

**Coral reef fish assemblages along a disturbance gradient in the northern Persian Gulf: a seasonal perspective<sup>1</sup>**

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**ABSTRACT**

Seasonal dynamics of coral reef fish assemblages were assessed along a gradient of potential anthropogenic disturbance in the Northern Persian Gulf. Overall, the attributes of coral reef fish assemblages showed seasonality at two different levels: seasonal changes irrespective of the magnitude of disturbance level (e.g. species richness), and seasonal changes in response to disturbance level (e.g. total abundance, and assemblage composition). The examined parameters mostly belonged to the second group, but the interpretation of the relationship between patterns of seasonal changes and the disturbance level was not straightforward. The abundance of carnivorous fishes did not vary among seasons. SIMPER identified the family Nemipteridae as the major contributor to the observed spatiotemporal variations in composition of coral reef fish assemblages in the study area.

**Keywords:** anthropogenic disturbance; seasonality; assemblage composition

## 1. Introduction

The Persian Gulf is a geologically young subset of the Indian Ocean, which is characterized by its depauperate fauna (Sheppard et al., 1992). The Gulf ecosystems are being increasingly impacted by a wide variety of disturbing natural (Price et al., 1993a; Sheppard, 1993) and anthropogenic processes (Price, 1993b; Sale et al., 2011). Coral reefs of the Gulf typically represent a good example of such perturbed ecosystems, suffering from loss of corals and their associated fauna (e.g., fish) (Sheppard et al., 2010).

Disturbing agents may directly impair health, growth, and reproduction in coral reef fishes (Donelson et al., 2014; Kokita and Nakazono, 2001; Loya and Rinkevitch, 1980; Munday et al., 2008; Pratchett et al., 2004; Reopanichkul et al., 2009; Wilson et al., 2006) or may exert indirect effects on recruitment, abundance, diversity, behavior of fish species through habitat degradation (Bellwood et al., 2006; Coker et al., 2009; Graham et al., 2006; Graham et al., 2007; Pratchett et al., 2011; Pratchett et al., 2008; Pratchett et al., 2009; Wen et al., 2010; Wilson et al., 2008; Wilson et al., 2006). The extent to which coral reef fishes are impacted by disturbance depends on the magnitude of disturbance, physiological limits of the organism, the degree of its reliance on live coral, and its interaction with others, which may vary between species (Pratchett et al., 2008; Wilson et al., 2006). Consequently, variable assemblage of coral reef fish communities may develop at different levels of disturbance (Jones and Syms, 1998; Pratchett et al., 2008). As such, considering the increasing trend in severity of disturbances, understanding how a coral reef fish community changes in time and space along a disturbance gradient is critical to determine the consequences of ongoing disturbances.

Research of coral reef fish community structure in the Gulf has been mainly limited to its southern parts. Gulf coral reef fishes were originally thought to be irregularly distributed along the Arabian region (Krupp and Muller, 1994), but later examinations indicated that natural coral reefs contain distinct assemblages of reef fishes when compared with artificial structures (Burt et al., 2009, 2013). Burt et al. (2011) has also found substantial dissimilarities in species composition of coral reef fish assemblages between the southern Persian Gulf and nearby Gulf of Oman or western Arabian Sea. Yet, studies on the effects of disturbance on structure of these communities yielded variable results. For example, Usseglio et al. (2008) concluded that live coral losses associated with coastal development would cause significant changes in species composition of coral reef fish communities. Similarly, Bauman et al. (2010) detected significant changes in assemblage composition of coral reef fish communities subjected to harmful algal bloom events, while Riegl (2002) failed to detect such differences after the 1998 bleaching event. With respect to the structure of reef fish assemblages on the northern Gulf coral reefs, Rezai and Savari (2004) recorded three types of coral reef fish assemblages along Iranian islands but also concluded that the exact effects of coral degradation on coral reef fishes are unknown in the region. Further studies attempted to assess the impacts of disturbance of coral reef fish, which were generally performed on the sub-community level rather than the whole assemblage. For example, Shokri et al. (2005) used a univariate approach to determine the degree of association between live coral cover and butterflyfishes, and Valavi et al. (2010) performed a multivariate redundancy analysis to investigate the effects of multiple stressors on the abundance of ReefChecks indicator species and concluded that only a subset of proposed species can be effectively used as indicators for multiple stressors.

