance and because they are the representative species in the region. Overall, a total of 29 and 22 fish species were caught in the mangrove-lined and un-vegetated sites, respectively and the Chao1 species richness estimator (S_{Chao1}) reached an asymptote in both sites (M. Shahraki Unpubl. data), emphasizing that the species richness of the intertidal fish communities was well-characterized by our sampling so that additional sampling should not have yielded additional species (Gotelli and Colwell, 2011). In our study, the low fish species richness and dominance of just a few species compared to other tropical regions is likely due to the extreme environmental conditions. Salinity averaged 38.3 ± 0.5 in the mangrove-lined site and 40.3 ± 2.3 in the un-vegetated site. Moreover, $>20^\circ\text{C}$ seasonal fluctuations in water temperature likely enhance the stressful condition for fishes (Table S2 in the Supplement).

Detritivores were the most abundant feeding guild in both sites (44% and 81% in the mangrove-lined and un-vegetated sites, respectively), followed by zooplanktivores (32%; 8%), macrobenthivores (18%; 7%), and omnivores (5%; <1%) (Table 1). The dominance of detritivores in our study sites suggests the importance of benthic (detritus) food webs in the intertidal creeks at Qeshm Island.

Isotopic composition of fish

The $\delta^{13}\text{C}$ values of different feeding guilds differed between the mangrove-lined and the un-vegetated sites (Table 3; TA, $p < 0.05$). However, differences in $\delta^{13}\text{C}$ values at the species level were only observed for *P. longimanus*, *A. latus*, and *Pomadasy kaakan* (Table 2; EV, $p < 0.05$). The spatial variability in isotopic values of the feeding guilds and some species could be explained by difference in $\delta^{13}\text{C}$ of sources between habitats. The spatial differences in $\delta^{13}\text{C}$ of benthic sources (e.g. MPB) were reflected in the $\delta^{13}\text{C}$ of fishes (DV and MB) and spatial shift in $\delta^{13}\text{C}$ of pelagic sources can be tracked in the $\delta^{13}\text{C}$ zooplanktivorous fishes. This was consistent with strong overall fish residency at the sites, even while recognizing fish make at least limited movements with tides to avoid being stranded (Lugendo et al., 2007; Kruitwagen et al., 2010).

Table 1 Dominant fish (species with relative abundance >1%) in mangrove-lined and un-vegetated sites in Qeshm Island, Iran. Relative abundance of dominant species (measured on the total number of fish in each habitat type) (RA). Trophic guilds (TG): detritivores (DV), zooplanktivores (ZP), macrobenthivores (MB) and omnivores (OV) according to available literature (see Material & Method section). Dash lines indicate 0.

Species	RA(Mangrove)	RA(Un-vegetated)	TG
<i>Liza klunzingeri</i>	41	47	DV ¹
<i>Leiognathus daura</i>	18	5	ZP ²
<i>Pentaprion longimanus</i>	10	5	MB ³
<i>Thryssa vitrirostris</i>	8	2	ZP ⁴
<i>Scatophagus argus</i>	5	-	OV ⁵
<i>Acanthopagrus latus</i>	4	2	MB ⁶
<i>Anodontostoma chacunda</i>	3	34	DV ⁷
<i>Sardinella longiceps</i>	3	-	ZP ²
<i>Pomadasy kaakan</i>	3	-	MB ^{1,2}
<i>Sardinella gibbosa</i>	2	-	ZP ²
<i>Lutjanus johnii</i>	1	-	MB ⁸
<i>Ilisha melastoma</i>	1	-	ZP ⁴
<i>Gerres longirostris</i>	-	2	MB ⁹
<i>Sillago sihama</i>	-	1	ZP ^{2,6}

1: Uddin et al (2012); 2: Hajisamae and Ibrahim (2008); 3: Yamashita et al (1987); 4. Elliot et al (2007), 5. Gandhi (2002); 6: Tse et al (2008); 7: Chew et al. (2012); 8: Kiso and Mahyam (2003); 9: Woodland (1984).

Table 2 Mean carbon and nitrogen isotope values (\pm SD) of food sources and consumers in mangrove-lined and un-vegetated intertidal creeks, Qeshm Island, Iran. N: Number of replicates. Differences were considered to be significant when $p < 0.05$ (bold values).

	Key	Mangrove-lined site			Un-vegetated site			p values	
		N	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	N	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$
Food Sources									
<i>Avicennia marina</i> (green)	ML(G)	20	4.6 \pm 0.7	-28.2 \pm 1.1					
<i>Avicennia marina</i> (yellow)	ML(Y)	6	5.4 \pm 1.0	-28.9 \pm 0.7					
Microphytobenthos	MPB	22	3.2 \pm 1.6	-17.9 \pm 1.9	11	2.0 \pm 1.2	-13.1 \pm 2.8	0.06	0.001
Sediment organic matter	SOM	12	3.6 \pm 1.2	-19.5 \pm 2.1	10	4.5 \pm 0.8	-17.4 \pm 2.4	0.08	0.4
Phytoplankton	PHY	26	6.9 \pm 0.7	-22.3 \pm 1.6	14	6.2 \pm 1.1	-21.8 \pm 1.6	0.7	0.001
Zooplankton	ZOO	24	7.0 \pm 0.5	-23.5 \pm 0.9	13	6.5 \pm 1	-22.6 \pm 1.3	0.1	0.01
Particulate organic matter	POM	30	5.0 \pm 1.1	-22.8 \pm 0.8	11	4.7 \pm 0.7	-19.1 \pm 1.2	0.3	0.001
Macrobenthos									
<i>Eurycarcinus spp.</i>	EUR	4	9.1 \pm 0.4	-14.6 \pm 0.5	3	6.8 \pm 2.5	-11.6 \pm 1.6	0.4	0.06
<i>Macrophetalmus spp.</i>	MAC	2	7.1 \pm 1.6	-12.1 \pm 2.3	2	6.5 \pm 1.7	-11.3 \pm 1.5	0.1	0.3
<i>Portunus spp.</i>	POR	2	6.9 \pm 0	-16.2 \pm 0.1	2	7.8 \pm 1.3	-17.1 \pm 3.2	0.2	0.5
<i>Penaeus merguinsis</i>	PM	16	8.2 \pm 1.9	-15.0 \pm 1.1					
Fish									
Detritivores (DV)									
			6.7 \pm 0.6	-14.1 \pm 0.7		7.6 \pm 1.4	-12.1 \pm 1.5		
<i>Liza klunzingeri</i>	LK	8	6.5 \pm 0.6	-14.3 \pm 0.8	12	8.0 \pm 1.7	-11.5 \pm 1.3	0.07	0.1
<i>Anodontostoma chacunda</i>	AC	6	7.0 \pm 0.5	-13.8 \pm 0.6	6	6.9 \pm 0.6	-13.5 \pm 1.0	0.03	0.7
Zooplanktivores (ZP)									
			12.1 \pm 1.1	-16.6 \pm 1.6		11.5 \pm 1	-15.6 \pm 2.1		
<i>Leiognathus daura</i>	LD	6	12.9 \pm 0.5	-19.0 \pm 1.3	5	12.3 \pm 0.7	-17.9 \pm 2.0	0.08	0.2
<i>Thryssa vitrirostris</i>	TV	5	11.4 \pm 0.7	-14.6 \pm 0.5	6	10.9 \pm 0.7	-14.2 \pm 0.5	0.03	0.8
<i>Sardinella longiceps</i>	SL	3	11.3 \pm 0.7	-17.9 \pm 0.3					

	Key	Mangrove-lined site			Un-vegetated site			p values	
		N	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	N	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$
<i>Sardinella gibbosa</i>	SG	2	11.4±0.6	-18.1±0.7					
<i>Ilisha melastoma</i>	IM	3	12.3±1.8	-16.5±1.6					
<i>Sillago sihama</i>	SS	3	13.1±0.2	-15.4±0.5	3	11.7±1.0	-14.5±0.8	0.3	0.7
Macrobenthivores (MB)			9.9±1.9	-16.5±1.5		11.1±1.6	-14.5±2.5		
<i>Pentaprion longimanus</i>	PL	6	12.5±1.1	-17.8±1.1	5	12.6±0.6	-16.7±0.9	0.3	0.001
<i>Pomadasys kaakan</i>	PK	8	9.9±1.7	-16.4±0.6	6	10.5±0.5	-13.3±0.9	0.3	0.004
<i>Acanthopagrus latus</i>	AL	8	8.0±0.7	-16.1±1.4	3	8.6±1.2	-12.2±0.7	0.3	0.001
<i>Lutjanus johnii</i>	LJ	8	9.9±1.0	-15.2±1.8					
Omnivores (OV)									
<i>Scatophagus argus</i>	SA	3	9.7±0.5	-13.9±0.8					

Table 3 Mean carbon and nitrogen isotope values (\pm SD) of main food source groups and feeding guilds (DV, ZP, MB) in mangrove-lined and un-vegetated intertidal creeks in winter and summer, Qeshm Island, Iran. Differences were considered to be significant when $p < 0.05$. Food sources were mangrove leaves, pelagic sources (phytoplankton, zooplankton and POM), benthic sources (MPB & SOM) and macrobenthos (crabs). Fish species considered for each trophic guilds are provided in brackets. Bold p values indicate significant differences.

$(\delta^{13}\text{C})$	Mangrove-lined site		Un-vegetated site		2 way ANOVA ($p < 0.05$)		
	winter	summer	winter	summer	site	season	site*season
Food sources							
<i>A. marina</i> (G & Y)	-27.3 \pm 0.7(11)	-29.7 \pm 0.7(15)	-	-	-	0.9	
Benthic sources	-18.3 \pm 2.7(14)	-18.5 \pm 1.2(20)	-16.1 \pm 3.1(10)	-14.3 \pm 3.7(11)	<0.001	0.7	0.9
Pelagic sources	-23.5 \pm 0.6(45)	-21.9 \pm 1.4(35)	-21.7 \pm 2.0(21)	-20.1 \pm 1.6(17)	<0.001	<0.001	0.04
Macrobenthos (crabs)	-15.8 \pm 0.7(5)	-12.0 \pm 3.8(3)	-15.3 \pm 3.2(2)	-12.2 \pm 1.5(5)	0.6	0.02	0.5
Feeding guilds							
Detritivores (LK, AC)	-14.2 \pm 0.9(8)	-14.1 \pm 0.4(6)	-12.0 \pm 2.1(9)	-12.1 \pm 0.8(9)	<0.001	0.2	0.1
Zooplanktivores (LD, TV)	-16.8 \pm 2.2(5)	-15.9 \pm 1.3(6)	-17.3 \pm 2.7(5)	-14.7 \pm 1.1(6)	0.007	0.6	0.1
Macrobenthivores (PL, PK, AL)	-16.6 \pm 1.5(13)	-16.8 \pm 0.6(9)	-14.8 \pm 3.2(7)	-14.2 \pm 0.3(6)	<0.001	0.06	0.4
($\delta^{15}\text{N}$)							
Food sources							
<i>A. marina</i>	4.2 \pm 0.8(11)	5.1 \pm 0.8(15)	-	-	-	0.2	
Benthic sources	3.3 \pm 1.7(14)	3.4 \pm 1.9(20)	3.1 \pm 1.5(10)	3.2 \pm 1.7(11)	0.7	0.3	0.1
Pelagic sources	6.0 \pm 1.4(45)	6.5 \pm 1.0(35)	5.4 \pm 1.2(21)	6.4 \pm 0.9(17)	0.1	0.004	0.2
Macrobenthos (crabs)	8.0 \pm 0.1(5)	8.1 \pm 1.9(3)	6.0 \pm 1.1(2)	7.4 \pm 2.0(5)	0.1	0.1	0.5
Feeding guilds							
Detritivores (LK, AC)	6.3 \pm 0.4(8)	7.2 \pm 0.2(6)	7.9 \pm 1.3(9)	7.4 \pm 1.6(9)	0.06	0.6	0.1
Zooplanktivores (LD, TV)	11.9 \pm 0.0 (5)	12.4 \pm 1.0(6)	12.0 \pm 0.4(5)	11.1 \pm 1.2(6)	0.06	0.2	0.1
Macrobenthivores (PL, PK, AL)	9.2 \pm 1.8(13)	10.9 \pm 2.3(9)	11.0 \pm 1.9(7)	11.2 \pm 1.2(6)	0.7	0.1	0.4

Regarding fish feeding guilds respectively, average $\delta^{13}\text{C}$ values were lowest for zooplanktivores ($\delta^{13}\text{C}_{\text{mean}} = -16.6 \pm 1.6\text{‰}$ and $-15.6 \pm 2.1\text{‰}$ respectively in the mangrove-lined and un-vegetated sites), intermediate for macrobenthivores ($\delta^{13}\text{C}_{\text{mean}} = -16.5 \pm 1.5\text{‰}$ and $-14.5 \pm 2.5\text{‰}$) and the highest for detritivores ($\delta^{13}\text{C}_{\text{mean}} = -14.1 \pm 0.7\text{‰}$ and $-12.1 \pm 1.5\text{‰}$), (Table 2; EV, $p > 0.05$). This pattern indicates that zooplanktivores rely on more ^{13}C -depleted food sources, while detritivores feed on the more ^{13}C -enriched food sources. This suggests high dietary reliance of detritivores on benthic sources and zooplanktivores on pelagic sources. Different carbon isotopic values for benthic and planktonic sources are the likely reason for the relative $\delta^{13}\text{C}$ enrichment of benthic and pelagic consumers, with heavier $\delta^{13}\text{C}$ values in the benthic than pelagic pathway. The $\delta^{13}\text{C}$ values of herbivorous, omnivorous and planktivorous fishes were more depleted than the predatory fish in fringe mangrove in the Caribbean region (Kieckbusch et al., 2004). This has been explained by the dietary reliance of non-predatory fish on more local sources.

The $\delta^{15}\text{N}$ values did not differ significantly between habitats at the species or trophic guild level, with exceptions observed in 2 species (*A. chacunda*, *T. vitrirostris*) (Table 2 & 3, TA, $p > 0.05$ and EV, $p < 0.05$). Mean $\delta^{15}\text{N}$ values of all fish species ranged between 6.5‰ and 13.1‰ in the mangrove-lined and from 6.6‰ to 12.6‰ in the un-vegetated site (Table 2). The $\delta^{15}\text{N}$ values differed significantly among trophic guilds in both sites (MWR; $p < 0.05$), with lowest values for detritivores ($\delta^{15}\text{N}_{\text{mean}} = 6.7 \pm 0.6\text{‰}$ in the mangrove-lined, and $7.6 \pm 1.4\text{‰}$ in the un-vegetated sites) and highest values for zooplanktivores ($\delta^{15}\text{N}_{\text{mean}} = 12.1 \pm 1.1\text{‰}$ in the mangrove-lined, and $11.5 \pm 1\text{‰}$ in the un-vegetated sites). Macrobenthivores and omnivores showed intermediate $\delta^{15}\text{N}$ values. Similar to other food web studies, the zooplanktivores in Qehsm Island had the highest $\delta^{15}\text{N}$ values, while detritivores had the lowest $\delta^{15}\text{N}$ values and carnivores had similar or even higher $\delta^{15}\text{N}$ than zooplanktivores. (Abrantes and Sheaves, 2009; Vaslet et al., 2012). These differences in $\delta^{15}\text{N}$ between zooplanktivores and detritivores are most likely due to the approximately 4‰ differences in $\delta^{15}\text{N}$ between phytoplankton and MPB (Table 2).

The isotope data and known feeding biology of the fish were consistent with the views that there were two main pathways for potential food sources to support the fish community in the area, irrespective of habitat type (mangrove-lined vs. un-vegetated site) (Fig. 3 a, b):

1- Pelagic pathway: plankton (phyto- and zooplankton) and POM contributing directly or indirectly to zooplanktivores.

2- Benthic pathway: MPB and SOM assimilated directly by detritivores (e.g. *L. klunzingeri*) or indirectly assimilated by shrimps and crabs and transferred to macrobenthivores and omnivores.

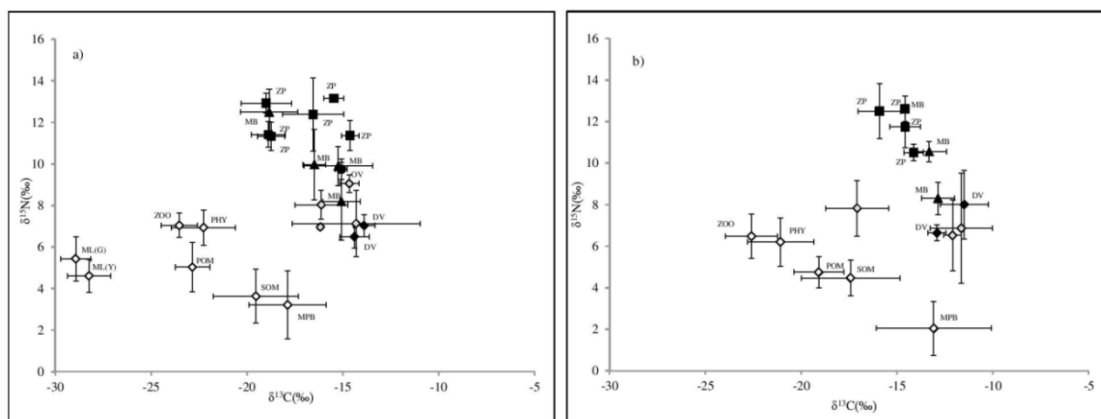


Figure 3 Plot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of food sources and consumers in (a) mangrove-lined and (b) un-vegetated sites. White dots represent food sources: Green and yellow mangrove leaves (ML-G and ML-Y, respectively), phytoplankton (PHY), zooplankton (ZOO), particulate organic matter (POM), sediment (SOM), microphytobenthos (MPB). Light gray dots symbolize macrobenthos (crabs & shrimps) and black dots represent different feeding guilds: Zooplanktivores (ZP), Macrobenthivores (MB), Detritivores (DV), Omnivores (OV).

The majority of fish species relied on the benthic pathway via feeding on MPB and organic sediment and also macrobenthos (i.e. crabs, shrimps). Carbon isotope values of macrobenthos and macrobenthivores widely overlapped and the values were very close to the values of MPB, suggesting that macrobenthos relied on MPB as a food source. Zooplanktivores relied on the pelagic pathway by feeding on plankton and particulate organic matter. The low $\delta^{13}\text{C}$ values of zooplanktivores corresponded to the low $\delta^{13}\text{C}$ values of zooplankton and phytoplankton, indicating that these items comprise the major food sources for these consumers. Also, zooplanktivores had their $\delta^{15}\text{N}$ close to the pelagic food sources, which had relatively high $\delta^{15}\text{N}$ values. On the other hand, detritivores relied on the more ^{13}C -enriched sources (MPB and SOM). The greater dependence of pelagic consumers on phytoplankton and of benthic consumers on benthic macroalgae and marsh vegetation also has been reported from an estuarine food web on the USA east coast (Deegan and Garritt, 1997).

Temporal variability in isotope composition of food sources and fish feeding guilds

There were few significant seasonal differences in the stable carbon and nitrogen isotope values of the potential food sources, although most $\delta^{13}\text{C}$ values were slightly higher in summer. Pelagic sources (phyto- zooplankton and POM) were the only food resource with significantly (TA, $p < 0.05$) higher $\delta^{13}\text{C}$ values in summer (Table 3), with an average summer increase in $\delta^{13}\text{C}$ of 1.6‰. The seasonal variability of plankton (phyto- and zooplankton) could be related to higher water temperatures in summer which provide suitable condition for photosynthetic production, which was reflected by a slightly higher phytoplankton biomass in summer ($0.35 \pm 0.08 \text{ mg ml}^{-1}$ in summer and $0.28 \pm 0.1 \text{ mg ml}^{-1}$ in winter). But further experiments are needed to confirm this hypothesis. Higher $\delta^{13}\text{C}$ in zooplankton during the periods of higher phytoplankton abundance and biomass has been reported from an Indian mangrove estuary (Bouillon et al., 2000).

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the different feeding guilds did not show any seasonal variability (TA, $p > 0.05$) (Table 3). The seasonal variability of plankton was also not reflected in the feeding guilds. However, seasonal variability in the carbon and nitrogen isotopic values of species from different trophic guilds (i.e., primary, secondary, and tertiary consumers) in an estuarine system in Florida were associated with food source availability (Olin et al., 2012). The lack of seasonal shifts in fish isotope values could be partly explained by no shifts in diet, habitat and stable isotope composition of sources. Our results of no seasonal shifts in fish isotopes contrast to those for a western Mediterranean lagoon where seasonal shifts were explained by dietary ontogenetic shift and intra-specific food partitioning (Vizzini and Mazzola, 2003). More studies are needed to elucidate controls of seasonal shifts in food webs.

Contribution of Mangrove leaves in aquatic food webs

At the level of the whole community and functional groups, maximum mangrove contributions ranged from 13 to 23%, with means and SE of $22 \pm 4\%$ for the whole community, $13 \pm 8\%$ for zooplanktivores, $18 \pm 3\%$ for detritivores, and $23 \pm 7\%$ for macrobenthivores (Fig. 4). For individual species caught at both mangrove and non-mangrove habitats, maximum potential mangrove contributions ranged from 3 to 35% with means and SE of $24 \pm 3\%$ for *L. klunzingeri*, $3 \pm 5\%$ for *A. chacunda*, $21 \pm 17\%$ for *L. daura*, $4 \pm 3\%$ for *T. vitrirostri*, $10 \pm 9\%$ for *Sillago sihama*, $17 \pm 9\%$ for *P.*

longimanus, 32 ± 3 for *P. kaakan*, and 36 ± 5 for *A. latus* (Fig. 4; see also Table S3 in the Supplement).

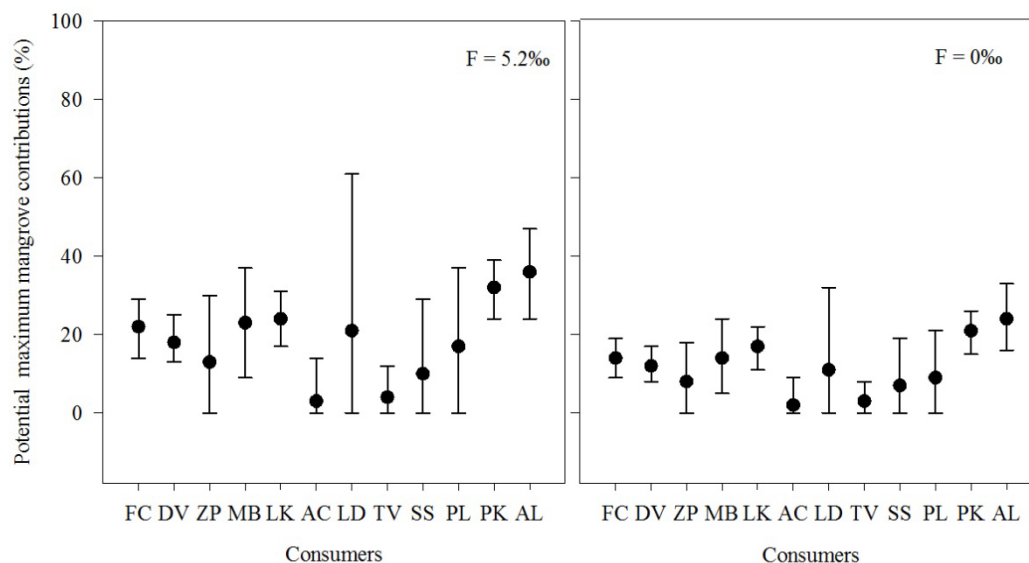


Figure 4 Potential maximum contributions of mangroves to fish diets (mean \pm 95% confidence interval) calculated by IsoError program for the whole fish community (FC), fish functional groups (DV, ZP, MB) and individual fish species (LK, AC, LD, TV, SS, PL, PK, AL; see Table 2 for full species name). Left panel includes a large 5.2‰ fractionation ($F = 5.2\text{‰}$) from mangroves to fish, and the right panel shows low estimates for potential mangrove contributions assuming no fractionation ($F = 0$) with from mangroves to fish. Cumulative trophic $\delta^{13}\text{C}$ fractionation from plants to fish diets (F). This figure shows potential maximum mangrove contributions; required minimum contributions to fish diets were 0% in all cases.

Among these averages for maximum possible mangrove contributions, there was no obvious pattern of detritivore species (*L. klunzingeri* and *A. chacunda*) being markedly more reliant on mangroves than other species, and as stated in Methods, no mangrove contribution was actually required to explain fish isotopes at the mangrove sites. The calculated maximum contributions were non-zero due to 1-4‰ negative shifts in average fish isotope values at the mangrove sites, but at these sites, MPB also shifted in the same negative direction by 4.8‰ (Table 2). Thus, reliance on MPB rather than mangroves could account for the negative isotope shifts for fish at the mangrove sites. Lastly, our maximum calculations for mangroves assumed a large 5.2‰ trophic fractionation between mangroves and fish, with this assumption based on a newly published study (Bui and Lee, 2014). However, older studies indicate that trophic fractionations are smaller for stable carbon isotopes (McCutchan et al., 2003), and values between 0 and 3‰ have been used for fish food webs (e.g., (Schwamborn et al., 2002; Abrantes and Sheaves, 2008). Using these smaller values reduces the

maximum food web support from mangroves, i.e., values would be half the maximum values given above if there is 0‰ trophic fractionation (Fig. 4). Also, if the isotope values for yellow leaves (-28.9‰) is used as the more appropriate value for mangrove detritus instead of the -28.3‰ average of yellow and green leaves, potential maximum mangrove contributions are slightly less than the maxima show in the left panel of Fig. 4, for example $20 \pm 3\%$ instead of $22 \pm 4\%$ for the whole fish community.

In summary, there were four reasons pointing to a conclusion that mangrove food web support is likely quite small or zero at the mangrove sites, i.e., 1) maximum potential contributions averaged only 21% for the mangrove fish community, 2) trophic fractionations, if smaller, would have resulted in lower maximum mangrove inputs, 3) there was not an obvious pattern of detritivorous fishes having a much higher potential trophic reliance on mangroves, and 4) shifts in isotope values of MPB provided a reasonable explanation for the relatively small shifts in fish isotope values at the mangrove sites.

Given the lack of other productive habitats in the proximities of the Qeshm Island mangroves, the low mangrove contribution to fish diets may be mainly due to the low overall productivity of arid mangrove systems, linked to a lack of freshwater input and very low precipitation. This finding is in line with previous observations in Gulf mangroves which pointed out the limited role of mangroves as primary food sources of epibenthic invertebrates (Al-Zaidan et al., 2006; Al-Maslamani et al., 2012). It was also argued that cyanophyta-dominated algal mats associated with tidal flats were a greater contributor to primary productivity in the Gulf as a whole compared to mangroves (Price et al., 1993). However, strong contributions of mangroves in aquatic food webs has been reported in the diet of an endemic shrimp species (*Palaemon khori*) from the east coast of Qatar (Al-Maslamani et al., 2013). Al-Maslamani et al. (2013) suggested that inwelling of external seagrass and plankton foods partially supported resident mangrove fauna. In contrast, invertebrates and fishes in several estuarine mangrove systems, such as in Brazil, Malaysia and Thailand showed a potentially higher reliance on mangroves, along with a generally mixed food web (Rodelli et al., 1984; Giarrizzo et al., 2011; Zagars et al., 2013). This suggests that the rainfall setting, tidal regime and habitat settings may influence how much mangroves contribute to coastal food webs. Furthermore, mangrove forests in Qeshm Island are flooded only during spring tides. This might also influence the role of mangrove as feeding habitat and provide less chance for fishes to utilize mangrove foods.

The mean C/N value of green mangrove leaves was high (C/N ratio of 20) and increased during the degradation (to values of up to 65) (see Fig. S2 in the Supplement). Apparently, there is a faster loss of N than C during mangrove leaf decomposition. The dissolved organic nitrogen (DON) might be preferentially leached and sustain the microbial food web in the mangrove site, which may lead to a high C/N ratio and heavier $\delta^{15}\text{N}$ values in decomposed mangrove leaves. Senescent mangrove leaf litter has been reported as an unattractive food for most animals because it is nutritionally poor (high C/N ratio) (Wolcott and O'Connor, 1992). The carbon of mangrove leaves was likely not stored in the sediment due to the low sediment C/N values (see Fig. S2 in the Supplement). Mangrove carbon might be exported out of the system by the tide probably in the form of dissolved organic carbon (DOC), DIC and particulate organic carbon (POC). Further measurements of $\delta^{13}\text{C}$ of DOC are likely needed to know the fate of most exported mangrove productivity in this region.

CONCLUSIONS

Our findings suggest that intertidal fish in Qeshm Island have little dependency on organic carbon produced by mangrove trees but a high dependency on planktonic and MPB sources. The overall reliance on mangrove carbon by fish was low for the dominant fish species in the mangrove-lined creeks. Organic matter formed by mangrove leaves contributed 0-36% to the fish diets in mangrove creeks whereas organic carbon produced by MPB and plankton contributed 64-100%. High salinities and a wide temperature range likely restrict mangrove productivity in the Gulf region. Detritivores were the most abundant feeding guild, with isotope measurements strongly linking them to MPB in both mangrove-lined and un-vegetated intertidal creeks. MPB thus appeared very important in structuring the aquatic food web in this arid coastal area. Both mangrove and un-vegetated sites act as feeding grounds for fishes via pelagic and benthic food pathways.