Reef fish communities of the southern Gulf has also been found to be seasonally regulated in the southern Gulf (Grandcourt, 2012). For example, Burt et al. (2009, 2013) found distinct fish assemblages on coral reefs of Dubai during cool and warm seasons but also demonstrated that the degree of seasonality in natural coral reef fish communities could be higher and lower than those communities inhabiting artificial structures. On the other hand, there has also been relatively little research dealing with seasonal changes in reef fish assemblages in the northern Gulf area, most of which is limited to artificial reefs and larval stages of fish. For example, Rabbaniha et al. (2013) observed consistent seasonal trends in the ratio of pelagic/demersal reef fish larvae and linked this to changes in water column chlorophyll concentration during warm and cool seasons. However, Pourjomeh et al. (2013) failed to detect such trends in composition of adult coral reef fish communities attracted to artificial reefs over the first two years of establishment and concluded that seasonal variability of reef fish assemblages may be less pronounced on younger artificial reefs. Yet, to our knowledge, there is no published data on the possible effects of disturbance on the seasonality of coral reef fish assemblages on natural reefs in the northern Gulf. The aim of the present study was to investigate seasonal patterns in assemblage structure coral reef fish along a potential human perturbation gradient in the northern Gulf region. The major question asked was whether the degree of seasonality in general attributes of coral reef fish assemblage structure varies along a gradient of disturbance.

## **2. Materials and methods**

### *2.1. Study area and data collection*

Mid-season baited remote under water video (BRUV) surveys were conducted from November 2013 to December 2014 on three nearshore coral patch reefs at an increasing along-shore distance from a petrochemical industry (a potential anthropogenic disturbance source location)

established in 1998. The three sampling sites included Assaluyeh port (near site; NS) located in the vicinity of industry, Southern Nayband Bay (far site; FS), 7 km from Assaluyeh port and Zahedeh Bay (farthest site; FSS), a further 13 km away from Assaluyeh port (Fig. 1). The coral fauna of the study area was dominated by *Platygyra* and *Porites* corals at ca. 5m depth. Mean live hard coral cover was 65%, 23%, and 17% at the Zahedeh Bay, Southern Nayband Bay Assaluyeh port, respectively. Prior to the study, a pilot experiment was conducted in the study area to optimize soak time and replicate numbers of BRUV surveys (Appendix A). Point intercept transect surveys were then performed on study sites to ensure that hard coral cover is homogenous within each site, since differences in coral cover can affect natural reef fish communities (Bell and Galzin, 1984). During the study, total of four replicate BRUV surveys were conducted at each study site (i.e., at a depth of ca. 5m) in each season. At each site, replicate BRUV deployments were done at randomly chosen stations which were at least 250m apart from each other (Langlois et al., 2010). This was done to ensure independency of replicate deployments and to avoid seasonal autocorrelation. Each survey included 65 minutes of front-view video recording from the boat using full-HD (1080p) mode and wide-viewing angle (170°). Approximately, 200g of fresh frigate tuna (*Auxis thazard thazard*) was used as bait for each survey (Hardinge et al., 2013). Sampling surveys were done during daylight hours (08:30 to 16:00 h) to avoid contributions of the crepuscular or nocturnal species to the sampling. Consecutive replicate surveys were conducted in 20-min intervals (Harvey et al., 2007). Water current velocities and vertical visibility were checked before each cast to ensure the constant dispersion rates of odor plume as well as equal chances of visual reinforcement of fish to the apparatus across the study. Recorded videos were observed on the computer screen by a single observer using GoPro Studio 2.0.0.285 player software. Analysis of each video started 3 minutes

after settlement of the filming apparatus on the seabed and continued for 60 minutes. For each video, number of sighted fish species and relative abundance of each species (MaxN; Willis and Babcock, 2000) were recorded by counting all the fish occupying near-filed distances (i.e., the distance between the camera lens and end of the bait arm=3m). Fish species were identified using illustrated fish catalogues (Al-Abdessalaam, 1995). Recorded fish species were then assigned to one of three trophic guilds (herbivore, planktivore/invertivore, or carnivore) at the family level according to (Halpern, 2003).