Supplementary data is given in Annex II

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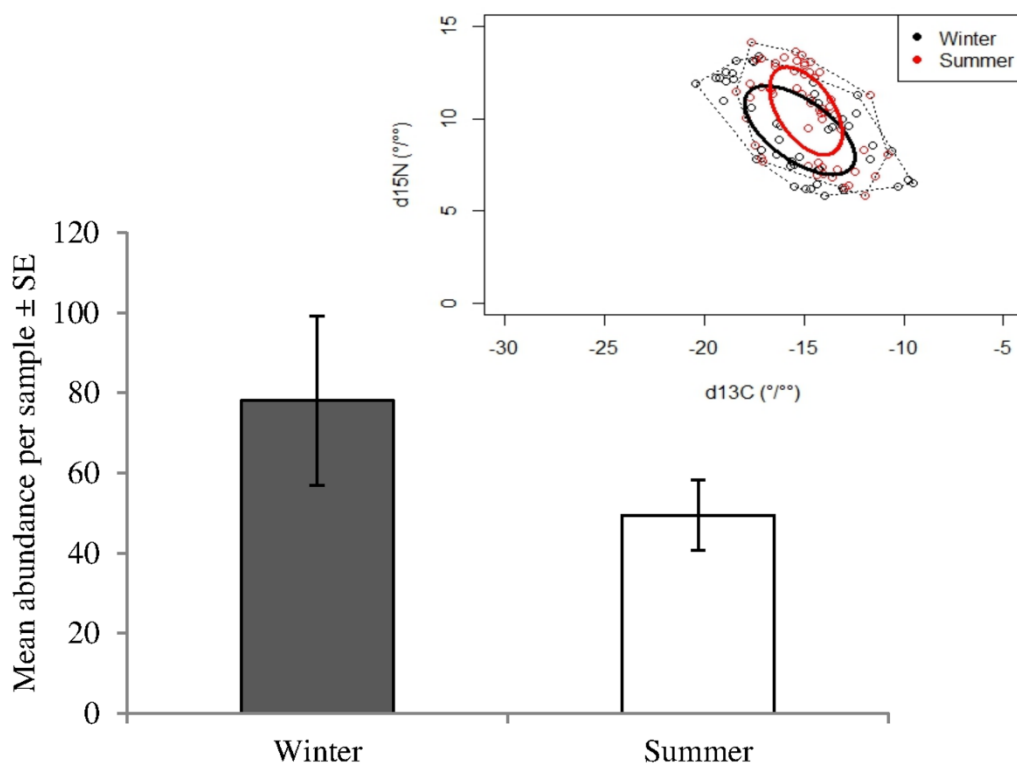
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CHAPTER IV

Seasonal Fisheries Changes in Low-Rainfall Mangrove Ecosystems



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Manuscript submitted

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 abundance 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. We found a general similarity in the diversity patterns, although slightly greater species richness occurred at mangrove sites. However, there were no consistent differences in fish abundance and 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.

Key words 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). Fish abundance in mangroves has been attributed to the diversity and availability of food sources in this habitat (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 mangrove 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 (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 fisheries.

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 fisheries, especially in the Caribbean and Gulf region (Nagelkerken and Velde 2004; Al-Maslamani et al. 2012). Factors that may help explain these divergent results include environmental parameters such rainfall and tidal regimes that may affect outwelling of mangrove derived organic carbon (Alongi 2009). This study focused on a low rainfall region in the Persian Gulf to test the idea that low rainfall might lead to low mangrove use in fisheries food webs. 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). Along the Iranian coast of Persian Gulf, natural mangroves stands are limited to 10 sites (Spalding et al. 2010) and the understanding of the relationship between mangroves and fisheries has received little study in this area.

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). Therefore, there was a need to assess the role of mangroves for fisheries in the Persian Gulf region. 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 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 also considered whether the high seasonal fluctuations in water temperature ($>20^{\circ}\text{C}$) in Qeshm mangroves might have strong impact on the variability of food sources with resultant in changes fish communities. Sampling was designed to contrast the effects of habitats (mangroves vs. non-mangroves) versus season as controls of fisheries food webs in the Persian Gulf. 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). 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; and non-mangrove sites included two intertidal creeks (C5 and C6) (Fig. 1C, D). The distance between the two sets of creeks was ca. 4 km.

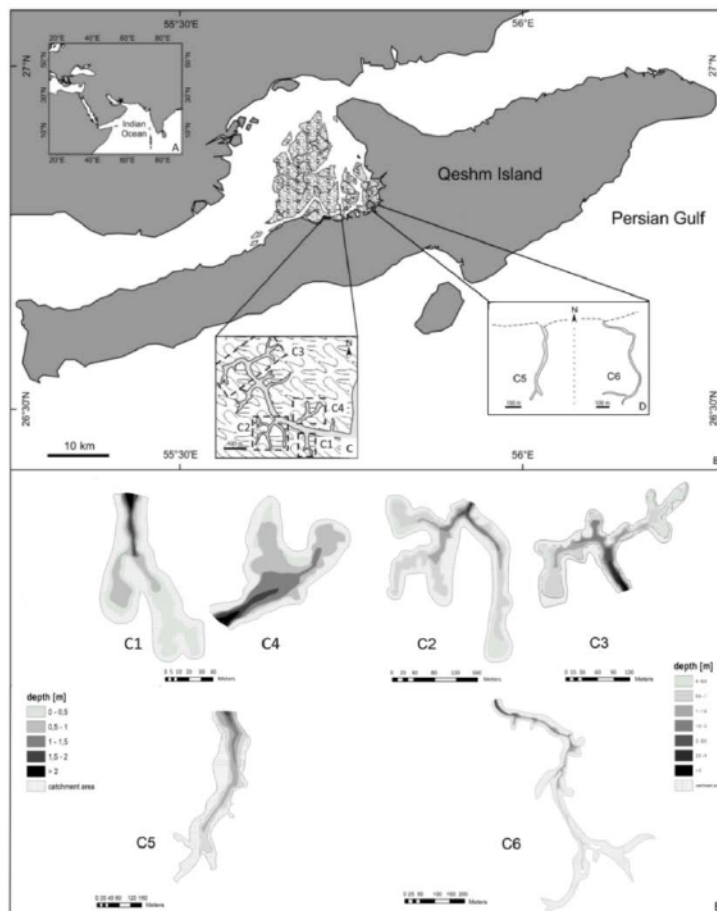


Figure 1 Study area in Qeshm Island, Iran. Location of the study area in the region (A), sampling sites (mangroves in light gray) (B), mangrove site (with 4 intertidal creeks) (C), non-mangrove site (with 2 intertidal bare creeks) (D), bathymetric maps of creeks 1, 2, 3, 4, 5 and 6 (E).

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. The block net method is regarded as highly efficient in recording the fish fauna using intertidal habitats (Bozeman and Dean 1980) and used for fish

collection in some mangroves studies e.g. in South Florida (Thayer et al. 1987) and Brazil (Barletta et al. 2003). Block net sampling is an area-based method and results are reported here both on a per sample and per area (m^{-2}) basis.

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. At high tide, the top of the nets were lifted onto wooden stakes. In the following low tide when the creeks 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 results were therefore excluded from this study.

All fish and prawns were transported on ice to the laboratory. They were identified to the lowest possible taxonomic level (Fischer and Bianchi 1984; Kuronuma and Abe 1986; Assadi et al. 1997), counted and weighed ($\text{g} \pm 0.1$). 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 name with # symbols, Table 1) 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 food sources (mangrove leaves, microphytobenthos (MPB), plankton, particulate organic matter (POM), sediment organic matter (SOM), 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 and 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, with the per m^2 comparisons more appropriate if fish were resident, and the per sample comparisons more appropriate if fish were 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 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 much 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 c. 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). 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 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). 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 sizes of food sources.

RESULTS

Community Overview

A total of 6120 individuals 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. 3471 fish were caught in winter and 2467 fish in summer, with 48 block net samples collected in each season. Generally small-sized fishes (5-15 cm) dominated catches (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).

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 the species/total individuals in the study; Occurrence (M %, NM %) are % samples where individuals of the species occurred (in mangrove and non-mangrove habitats). # symbols indicate large-sized species, and asterisks indicate the species considered for the SEA.

	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	0	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 vitrirostris</i> (Engraulidae)*	10 - 15	8	78	22
<i>Acanthopagrus cuvieri</i> (Sparidae)	15 - 20	0	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	0	60	40
<i>Scomberoides lysan</i> (Carangidae)	5 - 10	0	56	44
<i>Liza klunzingeri</i> (Mugilidae)*	5 - 20	38	34	66
<i>Pseudorhombus elevatus</i> (Paralichthyidae)	10 - 15	0	43	57
<i>Platycephalus indicus</i> (Platycephalidae)#	30 - 40	0	33	67
<i>Sphyraena putnamiae</i> (Sphyraenidae)#	30 - 40	0	20	80
<i>Hemiramphus archipelagicus</i> (Hemiramphidae)	12.5 - 15	0	33	67
<i>Sillago sihama</i> (Sillaginidae)*	10 - 17.5	1	19	81
<i>Upeneus sulphureus</i> (Mullidae)	10 - 15	0	20	80
<i>Anodontostoma chacunda</i> (Clupeidae)*	5 - 10	16	7	93
Mangroves only				
<i>Lutjanus johni</i> (Lutjanidae)	5 - 15	0	100	0
<i>Plectorhinchus pictus</i> (Haemulidae)	5 - 15	0	100	0
<i>Sardinella gibbosa</i> (Clupeidae)	5 - 10	2	100	0
<i>Scartelaos tenuis</i> (Gobiidae)	5 - 10	0	100	0
<i>Bathygobius fuscus</i> (Gobiidae)	5 - 10	0	100	0
<i>Epinephelus coioides</i> (Serranidae)#	30 - 40	0	100	0
<i>Abalistes stellatus</i> (Balistidae)#	20 - 30	0	100	0
<i>Lutjanus russelli</i> (Lutjanidae)	10 - 15	0	100	0
<i>Strongylura stronglura</i> (Belonidae)	10 - 15	0	100	0
Non-mangrove only				
<i>Terapon jarbua</i> (Terapontidae)	7.5 - 10	0	0	100
<i>Euryglossa orientalis</i> (Soleidae)	12.5 - 15	0	0	100
<i>Gerres poieti</i> (Gerreidae)	5 - 12.5	1	0	100
Crustacean				
<i>Penaeus merguensis</i> (Penaeidae)			100	0

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. This indicated that species richness of the intertidal fish communities was well-characterized by our sampling, and that additional sampling should not have yielded additional species (Gotelli and Colwell 2011).

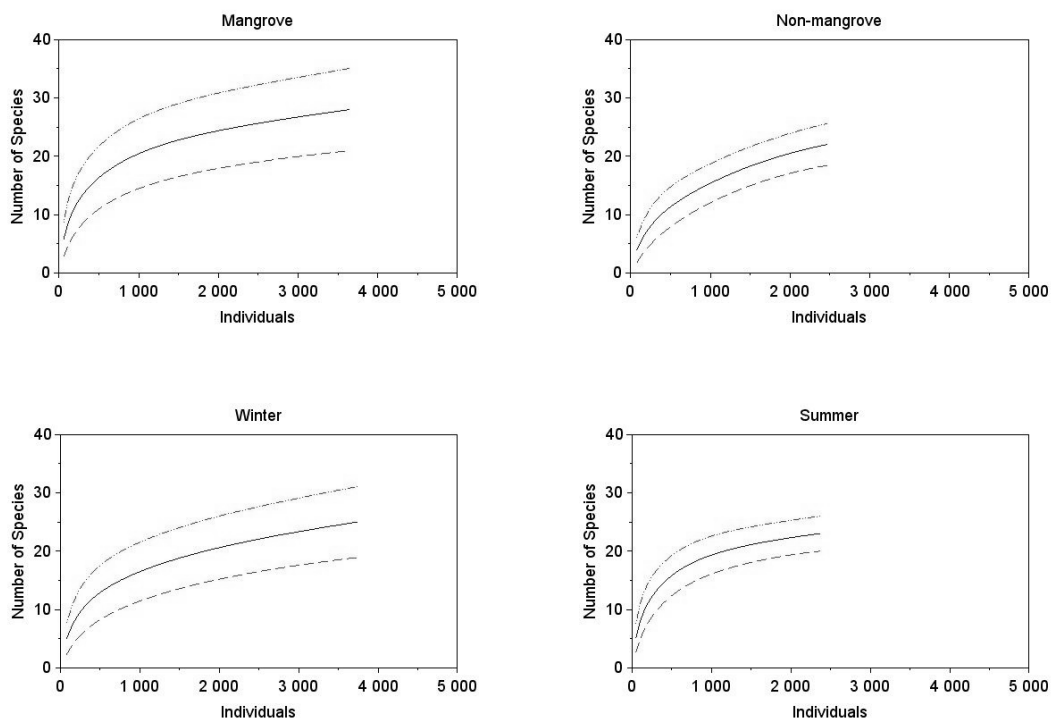


Figure 2 Individual-based rarefaction curves of fish species sampled in different habitats (mangrove vs. non-mangrove) and seasons (winter vs. summer). Dashed lines indicate 95% confidence intervals.

Nine species from seven families were caught only in mangrove creeks descending by abundance: *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 stronglura* (Belonidae). One species of

prawn (*P. 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). Regarding seasonal results, *G. poieti* was only found in summer, while *S. longiceps* and *S. gibbosa* were only found in winter. Most of these species 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. stronglura*, *T. jarbua*, *E. orientalis* and *B. fuscus* occurred 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 m² was dominated by Mugilidae (*L. 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 m² or per sample basis (Fig. 3). Thus, fish from mangroves showed higher abundance and biomass per m² 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 Figure 3; additional graphs for abundance and correlations relating abundance and biomass are presented in the Figures S1 and S2.