## *2.2. Data analysis*

Univariate variables (i.e., species richness, total abundance (total MaxN), and relative abundance (MaxN) of each trophic group) were standardized to maximum prior to analysis to account for possible inconsistency in size of sampling area (i.e., active space) (Colton and Swearer, 2010). A two-way (factor 1= site, fixed, three levels: FSS, FS, and NS, factor 2= season, fixed, four levels: fall, winter, spring, and summer) permutational MANOVA (PERMANOVA; Anderson, 2001), with a type I model, was used to analyze each data. Significant differences were tested by 9999 permutations with Euclidean distance measures (Dorman et al., 2012). For each trophic group, relative abundances of the next two groups were considered as covariates to account for possible inter-trophic group behavioral interactions around bait. In the case of significant differences for PERMANOVA main test, pair-wise a posteriori tests were used to compare levels of significant factors. The relationship between species richness and total abundance was assessed using Pearson correlation coefficients. PERMANOVA does not assume normality of errors but is sensitive to deviations from homoscedasticity. As such, PERMDISP was performed before running PERMANOVAs to test for homogeneity of multivariate dispersions (Anderson et al., 2006). PERMDISPs were significant for all response variables. As a result, abundance data were

square root transformed to meet the homoscedasticity assumption. Homoscedasticity of species richness data was not achieved through transformation. Thus, a more conservative significance level of  $p < 0.01$  was considered to account for heteroscedasticity (Zar, 1998).

The same process described for univariate data were used to analyses assemblages composition, except that a Bray-Curtis dissimilarity measure was applied instead of Euclidean distances. Data were standardized to total, and square root transformed before running the PERMANOVA. Also, a dummy variable was added to adjust for denuded samples at the “NS” sampling area (Clarke et al., 2006). In the case of significant differences, canonical analysis of principal coordinates (CAP) was used to visualize constrained patterns of the whole assemblage and to test within the levels of significant factors (Anderson and Willis, 2003). The default condition provided by PRIMER-E software was used to choose the number of PCO axes. The contribution of each family to the observed pairwise differences was determined using the routine. Values of  $\delta_i > 3\%$  and  $\delta_i / SD(\delta_i) > 1$  (where  $\delta_i$  is the mean contribution of the  $i^{\text{th}}$  species to the observed pairwise dissimilarity and SD is the standard deviation of the calculated mean) were considered as an indicator of strong contribution . The strongest contributors (i.e., principle families) were then used in a univariate approach (Terlizzi et al., 2005).

### **3. Results**

#### *3.1. Species richness*

A total of 27 taxa belonging to 23 families were sighted during the study (Appendix B). Both season and site were significant (site: pseudo- $F_{2,36} = 15.48$ ,  $p_{(\text{perm})} = 0.0001$ ; season: pseudo- $F_{3,36} = 8.61$ ,  $p_{(\text{perm})} = 0.0003$ ) in the PERMANOVA model, but there was no significant interaction between the two factors (pseudo- $F_{6,36} = 1.37$ ,  $p_{(\text{perm})} = 0.25$ ). The FSS and FS exhibited



significantly greater mean species richness than the NS (Fig. 2). Meanwhile, wintertime assemblages were significantly less specious than those of other seasons (Fig. 2).

### 3.2. Total MaxN

PERMANOVA was significant for site (pseudo- $F_{2,36}= 15.36$ ,  $p_{(\text{perm})}= 0.0001$ ), season (pseudo- $F_{3,36}= 7.39$ ,  $p_{(\text{perm})}= 0.0006$ ), and site  $\times$  season interaction (pseudo- $F_{6,36}= 2.93$ ,  $p_{(\text{perm})}= 0.017$ ), indicating that there was no main effect for site or season. The observed spatial differences were mainly driven by a higher mean number of individuals at the FSS/FS than the NS (Fig. 2). In terms of seasonal changes, significantly lower numbers of individuals were recorded during winter at the FS and NS, while total MaxNs were comparable across seasons at the FSS (Fig. 2). Total MaxN was significantly positively correlated with species richness at the NS ( $r= 0.83$ ,  $p= 0.000$ ) and FS ( $r= 0.76$ ,  $p= 0.002$ ), while there was a weak relationship between total MaxN and species richness at the FSS ( $r= 0.18$ ,  $p= 0.50$ ).

### 3.3. Relative abundance of trophic groups

Three families (Mugilidae, Ehippidae, Blenniidae) were excluded from the analysis, since they do not belong to single trophic groups (Halpern, 2003). Planktivores/invertivores were predominant in the study area, represented by nine families, followed by carnivores and herbivores.

The mean MaxNs of herbivores differed significantly across sites (pseudo- $F_{2,36}=12.68$ ,  $p_{(\text{perm})}= 0.0002$ ) and seasons (pseudo- $F_{3,36}= 3.91$ ,  $p_{(\text{perm})}= 0.019$ ), while the interaction term was also significant in the PERMANOVA model (pseudo- $F_{6,36}=2.69$ ,  $p_{(\text{perm})}= 0.029$ ). The observed spatiotemporal trends were rather ambiguous, and no clear image emerged (Fig. 2).