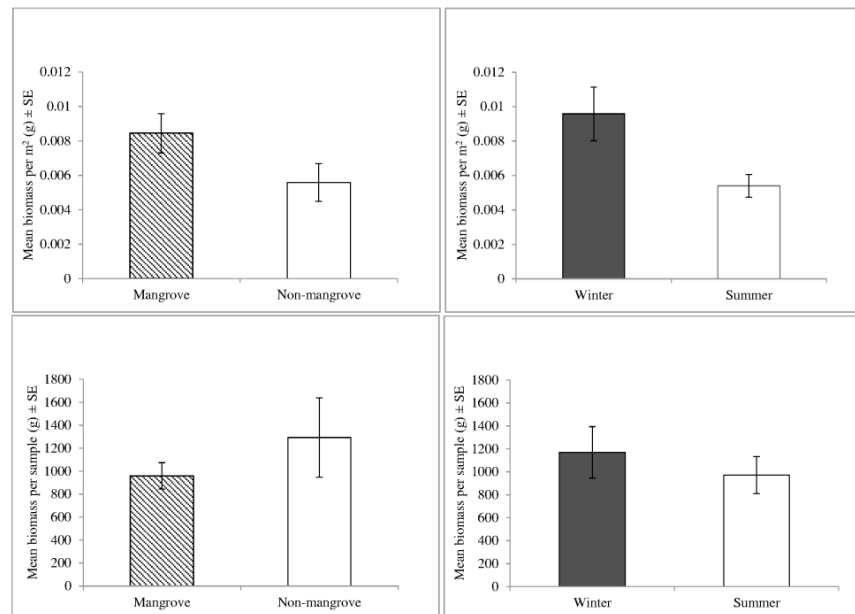


Figure 3 Mean fish biomass (g) per sample and per m² (±SE) in different habitats (left panels) and seasons (right panels). Left panels show fish can be more abundant at greater biomass when results are expressed on a per m² basis (top panels), but the opposite result pertains when results are expressed 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 m² basis used to scale the data.

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. Mean winter fish assemblages had higher biomass and abundance in all comparisons made on a per m² 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 (*A. chacunda*, *S. longiceps* and *S. gibbosa*) during winter. The rare species (e.g. *P. 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 Figure S3. Statistical tests showed no significant interactions between creeks and seasons (Table 2).

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

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	11222	11222	3.221	0.081	15	0.014	Habitat	1	13391	13391	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	13937	3484.1	1.792	0.006	998		Creek (Habitat)	4	13001	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)xSeason	4	6703.6	1675.9	0.862	0.664	999		Creek (Habitat) x Season	4	7824	1956	1.0314	0.412	998	
Residual	84	163320	1944.3					Residual	84	159300	1896.5				
Total	95	209670						Total	95	214110					
Biomass per m²	df	SS	MS	Pseudo-F	P(perm)	perms	P(MC)	Abundance per m²	df	SS	MS	Pseudo-F	P(perm)	perms	P(MC)
Habitat	1	11945	11945	4.0799	0.067	15	0.004	Habitat	1	16115	16115	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	11711	2927.8	1.5134	0.025	998		Creek (Habitat)	4	12543	3135.6	1.6583	0.016	998	
Habitat x Season	1	5420	5420	3.2722	0.038	999		Habitat x Season	1	10173	10173	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	162510	1934.6					Residual	84	158840	1890.9				
Total	95	208720						Total	95	217080					

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 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 *L. daura*, *S. longiceps* and *P. longimanus* were correlated with winter (Fig. 4). Detailed CAP results are presented in Table S3.

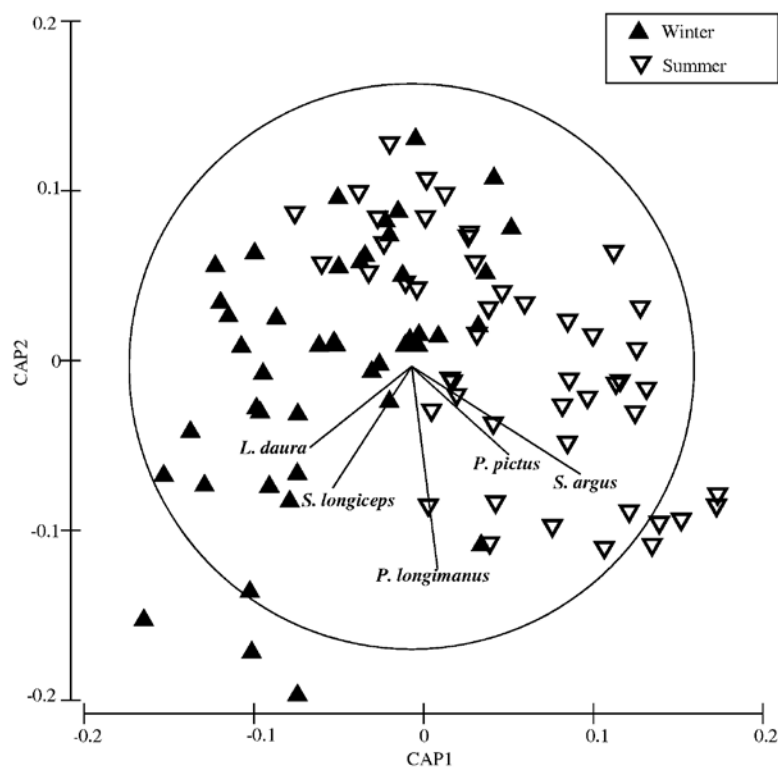


Figure 4 Canonical analysis (CAP) yielded two axes regarding factor season, with squared canonical correlations of $\delta_1^2=0.63$ and $\delta_2^2=0.50$. Symbols represent biomass (g m^{-2}) for individual block net samples and vectors show individual species correlations with the two CAP axes where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

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 fish 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 food isotopic values (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 Figure S4.

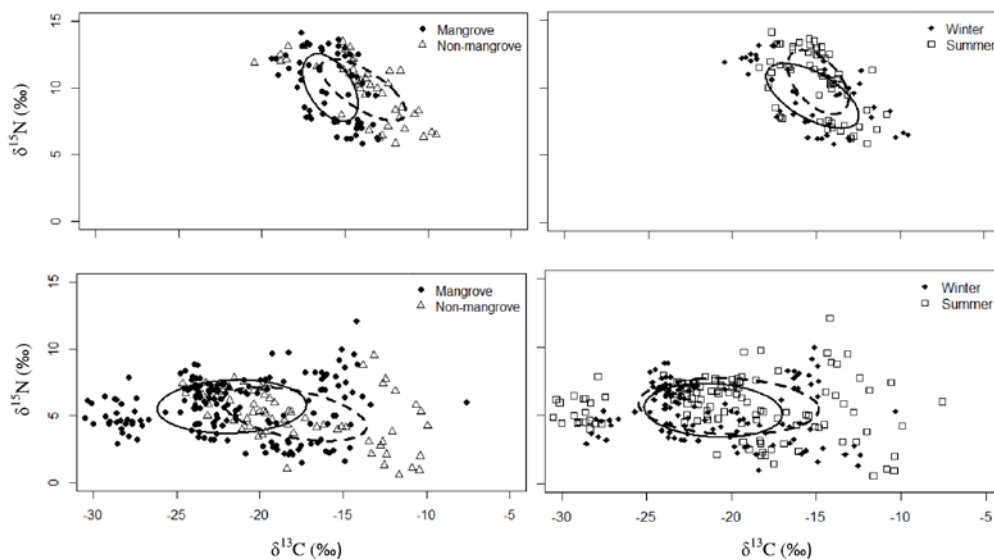


Figure 5 Standard ellipses areas (SEA) based on carbon and nitrogen stable isotope compositions of fish and food sources from different sites (left panels) and seasons (right panels); upper panels show data for fish, lower panels show data for potential foods. Solid and dashed lines enclose the standard 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 those when fish abundance and biomass were considered, 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).

Table 3 Small size-corrected standard ellipse areas (SEA_c) for food sources and fish. Probability that the SEA of food sources and fish from one group is smaller than the other group (habitats & 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. Bold numbers indicate the high probability of significant differences in SEA.

Groups	Food sources			Fish			Ratios
	SEA_c ($\%_{00}^2$)	SEA_B non-mangrove < SEA_B mangrove	SEA_B winter < SEA_B summer	SEA_c ($\%_{00}^2$)	SEA_B mangrove > SEA_B non-mangrove	SEA_B winter > SEA_B summer	Ratios of SEA_c (fish) / (food source)
Mangrove	28.0	0.12	-	11.6	0.30	-	0.4
Non-mangrove	24.0			13.1			0.5
Winter	25.0	-	0.99	16.5	-	0.96	0.7
Summer	34.3			11.6			0.3

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 (salinities of 39 and above), and summer water temperatures are often high $>33^{\circ}\text{C}$ (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 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). The lack of seagrass in the area may also partly explain the observed low fish diversity (Pittman et al. 2004).

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, with 8 of these found only in mangrove habitats. In contrast, only two of the rarer species were found in the non-mangrove habitats, 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 some species only in mangroves may be significant for fisheries in some cases, with mangrove snapper and a commercial shrimp (Vance et al. 1996; Rönnbäck 1999). The fact that many species occurred in the mangrove creeks but only a few were abundant seems to be a common feature observed also in other mangroves studies (Little et al. 1988; Chong et al. 1990). This can be related to the opportunistic species that shift their habitats based on food availability and predation risk (Hammerschlag-Peyer and Layman 2010). 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 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/abundance per sample, but a more biomass/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 abundance and biomass in mangroves with different environmental settings, limiting direct comparisons to this study. Nevertheless, we did not define the life history of fish in this study, and future surveys need to consider fish residency status.

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 and their presence increased the isotopic niche size. High $\delta^{15}\text{N}$ values for zooplanktivores are reported in other food webs studies (Abrantes and Sheaves 2009; Vaslet et al. 2012). If these fish were removed from the 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 (>31°C) 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 (Abrantes et al. 2014). 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 foods, not just important foods, seemed to be a reasonable first approach.

Our findings emphasized that fish 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.

Supplementary data is given in Annex III

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CHAPTER V

Synoptic Discussion and Outlook



Synoptic discussion and outlook

This thesis provides new information on variables structuring fish assemblages in the low-rainfall coastal ecosystem of Qeshm Island, Iran, and helps to fill a gap in knowledge regarding fish communities in the northern edge of mangrove distribution in the Indian Ocean. The findings show the influence of environmental variables (e.g. tide and temperature) in structuring fish assemblages in a meso-tidal area of the Persian Gulf (Chapters II and IV). The unique aspect of this study is to combine the community descriptors and isotopic niche diversity to determine the patterns of changes in the fish assemblages of Qeshm Island. With respect to this, the structuring effect of seasonality is more important than habitat in determining the fish distribution patterns (Chapter IV). Moreover, the outcomes of this dissertation demonstrate the main food pathways sustaining fish communities in mangrove and non-mangrove intertidal creeks (Chapters III). The conceptual framework describing the factors structuring Qeshm Island fish communities and food web dynamics is shown in figure 1.

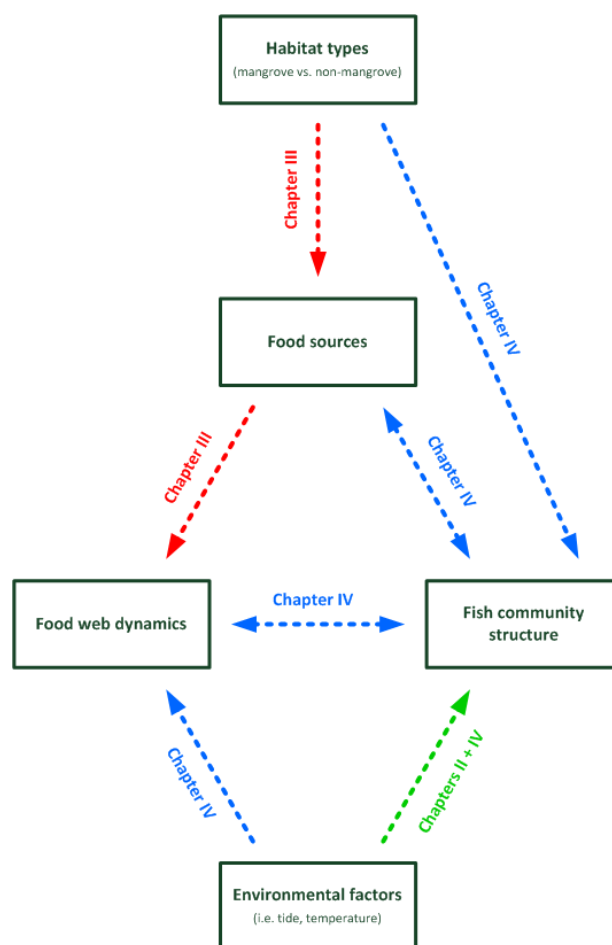


Figure 1 Simplified model of the factors shaping fish communities and food webs in Qeshm Island, Iran. Arrows indicate the direction of the influence.

Factors determining structural changes in fish communities

Environmental factors

Changes in environmental variables cause a structural alteration among fish assemblages, although the relative importance of different factors is variable between the biogeographical regions (Blaber and Blaber 1980; Blaber 2002). While seasonal fluctuations of salinity structure fish communities in humid regions (Barletta et al. 2003; Barletta and Saint-Paul 2010), this effect is negligible in the low-rainfall system of Qeshm Island. Given the fact that the coasts of the Persian Gulf are subjected to mesotides, the regular changes in the water level cause significant variance in fish distribution. The results of this study show that the interaction between tides (spring and neap) and day-night cycles influence the organization of fish assemblages. The highest fish biomass, abundance and diversity are observed during spring tide night. Qeshm Island presents mangroves where much larger intertidal areas are inundated at spring, rather than at neap tides. Therefore, high inundation during spring tide coinciding with the darkness provided favorable conditions for fish. This minimizes the predation effect and provides longer habitat accessibility for fish. These findings are not unexpected and are consistent with other studies that have viewed tidal cycles as one of the major factors in determining the dynamics of mangrove fish assemblages in tidal coasts e.g. in the Indo-West Pacific (Laroche et al. 1997; Rönnbäck et al. 1999; Wilson and Sheaves 2001). Conversely, in the Caribbean, the tidal cycle plays a negligible role in structuring fish assemblages, and instead, the diel cycle is the major rhythm driving short-term changes in mangrove fish assemblages (Nagelkerken et al. 2000). Thus, tidal dynamics' effect on Qeshm fish assemblages is similar to other mangroves exposed to median to large tidal regimes (range 2 to >5).

There, exist a unique attribute of high seasonal fluctuations in water temperatures (>20°C). Thereby, this contrasting characteristic of arid mangroves is crucial for structuring fish assemblages. In this context, low fish abundance and biomass are observed in summer. Extreme summer water temperatures (>33°C) likely limit the fish abundance and biomass. The observation of a decline in fish assemblages in summer due to an increase in water temperature is characteristic in the Gulf's shallow water habitats (Wright 1989).

Also, intertidal mangrove creeks in Qeshm Island do not support many fish species. Seasonal fluctuations in water temperatures of >20°C likely limit the suitability of this shallow-water habitat for coastal-marine fish species in Qeshm

mangroves. Therefore, the diversity of fish may also be closely linked to the environmental conditions. While high species diversity (>80 species) has been reported among the humid mangroves in the Indo-Malaysian region (Tongnunui et al. 2002; Ikejima et al. 2003), the species richness is relatively low in the arid mangroves of Qeshm Island (<30 species). This difference in species richness could partly reflect the effect of different environmental settings across regions e.g., the lack of fresh water and rainfall in the Persian Gulf as compared to South East Asia's high precipitation rate. The low species diversity could also be driven by the lack of other productive habitats in the proximities of the Qeshm mangroves, such as seagrass and coral reef. However, at a global scale, the low species diversity in the western Indian Ocean reflects the standard species gradient from the center of shallow water species richness in the coral triangle in all directions (Blaber 2000; Carpenter and Springer 2005).