With respect to the relative abundance of planktivores/invertivores, significant spatial (pseudo- $F_{3,36}= 18.73$ ,  $p_{(\text{perm})}= 0.0001$ ) and seasonal differences (pseudo- $F_{2,36}= 14.34$ ,  $p_{(\text{perm})}= 0.0001$ ) were

detected, while the interaction term was also significant (pseudo- $F_{6,36} = 9.23$ ,  $p_{(\text{perm})} = 0.0002$ ).

The observed spatiotemporal trends were to some extent similar to the total MaxN data (Fig 2).

The mean MaxNs of carnivores were comparable across sites (pseudo- $F_{2,36} = 1.22$ ,  $p_{(\text{perm})} = 0.31$ ) and seasons (pseudo- $F_{3,36} = 0.79$ ,  $p_{(\text{perm})} = 0.51$ ). The season  $\times$  site interaction was also nonsignificant (pseudo- $F_{6,36} = 0.97$ ,  $p_{(\text{perm})} = 0.46$ ).

### 3.3. *Assemblage composition*

The obtained CAP plots illustrated some separation between the study sites, while separations between seasons were poorly represented (Fig. 3). PERMANOVA detected significant effects of season (Pseudo- $F_{3,36} = 3.70$ ,  $p_{(\text{perm})} = 0.0001$ ), site (Pseudo- $F_{2,36} = 8.00$ ,  $p_{(\text{perm})} = 0.0001$ ) and their interactive term (Pseudo- $F_{6,36} = 2.73$ ,  $p_{(\text{perm})} = 0.0001$ ) on assemblage composition. The PERMDISP test also detected significant ( $p < 0.05$ ) differences in multivariate dispersions among different seasons and sites. Together, results of PERMANOVA and PERMDISP revealed an interactive pattern which may be due to differences in study site, season, dispersion and/or their combination. Detected pairwise spatial differences included fully variable assemblages in autumn and a significant difference between FSS and NS during other seasons (Table 1). In terms of seasonal changes, the species composition was comparable along succeeding seasons at the FSS and FS, whereas there was a difference between fall and winter at the NS study area. SIMPER analyses revealed five families as the weightiest taxa to distinguish spatial and temporal patterns (Table 1) amongst which only two (Nemipteridae and Carangidae) were responsible for both spatial and temporal changes. Results of univariate PERMANOVAs revealed significant spatial (Pseudo- $F_{3,36} = 33.38$ ,  $p_{(\text{perm})} = 0.0001$ ) and seasonal (Pseudo- $F_{2,36} = 9.73$ ,  $p_{(\text{perm})} = 0.0005$ ) differences for mean MaxN of Nemipteridae, while the interactive term was also significant (Pseudo- $F_{6,36} = 14.39$ ,  $p_{(\text{perm})} = 0.0001$ ). The observed interactive trends were

mainly driven by significant increases in numbers of individuals during autumn at the FS site and during summer at the NS site (Fig. 4). The mean MaxNs of Carangidae did not differ significantly across sites (Pseudo- $F_{6,36}=14.39$ ,  $p_{(\text{perm})}=0.0001$ ) or seasons (Pseudo- $F_{6,36}=0.16$ ,  $p_{(\text{perm})}=0.92$ ) but there was an apparent interaction between two factors (Pseudo- $F_{6,36}=2.6$ ,  $p_{(\text{perm})}=0.028$ ).

In total, replicate samples taken from Assaluyeh port showed higher variability (MVDISP= 1.20) than Southern Nayband Bay (MVDISP= 0.93) or Zahedeh Bay (MVDISP=0.86).

#### **4. Discussion**

Overall, the results of our study indicated that the attributes of coral reef fish assemblage may show seasonality at two different levels: seasonal changes irrespective of the disturbance level, and seasonal changes in response to disturbance level. The examined parameters mostly belonged to the second group, but the interpretation of the relationship between patterns of seasonal changes and the disturbance level was not straightforward.