Changes in fish communities are most likely linked to the biogeography of the mangroves, whereby distinctive environmental factors contribute to the organization of fish distribution patterns. Qeshm mangroves are characterized by stable salinities and other variables such as tide-diel cycle, and seasonal changes in water temperature have been shown to be an important determinant in shaping fish community structure in this region (see Chapters II and IV). Also, stressful environmental conditions at the northern edge of mangrove distribution in the Western Indian Ocean influence fish species diversity in this region.

Food sources

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. This can be linked to higher fish abundance and biomass during spring tide in Qeshm's intertidal mangrove creeks. It has been observed that during high tide, fish from adjacent habitats such as mud flats and seagrass beds migrate into the mangroves to feed (Vance et al. 1996; Sheaves and Molony 2000). Depending on local conditions, phytoplankton, algae and seagrass detritus imported with tides may represent a significant supplementary food input (Kristensen et al. 2008; Nagelkerken et al. 2008). In Qeshm's mangrove-lined creeks, mangrove leaves are isotopically distinct from other food sources. The findings of this study do not support mangrove litter as a major feeding source for fish in Qeshm Island; and algal sources sustain food webs in intertidal arid habitats (Shahraki et al. 2014). Algal material could be a readily

available food source for fish and invertebrates on flooding tides. Also, the large amounts of algae covering the pneumatophore provide food for many invertebrates and juvenile fish (Laegdsgaard and Johnson 2001).

High fish abundance in mangroves has been attributed to the availability of food sources in this habitat (Laegdsgaard and Johnson 2001; Chong 2007). To reliably assess the role of mangrove ecosystems in supporting aquatic food webs, mangrove habitats should be compared with habitats of the same type but without mangrove cover, recognizing that this may be a somewhat artificial comparison if the habitat type strongly shifts foraging opportunities. When comparing mangrove vs. non-mangrove food webs, both habitats fuel fish with similar food sources. Fish compositions are very similar between mangroves and non-mangroves, both in terms of species richness and especially in the contribution of dominant species (see Chapter IV). Also, community trophic diversity measured as size-corrected standard ellipse areas show no significant difference between mangrove and non-mangrove sites in Qeshm Island.

Moreover, food sources of different origins can be seasonally important for consumers (Vizzini and Mazzola 2003; Olin et al. 2012). In the current work, food standard ellipse areas (SEA) values indicate wider diversity in food values in summer. Also, the $\delta^{13}\text{C}$ of pelagic food sources (e.g. plankton) show seasonal variations, which are reflected in seasonal isotopic variations of zooplanktivores. In summer, temperature stress decreases fish trophic diversity, and fish communities are characterized by low biomass and abundance. In contrast, higher SEA values for fish communities in winter indicate a broader use of foods, though this is mostly due to presence of zooplanktivores, which are not abundant in summer months.

In addition, seasonal changes in fish/food isotope niche ratios confirm and magnify the seasonal patterns in fish isotope diversity in this study. Thus, the coarse-level view of food isotope diversity based on all foods, not just important foods, seemed to be a reasonable first approach. However, these findings should be interpreted with some caution because the isotope values are usually (as in this study) measured for many potential foods rather than the actual 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).

Based on these conclusions, the structure of fish assemblages of species which use mangrove and non-mangrove intertidal creeks is mostly influenced by seasonal changes in water temperatures. These seasonal developments influence the

accessibility of food sources, resulting in changes among fish assemblages. Also, similarities in the food resources across habitats may partially account for similarities in fish communities in the mangrove and non-mangrove creeks of Qeshm Island.

The main sources of energy for fish

The fish food web's support of mangrove and non-mangrove intertidal creeks seem to be energetically driven by pelagic and benthic food pathways in Qeshm Island (Fig. 2). The fish community result is indicated by the dominance of detritivores in this arid environment. However, there is not an obvious pattern of detritivorous fish having a much higher potential trophic reliance on mangrove leaves.

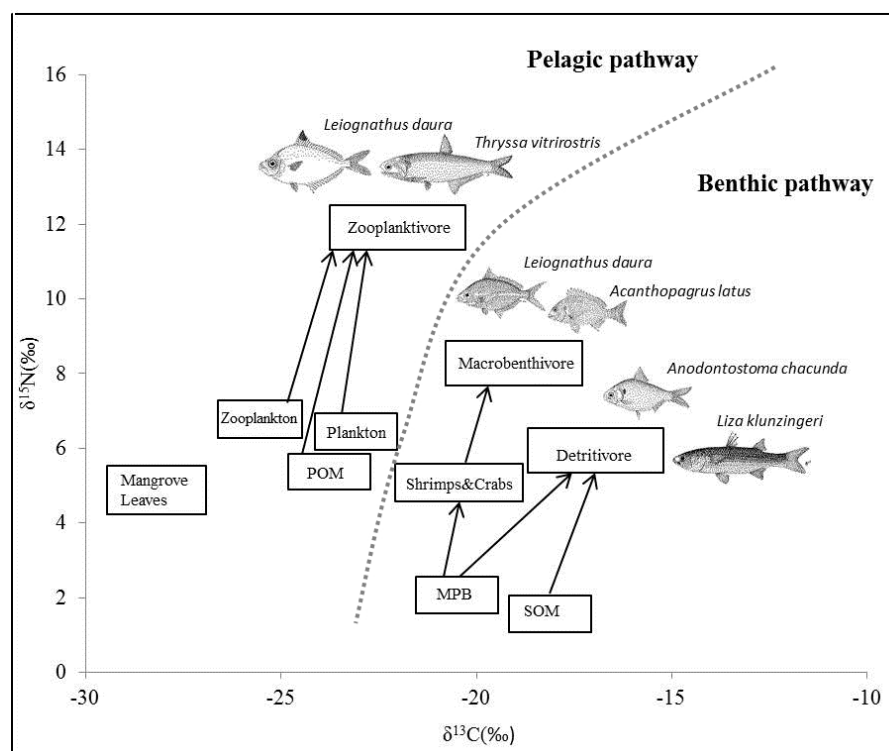


Figure 2 Simplified mangrove food webs indicating two food pathways in Qeshm mangroves, Persian Gulf. Arrows indicate the destination of food sources (particulate organic matter (POM), sediment (SOM), microphytobenthos (MPB) to macrobenthos (crabs and shrimps) to fish (detritivores, zooplanktivores, macrobenthivores); Modified from Shahraki et al. (2014).

As it is shown in Chapter III, fish show low reliance on organic matter derived by mangrove trees at multiple levels, from species to trophic guilds to communities. Overall, the minimum and maximum mangrove contributions range between 0% and 36%, respectively, for the various fish groups and species tested in this study. Other

food sources are aggregated in the 2-source model as various types of “algae”, and “algal” contributions to the various fish groups ranged from a minimum of 64% to a maximum of 100%. A global overview of the contribution of food sources supporting mangrove food webs reveals a high importance of mangrove litter to fish diet in the Indo-Malaysian region, indicated by high precipitation (Rodelli et al. 1984; Zagars et al. 2013) and low mangrove litter contributions for the African region, which is characterized by the moderate to low rainfalls (Nyunja et al. 2009; Kruitwagen et al. 2010). Elsewhere, such as in the Caribbean where mangroves are permanently inundated, this role is also limited (Nagelkerken and Velde 2004). These divergent results suggest that environmental parameters e.g., the precipitation regime may affect the outwelling of mangrove derived organic carbon (Alongi 2009). In this study area, the low mangrove litter contribution to fish food webs could be mainly related to a lack of freshwater input and very low precipitation. Similarly, the possible contribution of mangroves as a source of nutrition for benthic and epibenthic invertebrates was less than other primary producers in some other studies in the Gulf region (Al-Zaidan et al. 2006; Al-Maslamani et al. 2012). These results therefore suggest that attributes of an arid environment, in other words, the dearth of rainfall, may largely reduce the outwelling of mangrove derived organic carbon, and thus influence the use of mangrove litter in aquatic food webs.

Furthermore, the dominance of detritivores in both mangrove and non-mangrove intertidal creeks suggests the importance of benthic (detritus) food webs in the intertidal creeks at Qeshm Island.

Mangroves fisheries support

Benefits to fisheries from mangroves are derived from a high availability of food sources as well as physical attributes (shelter from predation), as demonstrated by high fish abundance and diversity (Manson et al. 2005; Chong 2007). But, when mangrove fish food webs are compared with the non-mangroves, there is a low estimated role of mangrove detritus and a likely shared dependence on mudflat algal food resources in both sites in Qeshm Island (Shahraki et al. 2014).

The estimates of fish abundance and biomass vary depending on whether results are expressed on a per sample basis or a per m² basis, with mangrove creeks supporting less abundance and biomass per sample, but more abundance and biomass per m². This may seem somewhat contradictory, but reflects a real dichotomy in results

presented in other studies where it has been also 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. This reinforces the need for an integrated approach to evaluate the role of mangrove as fish habitats.

A somewhat more mangrove-centric view of this study is the presence of some economically important species (e.g. snapper and a commercial shrimp) found only in mangroves, suggesting Qeshm mangroves are particularly important habitats for associated-mangrove fisheries. Also, the numbers of rarer species (species with relative abundance of <1%) occur more frequently in mangroves than in non-mangroves, which is consistent with the idea that the higher complexity and shelter of mangroves may attract more fish species (Verweij et al. 2006; Nanjo et al. 2014b).

Perspectives and future directions

This study compliments previous studies in the western Indian Ocean by contributing to the understanding of fish community patterns in relation to changes in the abiotic variables. Tide and season emerged as important factors for structuring fish assemblages in the low-rainfall mangroves of Qeshm Island. However, there is still a lack of ecological knowledge regarding mangrove habitat use by fish in an arid system and further studies, especially in the Gulf region, are needed for a more widespread understanding of the relationship between mangrove complexity and fish distribution patterns. In this study, the fish abundance and biomass comparisons are made on both a per m² basis and on a per sample basis, revealing an interesting difference between the two expressions of the data. These contrasting results are addressed in this thesis.

However, the challenge lies in identifying the life history of fish to assess the importance of the mangroves to fish population. Further research is needed to know which species, when, and at what life stages rely on mangroves. Also, future research will address turnover rates for fish population to estimate fish productivity in Qeshm mangroves.

There exists a small body of research which surveys food webs from a low rainfall ecosystem, like Qeshm Island, and this study not only records the first fish food webs knowledge based on the isotope approach for the Iranian coast of the Persian Gulf, but also provides valuable benchmarks for the comparison of trophic diversity with comparable arid and humid systems. However, it should be noted that only abundant fish species are included for determining fish food webs in this study. For having a complete picture of food web dynamics, all fish species should be incorporated for the stable isotope measurements. Also, future studies should be conducted in concert with gut content analysis to better identify important food sources and the relationship between fish isotope diversity and the diversity of those foods.

The reason for the $\delta^{13}\text{C}$ depletion in benthic and pelagic pathways of mangrove as compared to non-mangrove sites remains unknown in this study, although it may be related to differences in the microphytobenthos community itself. Cyanobacteria dominate the microphytobenthos at the non-mangrove sites. This might be the impact of an enhanced proportion of nitrogen-fixing cyanobacteria within the microphytobenthos. The dominant role of nitrogen-fixing cyanobacteria is also reflected in the nutrient concentrations (Shahraki Unpubl. data). Relatively high nitrate and low phosphate concentrations indicate the preferential uptake of phosphates that is leached from the sediments by the cyanobacteria mats, leading to phosphate-limiting conditions in the non-mangrove intertidal creeks (Shahraki Unpubl. data). The shading effect of mangrove might explain why diatoms dominated over cyanobacteria in the mangrove site. But, further studies are needed to clarify these hypotheses.

It has been believed that large amounts of mangrove leaves, detritus and particulate organic matter are exported to adjacent habitats and drive offshore fisheries production (Odum and Heald 1972; Lee 1995). However, recent stable isotope studies find that it is not the case in humid mangroves (Rodelli et al. 1984; Newell et al. 1995; Chong et al. 2001). Because the export of mangrove detritus to adjacent habitats might be limited due to lack of fresh water input, this pattern could be more complex in arid mangroves. Therefore, our understanding of the role of organic matter produced by

mangrove trees for food webs of adjacent habitats, to which they are linked through tidal flows, remains restricted. Mangrove carbon might be exported out of the system by the tide, probably in the form of dissolved organic carbon (DOC), dissolved inorganic carbon (DIC) and particulate organic carbon (POC). Measuring isotopic values of fish along a gradient from the mangrove creeks towards open marine waters should be considered in future studies. Also, further measurements of $\delta^{13}\text{C}$ of DOC are needed to know the fate of most exported mangrove carbon in this low rainfall region.

Lastly, the possible roles played by benthos within Iranian mangrove systems in the transfer and processing of organic matter remain largely unknown. Biogenic activities such as bio-turbation and bio-irrigation could drive sediment–water exchange of nutrients and organic matter (Stieglitz et al. 2000), therefore contributing to the aquatic food webs. Spatio-temporal variability of solute fluxes (O_2 , CO_2 , nutrients) at the sediment-water interface, could act as indicators of ecosystem functioning (e.g., nutrient cycling) and thereby affecting the biodiversity, in particular the production of fish communities. Hence, further analyses and monitoring of the biogeochemical fluxes along the sediment-water system hold the potential to delineate the supply of organic matter into the food web.

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ANNEX

Annex I. Supplements for Chapter II

Annex II. Supplements for Chapter III

Annex II. Supplements for Chapter IV

Annex I. Supplements for Chapter II**Table S1** Mean \pm SD of environmental parameters measured in different months at the water surface during slack high tide at the mouth of intertidal mangrove creeks in Qeshm Island, Iran. N: Number of measurements for each variable.

Sampling Time	N	Salinity	Water temperature (°C)	pH	Oxygen concentration (mgL ⁻¹)
December 2011 - January 2012	32	38.3 \pm 0.6	19.9 \pm 1.2	8.1 \pm 0.1	8.7 \pm 0.5
February - March 2012	32	37.9 \pm 0.4	19.4 \pm 1.7	8.2 \pm 0.7	9.3 \pm 0.7
August- September 2012	32	38.7 \pm 0.3	33.7 \pm 1.5	8.2 \pm 0.2	6.5 \pm 1.2

Table S2 Canonical analysis of principal coordinates (CAP) testing the effect of tide-time of day (spring tide-night, spring tide-day, neap tide-night, neap tide-day) and months (December, February and August). %Var = percentage of the total variation explained by the first *m* principal coordinate axes; allocation success = percentage of points correctly allocated into each group; δ^2 = square canonical correlation.