##### *4.1. Variations in species richness*

The season had a significant overall effect on species richness, irrespective of the disturbance level. Seasonality in species richness (and also species richness) has been documented for tropical (e.g. Munga et al., 2011), subtropical (e.g. Tremain and Adams, 1995), and temperate (e.g. ter Hofstede et al., 2010) fish communities. Previous studies of the southern Gulf reef fish communities have also recorded seasonal fluctuations (i.e., decline in winter and rise in summer) in species richness (e.g. Burt et al., 2013; Coles and Tarr, 1990; Krupp and Muller, 1994), but observations were not always consistent (e.g. Burt et al., 2009). Off-reef migrations (Coles and

Tarr, 1990) and die-off events (Krupp and Muller, 1994) have been considered the main drivers of declines in species richness during winter. We did detect a significant decline in species richness during winter, which seemed to be mainly driven by off-shore migrations of fish, since no signs of within-site mortality were found in the study area.

In terms of spatial variations, our findings were consistent with the general idea that disturbance would result in decreased diversity of coral reef fish (Pratchett et al., 2011; Pratchett et al., 2008; Wilson et al., 2006). This may be mainly due to loss of live coral cover, lower topographical complexity, and/or lower coral species richness in disturbed areas (Chabanet et al., 1997; Komyakova et al., 2013; Pratchett et al., 2011). Pratchett et al. (2011) concluded that >40% absolute decrease in live coral cover would lead to a considerable decline in species richness. In our study, the estimated mean live coral cover at the NS was 43% lower than at the FS, and a further 32% lower than at the FSS. Coral cover was also markedly different between the FSS and FS (64% lower at the FSS), but mean species richness at the FSS and FS was comparable. Further observation of the habitat structure in obtained videos indicated that corals were more patchily distributed at the FS than at the FSS, which was mainly characterized by continuous corals. In this case, higher habitat fragmentation at the FS may positively affect species richness of its reef fish assemblage by alleviation of agonistic actions between competing species (Bonin et al., 2011). Furthermore, Bellwood et al. (2006) indicated that moderate levels of disturbance may have limited (or even positive in the case of generalist species) effects on species richness. This may also hold for our study, since the number of planktivorous/invertivorous fish (commonly considered to be generalist) species was higher at the FS than at the FSS. Although variations in topographical complexity and coral species richness were not directly examined in our study, one may expect that both decreased topographical complexity and coral species

richness would eventually occur due to the loss of live coral cover (Komyakova et al., 2013; McCook, 2002). Yet, the overall diversity of coral growth forms was very low in the study area (including mainly massive and columnar corals) which may, along with other factors (e.g. shallow depth, high turbidity), explain the small number of species in this area, compared with other parts of the Gulf (e.g. Rezai and Savari, 2004). It should be noted that the observed differences in total number of species between our study and other studies may be partially due to differences in the sampling methods applied (BRUV vs. underwater visual census; UVC), since BRUV generally records a smaller number of species than UVC (Lowry et al., 2012).

#### *4.2. Variations in Abundance*

Seasonal trends in the total MaxN, MaxN of herbivores and MaxN of planktivores/ invertivores were dependent on disturbance levels. Perhaps the most striking pattern occurred at the lowest levels of disturbance (i.e., the FSS), the comparable mean abundances throughout the year. In contrast, the total abundance and the relative abundance of trophic groups fluctuated seasonally at both moderately (i.e., the FS) and highly impacted (i.e., the NS) sites. Nevertheless the trends were inconsistent. Previous research in the southern Gulf area demonstrated that seasonal variations in total abundance and to some extent the abundance of trophic groups followed the same pattern as the species richness, a summertime rise followed by a winter time decline (Burt et al., 2013; Coles and Tarr, 1990; Krupp and Muller, 1994). However, Burt et al. (2009) failed to detect such variations in the natural reef fish community in Dubai, whilst these changes were significant on breakwaters of the same area. It has been concluded that mortality and, migration, may contribute to the decreased abundances during the winter time, similar to the trends with regards to species richness (Burt et al., 2013). Yet, Coles and Tarr (1990) argued that fish may be able to survive winters by seeking shelter in near-shore coral reefs. As such, the

availability of sufficient shelter (probably by higher coral cover) would result in no changes in total abundance in the winter - the case in the FSS community in our study. However, these results were seemingly contradictory with the species richness data at the FSS which indicated a significant decrease in mean number of species in the winter. Furthermore, at the time there was a poor correlation between species richness and abundance in the FSS fish community, although these correlations were significant at the FS and NS communities. As such, factors other than simply colonization and mortality (e.g. competition and predation) may contribute to changes in the abundance of fish at the FSS (Sale, 1980).