Factor	m	Var %	Allocation success (%)				Total	δ^2	P
			SN	SD	NN	ND			
Tide-Time	12	97	70.8	79.1	45.8	79.1	68.7	0.7	0.001
Month			Dec	Feb	Aug				
	6	96	50	71.8	68.7	61.9	0.4	0.01	



Figure S1 Intertidal mangrove creek at low water (on the left) and in high water (on the right), Qeshm Island, Iran. The photos on the tops indicate the low-lying creeks and high-lying creeks are shown in the bottom.

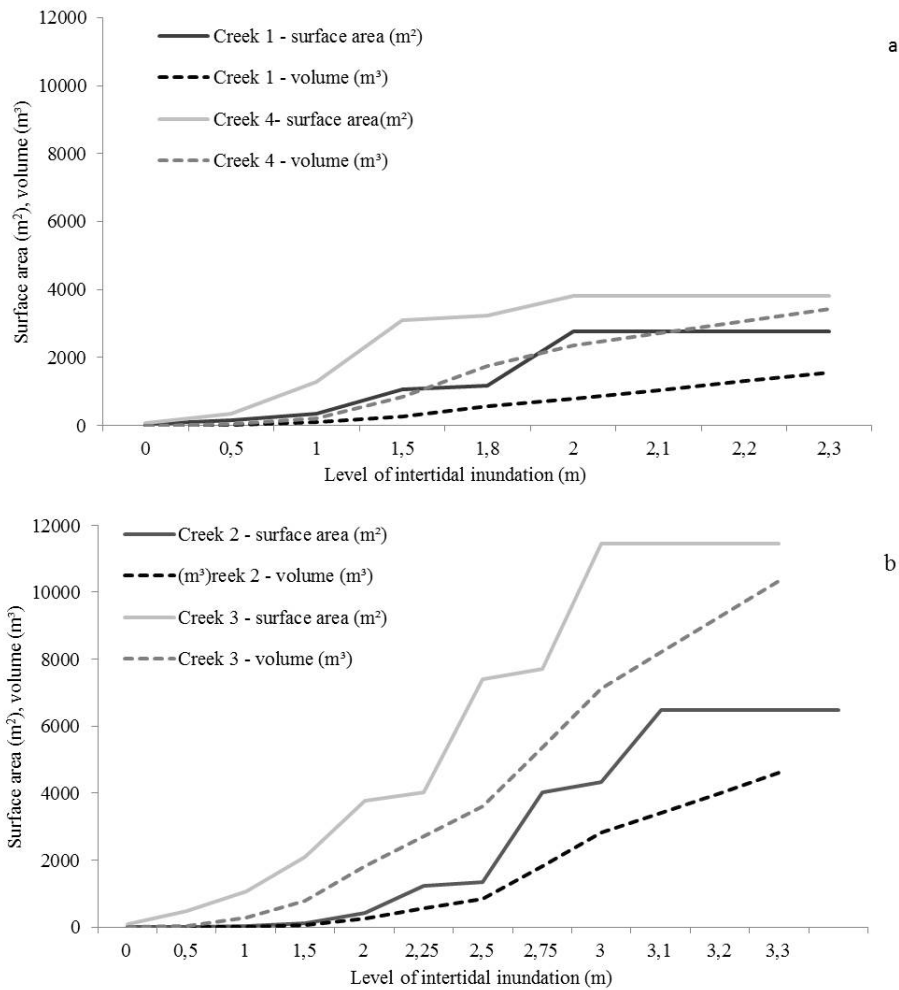


Figure S2 Relationship between level of intertidal inundation and GIS-generated surface area (m²) and volume (m³) in two high-lying (a) and two low-lying (b) intertidal mangrove-lined creeks in Qeshm Island, Iran (Note: different x axis scales).

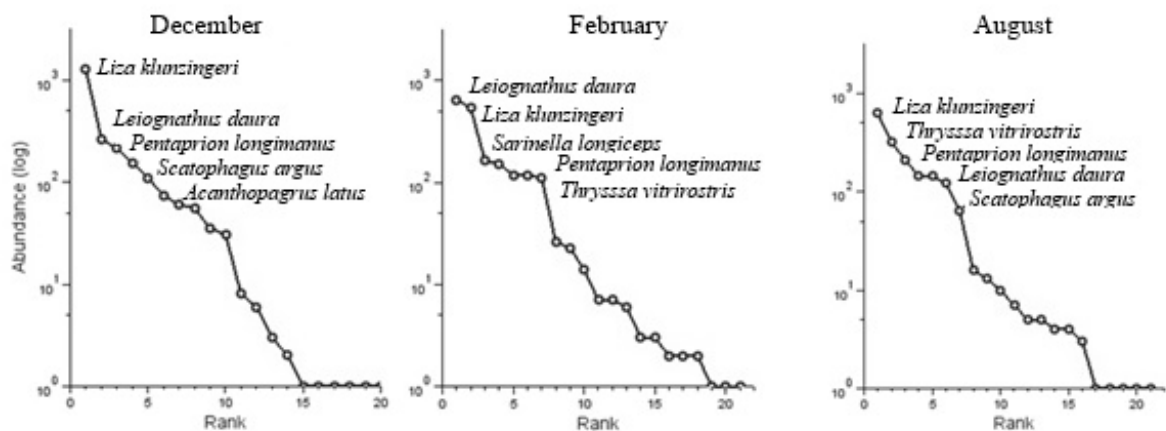


Figure S3 Rank-abundance plot of fishes captured from intertidal mangrove-lined creeks at different tide-time of day combinations during a lunar cycle in December 2011, February and August 2012 in Qeshm Island, Iran.

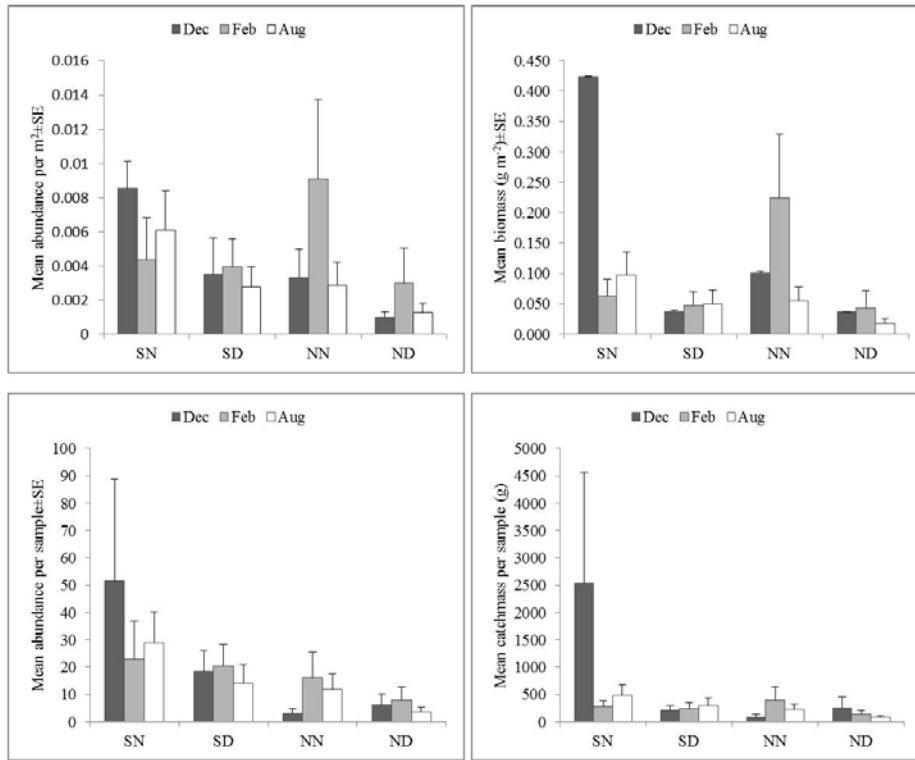


Figure S4 Mean abundance and biomass per sample and per $m^2 \pm 1SE$ of fish at different combination of the tidal-diel cycles and months.

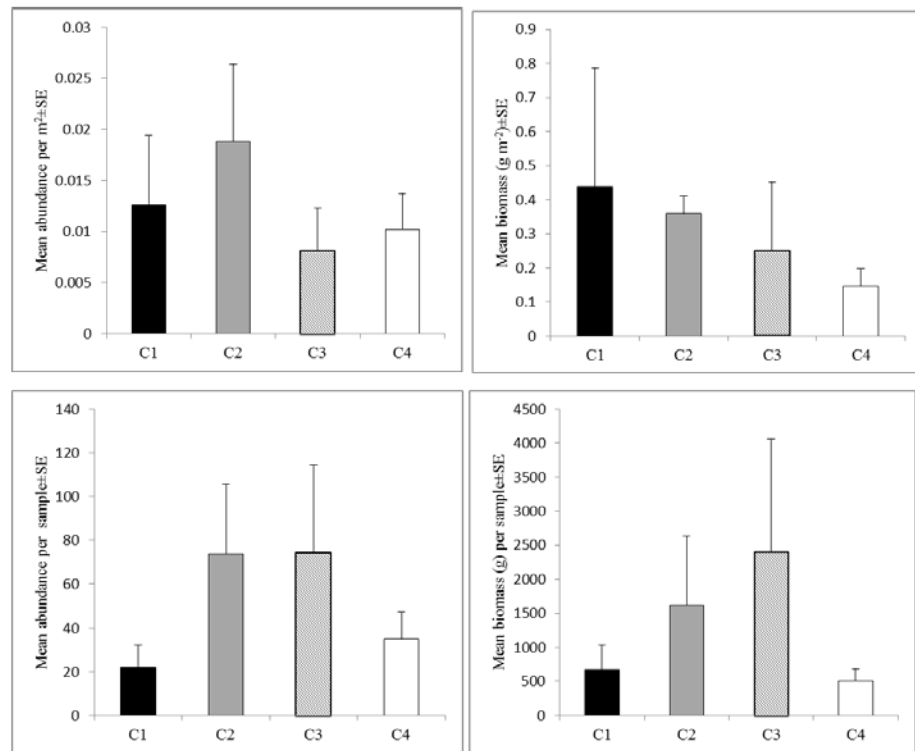


Figure S5 Mean abundance and biomass per sample and per $m^2 \pm 1SE$ of fish from two low-lying (C2, C3) and two high-lying (C1, C4) intertidal mangrove-lined creeks in Qeshm Island, Iran.

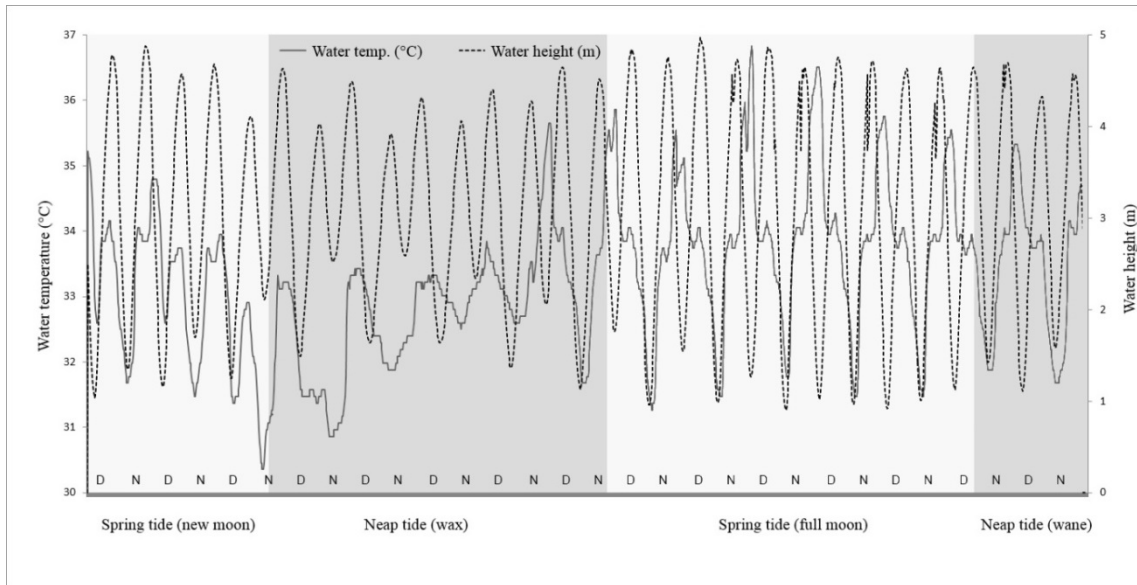


Figure S6 Continuous 15 min measurements of water temperature and water height (m) with a HOBO water level data logger installed in the subtidal area at the mouth of the main channel from 21.08.2012 at 6:30 PM until 5.09.2012 at 7:30 PM (August - September 2012).

Annex II. Supplements for Chapter III**Table S1** List of microphytobenthos genera in mangrove-lined and un-vegetated sites. The numbers indicate the relative cell abundance. Bold numbers highlight site differences.

<i>Taxa</i>	Mangrove-lined	Un-vegetated
<i>Navicula spp.</i>	62.2	2.3
<i>Nitzschia spp.</i>	12.2	-
Bacillariophyceae (Total)	74.4	2.3
<i>Anabaena spp.</i>	-	0.8
<i>Chroococcus spp.</i>	1.4	12.3
<i>Gloeocapsa spp.</i>	-	0.8
<i>Microcoleus spp.</i>	13.5	49.8
<i>Oscillatoria spp.</i>	10.7	34.1
Cyanophyceae (Total)	25.6	97.8

Table S2 Physico-chemical characteristics of the seawater from the mangrove-lined and un-vegetated sites, Qeshm Island, Iran.

Site	Season	pH	Do (mg/l)	Salinity	Temperature (°C)
Mangrove-lined	Winter	8.1 ±0.1	9.06±0.7	38.1±0.5	19.6±1.5
	Summer	8.2±0.2	6.6±1.2	38.7±0.3	33.7±1.4
Un-vegetated	Winter	8.0±0.1	9.4±0.3	40.8±4.2	19.6±2.0
	Summer	8.2±0.0	7.2±0.9	40.4±1.1	34.0±2.0

Table S3 Potential contributions of mangroves to fish diets (mean ± 95% confidence interval) calculated by IsoError program and two-source mixing models for the whole fish community, fish functional group and individual fish species using $\delta^{13}\text{C}$ values.

	Sample (Mangrove fish)	Source 1 (Non- mangrove sources)	Source 2 (Mangrove Leaves- green & yellow)
Whole fish community			
$\delta^{13}\text{C}$ [‰] (SD)	-15.8 (1.7)	-13.8 (2.5)	-28.3 (1.09) -23.1 (1.09)
Sample size	66	46	26
Source proportions (No fractionation)		87-100	0-13
Source proportions [%] (SE)		86 (03)	14 (03)
95% Confidence limits (%)		81-91	09-19
Source proportions (Max fractionation)		79-100	0-21
Source proportions [%] (SE)		78 (04)	22 (04)
95% Confidence limits (%)		71-86	14-29
Functional groups			
Detritivores (DV)			
$\delta^{13}\text{C}$ [‰] (SD)	-14.1 (0.7)	-12.1 (1.5)	-28.3 (1.09) -23.1 (1.09)
Sample size	14	18	26
Source proportions (No fractionation)		88-100	0-12

	Sample (Mangrove fish)	Source 1 (Non- mangrove sources)	Source 2 (Mangrove Leaves- green & yellow)
Source proportions [%] (SE)		88 (02)	12 (02)
95% Confidence limits (%)		83-92	08-17
Source proportions (Max fractionation)		82-100	0-18
Source proportions [%] (SE)		82 (03)	18 (03)
95% Confidence limits (%)		75-88	12-25
Zooplanktivores (ZP)			
$\delta^{13}\text{C}$ [‰] (SD)	-16.6 (1.6)	-15.6 (2.1)	-28.3 (1.09) -23.1 (1.09)
Sample size	22	14	26
Source proportions (No fractionation)		93-100	0-7
Source proportions [%] (SE)		92 (05)	08 (05)
95% Confidence limits (%)		82-100	00-18
Source proportions (Max fractionation)		87-100	0-13
Source proportions [%] (SE)		87 (08)	13 (08)
95% Confidence limits (%)		70-100	00-30
Macrobenthivores (MB)			
$\delta^{13}\text{C}$ [‰] (SD)	-16.5 (1.5)	-14.5 (2.5)	-28.3 (1.09) -23.1 (1.09)
Sample size	30	14	26
Source proportions (No fractionation)		86-100	0-14
Source proportions [%] (SE)		86 (05)	14 (05)
95% Confidence limits (%)		76-95	05-24
Source proportions (Max fractionation)		77-100	0-23
Source proportions [%] (SE)		77 (07)	23 (07)
95% Confidence limits (%)		63-91	09-37
Fih species			
<i>Liza klunzingeri</i>			
$\delta^{13}\text{C}$ [‰] (SD)	-14.3 (0.8)	-11.5 (1.3)	-28.3 (1.09) -23.1 (1.09)
Sample size	8	12	26
Source proportions (No fractionation)		84-100	0-16
Source proportions [%] (SE)		83 (03)	17 (03)
95% Confidence limits (%)		78-89	11-22
Source proportions (Max fractionation)		76-100	0-24
Source proportions [%] (SE)		76 (03)	24 (03)
95% Confidence limits (%)		69-83	17-31
<i>Anodontostoma chacunda</i>			
$\delta^{13}\text{C}$ [‰] (SD)	-13.8 (0.6)	-13.5 (1)	-28.3 (1.09) -23.1 (1.09)
Sample size	6	6	26
Source proportions (No fractionation)		98-100	0-2
Source proportions [%] (SE)		98 (03)	02 (03)
95% Confidence limits (%)		91-100	00-09
Source proportions (Max fractionation)		97-100	0-3
Source proportions [%] (SE)		97 (05)	03 (05)
95% Confidence limits (%)		86-100	00-14
<i>Leiognathus daura</i>			
$\delta^{13}\text{C}$ [‰] (SD)	-19 (1.3)	-17.9 (2)	-28.3 (1.09) -23.1 (1.09)
Sample size	6	5	26
Source proportions (No fractionation)		90-100	0-10
Source proportions [%] (SE)		89 (09)	11 (09)
95% Confidence limits (%)		68-100	00-32
Source proportions (Max fractionation)		79-100	0-21
Source proportions [%] (SE)		79 (17)	21 (17)
95% Confidence limits (%)		39-100	00-61

	Sample (Mangrove fish)	Source 1 (Non- mangrove sources)	Source 2 (Mangrove Leaves- green & yellow)
<i>Thryssa vitirostris</i>			
$\delta^{13}\text{C}$ [‰] (SD)	-14.6 (0.5)	-14.2 (0.5)	-28.3 (1.09) -23.1 (1.09)
Sample size	5	6	26
Source proportions (No fractionation)		98-100	0-2
Source proportions [%] (SE)		97 (02)	03 (02)
95% Confidence limits (%)		92-100	00-08
Source proportions (Max fractionation)		96-100	0-4
Source proportions [%] (SE)		96 (03)	04 (03)
95% Confidence limits (%)		88-100	00-12
<i>Sillago sihama</i>			
$\delta^{13}\text{C}$ [‰] (SD)	-15.4 (0.5)	-14.5 (0.8)	-28.3 (1.09) -23.1 (1.09)
Sample size	3	3	26
Source proportions (No fractionation)		94-100	0-6
Source proportions [%] (SE)		93 (04)	07 (04)
95% Confidence limits (%)		81-100	00-19
Source proportions (Max fractionation)		90-100	0-10
Source proportions [%] (SE)		90 (06)	10 (06)
95% Confidence limits (%)		71-100	00-29
<i>Pentaprion longimanus</i>			
$\delta^{13}\text{C}$ [‰] (SD)	-17.8 (1.1)	-16.7 (0.9)	-28.3 (1.09) -23.1 (1.09)
Sample size	6	5	26
Source proportions (No fractionation)		80-100	0-20
Source proportions [%] (SE)		91 (05)	09 (05)
95% Confidence limits (%)		79-100	00-21
Source proportions (Max fractionation)		83-100	0-17
Source proportions [%] (SE)		83 (09)	17 (09)
95% Confidence limits (%)		63-100	00-37
<i>Pomadasy kaakan</i>			
$\delta^{13}\text{C}$ [‰] (SD)	-16.4 (0.6)	-13.3 (0.9)	-28.3 (1.09) -23.1 (1.09)
Sample size	8	6	26
Source proportions (No fractionation)		76-100	0-24
Source proportions [%] (SE)		79 (02)	21 (02)
95% Confidence limits (%)		74-85	15-26
Source proportions (Max fractionation)		69-100	0-31
Source proportions [%] (SE)		68 (03)	32 (03)
95% Confidence limits (%)		61-76	24-39
<i>Acanthopagrus latus</i>			
$\delta^{13}\text{C}$ [‰] (SD)	-16.1 (1.4)	-12.2 (0.7)	-28.3 (1.09) -23.1 (1.09)
Sample size	8	3	26
Source proportions (No fractionation)		76-100	0-24
Source proportions [%] (SE)		76 (04)	24 (04)
95% Confidence limits (%)		67-84	16-33
Source proportions (Max fractionation)		65-100	0-35
Source proportions [%] (SE)		64 (05)	36 (05)
95% Confidence limits (%)		53-76	24-47

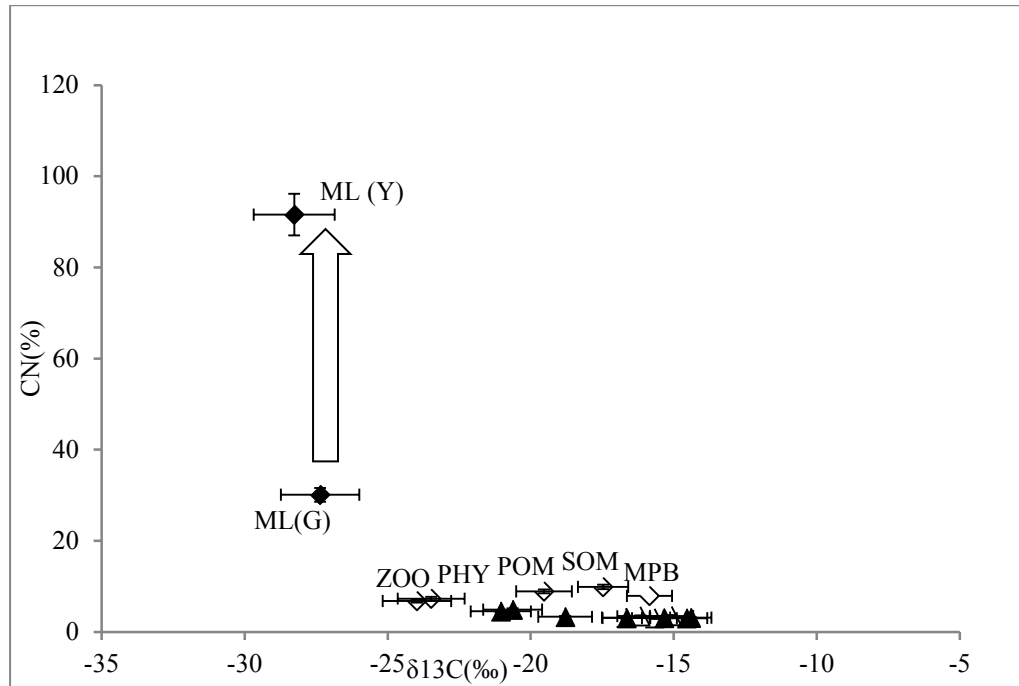


Figure S1 Plot of $\delta^{13}\text{C}$ and CN% values of food sources and consumers in the mangrove site of Qeshm Island, Iran. Green and yellow mangrove leaves: ML (G), ML (Y), phytoplankton (PHY), zooplankton (ZOO), particulate organic matter (POM), Sediment (SOM), Microphytobenthos (MPB), Δ : Macrobenthos, \blacktriangle : Fishes. Arrow indicates CN% shift from green to yellow (decomposed) leaves.

Annex III. Supplements for Chapter IV**Table S1** Mean inundation area and volume of water for each creek during spring and neap high tides.

Creeks	Spring tide		Neap tide	
	Area(m ²)	Volume(m ³)	Area(m ²)	Volume(m ³)
C1	2774	1562	338	102
C2	6481	4600	815	165
C3	11460	10327	2937	1807
C4	3811	3439	1281	220
C5	5672	2240	282	54
C6	10822	6034	1362	240

Table S2 Detailed species data for total abundance and biomass of fish and prawn on a per sample and per m² basis for each habitat and season.

Factor	m	Var %	Allocation success (%)						Total	δ^2	P
			mangrove		non-mangrove						
Habitat											
	5	95	76.5	78.1					74.9	0.3	0.004
Season											
	9	97	75	81.2					75.9	0.6	0.02
Creek (habitat)											
	11	97	18.7	37.5	31.2	25	25	43.7	29.9	0.4	0.02

Table S3 Table S3. Canonical analysis of principal coordinates (CAP) testing the effect of habitat (mangrove and non-mangrove), season (winter and summer) and creeks (C1, C2, C3, C4, C5, C6). %Var = percentage of the total variation explained by the first m principal coordinate axes; allocation success = percentage of points correctly allocated into each group; δ^2 = square canonical correlation.

	Total abundance per sample				Total abundance per m ²				Total biomass per sample				Total biomass per m ²			
	Habitat		Season		Habitat		Season		Habitat		Season		Habitat		Season	
	Mangrove	Non-mangrove	Winter	Summer	Mangrove	Non-mangrove	Winter	Summer	Mangrove	Non-mangrove	Winter	Summer	Mangrove	Non-mangrove	Winter	Summer
Mangrove and non-mangrove																
<i>Scatophagus argus</i> (Scatophagidae)	2.30	0.09	0.13	3.00	0.040	0.001	0.00	0.04	25.0	1.0	4.2	29.76	0.27	0.01	0.06	0.21
<i>Pomadasyys kaakan</i> (Haemulidae)	1.36	0.16	0.52	1.40	0.021	0.001	0.01	0.02	20.4	3.9	7.7	22.10	0.32	0.02	0.09	0.26
<i>Ilisha melastoma</i> (Clupeidae)	0.28	0.06	0.29	0.13	0.003	0.000	0.00	0.00	4.8	0.7	6.0	0.80	0.03	0.00	0.03	0.01
<i>Sarinella longiceps</i> (Clupeidae)	2.58	0.34	3.67	0.00	0.066	0.001	0.07	0.00	29.9	2.3	41.4	0.00	0.85	0.01	0.85	0.01
<i>Leiognathus daura</i> (Leiognathidae)	12.39	4.16	16.25	3.04	0.230	0.014	0.21	0.03	54.0	14.8	61.3	20.55	1.07	0.06	0.88	0.19
<i>Thryssa vitrirostris</i> (Engraulidae)	6.83	1.88	2.88	7.48	0.118	0.009	0.06	0.07	176.8	48.2	105.0	162.92	3.09	0.23	1.79	1.54
<i>Acanthopagrus cuvieri</i> (Sparidae)	0.23	0.06	0.04	0.31	0.003	0.000	0.00	0.00	1.7	6.7	0.1	6.71	0.02	0.03	0.03	0.05
<i>Pentaprion longimanus</i> (Gerreidae)	5.69	3.75	5.60	4.48	0.092	0.014	0.05	0.06	55.2	36.2	54.3	43.39	0.91	0.14	0.41	0.52
<i>Acanthopagrus latus</i> (Sparidae)	2.30	1.88	1.63	2.69	0.046	0.008	0.02	0.03	62.4	52.8	58.3	60.12	1.69	0.20	1.12	0.62
<i>Eleutheronema tetradactylum</i> (Polynemidae)	0.09	0.06	0.13	0.04	0.005	0.000	0.00	0.00	0.9	1.3	1.2	0.85	0.05	0.00	0.05	0.00
<i>Scomberoides lysan</i> (Carangidae)	0.08	0.06	0.00	0.15	0.001	0.000	0.00	0.00	1.1	1.3	0.0	2.27	0.01	0.00	0.00	0.01
<i>Liza klunzingeri</i> (Mugilidae)	18.20	36.09	24.98	23.3	0.277	0.164	0.26	0.18	402.7	793.2	590.5	475.16	6.58	3.70	5.59	3.45
<i>Pseudorhombus elevatus</i> (Paralichthyidae)	0.05	0.06	0.10	0.00	0.001	0.000	0.00	0.00	5.2	7.8	12.2	0.00	0.05	0.02	0.05	0.00
<i>Platycephalus indicus</i> (Platycephalidae)	0.06	0.13	0.00	0.17	0.001	0.001	0.00	0.00	8.6	45.0	0.0	41.46	0.14	0.24	0.24	0.38
<i>Sphyraena putnamiae</i> (Sphyraenidae)	0.02	0.06	0.00	0.06	0.000	0.000	0.00	0.00	10.0	12.8	0.0	21.85	0.22	0.08	0.08	0.30
<i>Hemiramphus archipelagicus</i>	0.02	0.03	0.02	0.02	0.001	0.000	0.00	0.00	0.9	0.3	0.2	1.15	0.01	0.00	0.00	0.01