On other hand, we failed to detect any increase in fish abundance in summer, which has been found as a common phenomenon in the southern Gulf area (Burt et al., 2013; Coles and Tarr, 1990; Krupp and Muller, 1994). Moreover, Seasonal recruitment and colonization has been suggested as the main driving forces that increased fish abundance during warm seasons (Burt et al., 2009; Burt et al., 2013). The observed disparity between our findings and previous results may be partially explained by the incidence of more extended spawning seasons for fish in northern communities, which results in later recruitment events. For example, Taghavi Motlagh et al. (2010) found that *Lethrinus nebulosus* spawns in Iranian waters between March and June, while the spawning period for the same species in Dubai is from April to May. This might be due to the higher temperature in the northern Gulf area during the winter compared to the southern parts ( $22.7 \pm 1.2$  in the northern Gulf vs.  $21.9 \pm 0.07$  in the southern Gulf; mean  $\pm$  SD) (Swift and Bower, 2003), since an increased temperature would trigger an earlier start of spawning and a longer duration of the spawning season (Munday et al., 2008).

#### 4.3. Variations in assemblages

In general, seasonal variations in composition of natural fish assemblages have been mainly contributed to feeding/breeding migrations and recruitment processes (Friedlander and Parrish, 1998). Meanwhile, the effects of anthropogenic disturbance on seasonality of fish assemblages have been found to vary according to the type of disturbing agent, its timing, duration, and frequency (Chen et al., 2004; González-Sansón et al., 2008; Guidetti et al., 2003; Reopanichkul et al., 2009). Results of our study indicated that, the degree of seasonality in composition of coral reef fish assemblage may to some extent depend on the disturbance level.

Contrary to expectations from previous studies on the southern Gulf (Burt et al., 2009, 2013), diverged fish assemblages seemed to occur during fall and summer in the northern Gulf, irrespective of the disturbance level. According to the results derived from SIMPER analysis, these changes seemed to be mainly driven by seasonal influx and/or colonization of the emperors to coral reefs at the FSS during fall (considering similar interannual recruitment patterns in the northern Gulf area). The emperors (Lethrinidae) are a generalist carnivores which generally settle into sea grass beds and then migrate to the nearshore coral reefs as adult (Arvedlund and Takemura, 2006). Although, sea grass beds were present at the proximity of all study sites, no specimens of Lethrinidae were recorded from the FS or NS during the study period, but this phenomenon seemed less likely to have been attributed to higher coral cover at the FSS, since generalist species have been found not to be highly associated with live corals (Graham et al., 2007). On the other hand, distribution of Lethrinids has been found to be restricted by upper thermal limits (e.g. Williams et al., 2003) and it has been suspected that their distributions might be affected by global warming (Munday et al., 2008). As such, the absence of Lethrinids from the FS and FSS might be explained by higher water temperature in the Nayband bay area compared to the Zahedeh Bay (Ardakani et al., 2014) which is primarily due to thermal

pollution. Additional seasonal assemblage composition transitions at the NS generally included divergences between fall and other seasons. Although, several families were found as principle contributors to the observed seasonal changes in assemblages composition, the general trend seemed to be characterized by declined abundances in autumn assemblages. Assuming that recruitment occurs during fall in the northern Gulf communities, the observed divergence between fall and other seasons may be implicitly linked to impaired recruitments of fish species to the NS area during autumn and causal colonization of the area by different species during succeeding seasons. This was somewhat apparent for Lutjanidae, since the observed differences in assemblage composition between FSS and NS during autumn was found to have been attributed to absence of Lutjanids at the NS. Yet, these interpretations should be viewed with caution, since assemblages were highly variable within each season and/or study site. It should also be noted that the observed magnified effects might be due to inherent sampling errors, since fish abundances were naturally rare at the NS sampling area.

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Table 1. Results of canonical analysis of principal coordinates (CAP) analysis examining spatiotempral changes in composition of coral reef fish assemblages, along with contribution of the principle species to significant pairwise differences. FSS, farthest site (Zahedeh Bay); FS, far site (Sothern Nayband Bay); NS, near site (Assaluyeh Port);  $\delta_i$ , mean present dissimilarity



Table 1

Results of canonical analysis of principal coordinates (CAP) examining spatiotemporal changes in the composition of coral reef fish assemblages, along with contribution of the principle species to significant pairwise differences. FSS, farthest site (Zahedeh Bay); FS, far site (Sothern Nayband Bay); NS, near site (Assaluyeh Port);  $\delta_i$ , mean present dissimilarity.

		G1 Vs. G2	(tr(Q_m'HQ_m))	$p_{(perm)}$	