	Total abundance per sample				Total abundance per m ²				Total biomass per sample				Total biomass per m ²			
	Habitat		Season		Habitat		Season		Habitat		Season		Habitat		Season	
	Mangrove	Non-mangrove	Winter	Summer	Mangrove	Non-mangrove	Winter	Summer	Mangrove	Non-mangrove	Winter	Summer	Mangrove	Non-mangrove	Winter	Summer
(Hemiramphidae)																
<i>Sillago sihama</i> (Sillaginidae)	0.16	0.69	0.58	0.08	0.004	0.004	0.01	0.00	5.4	21.2	17.6	3.79	0.16	0.12	0.14	0.04
<i>Upeneus sulphureus</i> (Mullidae)	0.02	0.06	0.04	0.02	0.000	0.000	0.00	0.00	0.0	1.3	0.8	0.05	0.00	0.01	0.00	0.00
<i>Anodontostoma chacunda</i> (Clupeidae)	2.00	26.06	18.40	1.65	0.016	0.089	0.09	0.01	31.6	221.2	163.1	26.44	0.24	0.78	0.27	0.18
Mangroves only																
<i>Lutjanus johni</i> (Lutjanidae)	0.27	0.00	0.15	0.21	0.008	0.000	0.01	0.00	31.0	0.0	17.1	24.24	0.97	0.00	0.73	0.24
<i>Plectorhinchus pictus</i> (Haemulidae)	0.11	0.00	0.00	0.15	0.002	0.000	0.00	0.00	6.2	0.0	0.0	8.27	0.12	0.00	0.00	0.12
<i>Sardinella gibbosa</i> (Clupeidae)	1.84	0.00	2.46	0.00	0.029	0.000	0.03	0.00	16.0	0.0	21.4	0.00	0.24	0.00	0.24	0.00
<i>Scartelaos tenuis</i> (Gobiidae)	0.11	0.00	0.04	0.10	0.002	0.000	0.00	0.00	1.9	0.0	0.8	1.72	0.04	0.00	0.01	0.02
<i>Bathygobius fuscus</i> (Gobiidae)	0.03	0.00	0.04	0.00	0.001	0.000	0.00	0.00	0.6	0.0	0.8	0.00	0.01	0.00	0.01	0.00
<i>Epinephelus coioides</i> (Serranidae)	0.02	0.00	0.00	0.02	0.000	0.000	0.00	0.00	3.1	0.0	0.0	4.17	0.07	0.00	0.00	0.07
<i>Abalistes stellatus</i> (Balistidae)	0.02	0.00	0.02	0.00	0.000	0.000	0.00	0.00	0.3	0.0	0.3	0.00	0.01	0.00	0.01	0.00
<i>Lutjanus russelli</i> (Lutjanidae)	0.03	0.00	0.02	0.02	0.001	0.000	0.00	0.00	1.4	0.0	1.7	0.16	0.10	0.00	0.10	0.00
<i>Strongylura stronglura</i> (Belonidae)	0.02	0.00	0.02	0.00	0.000	0.000	0.00	0.00	2.0	0.0	2.7	0.00	0.01	0.00	0.01	0.00
Non-mangrove only																
<i>Terapon jarbua</i> (Terapontidae)	0.00	0.03	0.02	0.00	0.000	0.000	0.00	0.00	0.0	1.1	0.7	0.00	0.00	0.00	0.00	0.00
<i>Euryglossa orientalis</i> (Soleidae)	0.00	0.03	0.02	0.00	0.000	0.000	0.00	0.00	0.0	0.4	0.3	0.00	0.00	0.00	0.00	0.00
<i>Gerres poieti</i> (Gerreidae)	0.00	1.34	0.00	0.90	0.000	0.004	0.00	0.00	0.0	20.5	0.0	13.66	0.00	0.06	0.06	0.06
Crustacean																
<i>Penaeus merguensis</i> (Penaeidae)	25.547	0	31.04	3.02	0.4	0	0.37	0.04	126.5	0	157.8	11.53	0.03	0	0.04	0.002
Number of species	28	22	25	23												

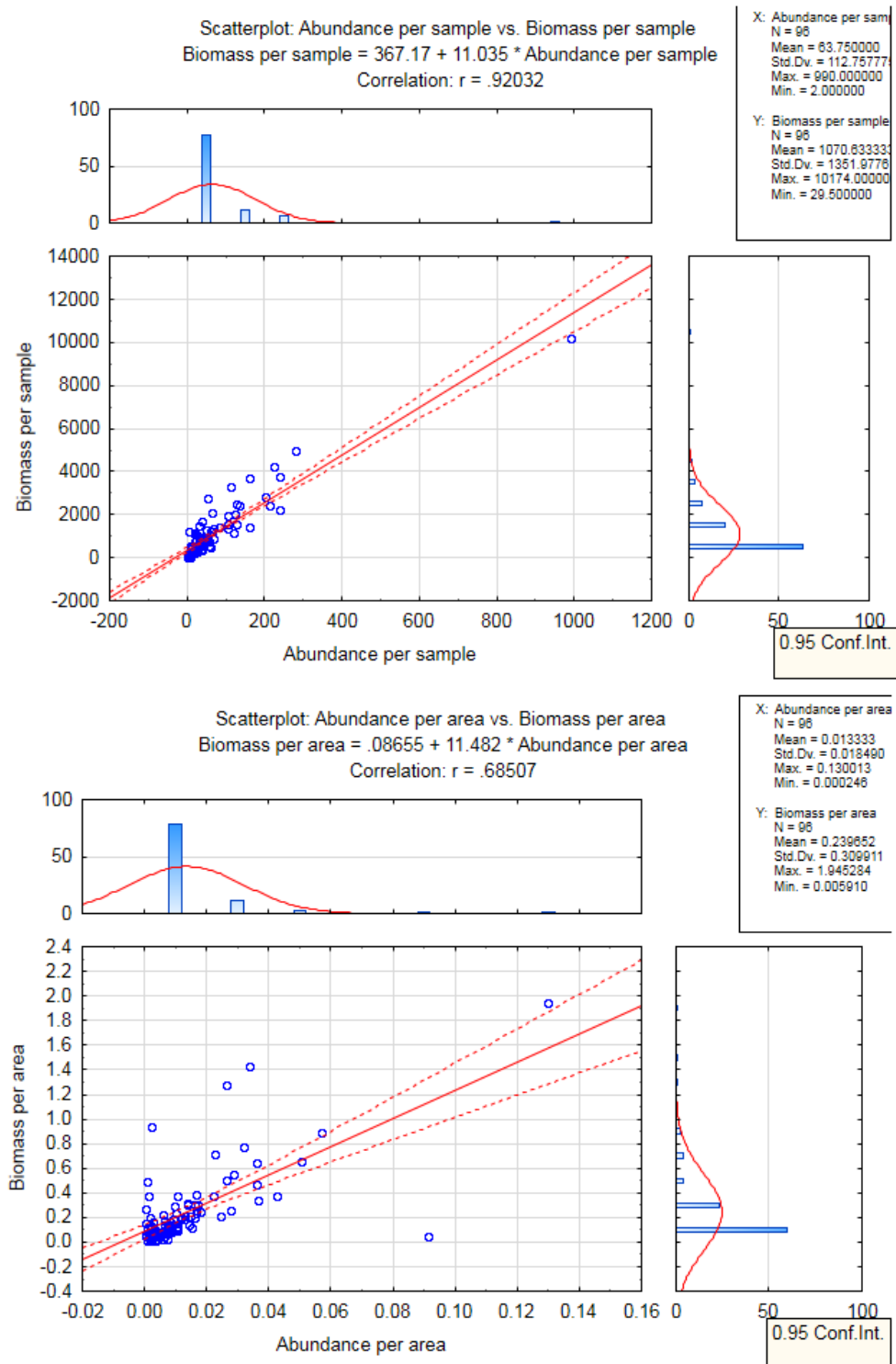


Figure S1 Correlation analyses between abundance and biomass per sample and per area. The correlation between abundance and biomass are significant for both per sample ($r=0.9$, $N=96$, $P<0.05$) and per area ($r=0.6$, $N=96$, $P<0.05$).

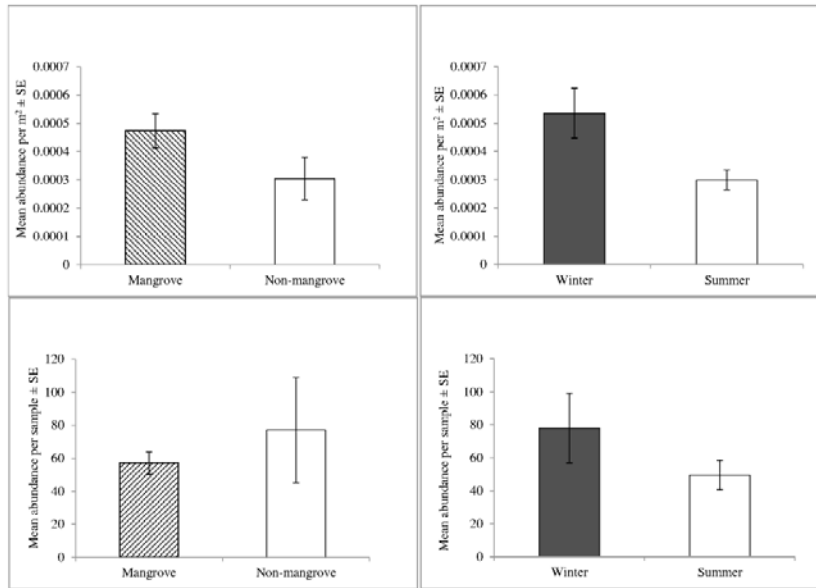


Figure S2 Mean fish abundance per sample and per m² (±SE) in different habitats (left panels) and seasons (right panels).

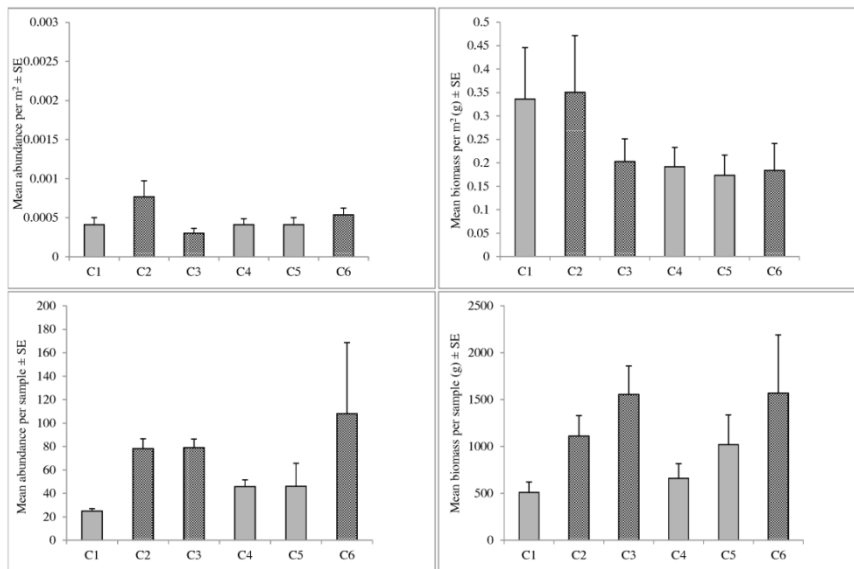


Figure S3 Mean fish abundance and biomass (±SE) per m² (upper panels) and per sample (lower panels), indicates inconsistent patterns between creeks (Note: different y axis scales).

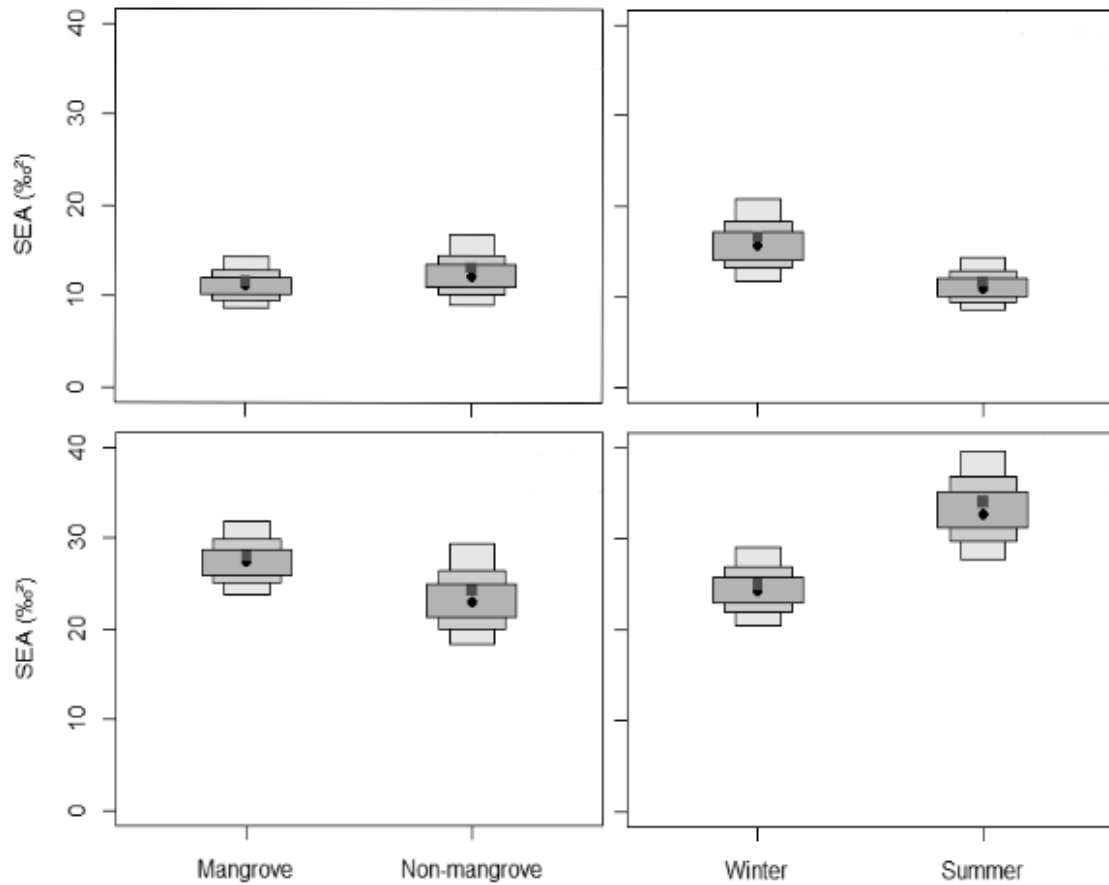


Figure S4 Density plots showing the credibility intervals of the standard ellipses areas (SEA) for fish species (upper panels) and food sources (lower panels). Black circles are the mode SEA, gray squares are the small sample size corrected SEA (SEA_c), and boxes indicate the 50%, 75% and 95% credibility intervals.

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Eidesstattliche Erklärung

(Gem. § 6(5) Nr. 1-3 PromO)

Hiermit versichere ich, dass ich die vorliegende Arbeit:

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Bremen, März 2015

Maryam Shahraki

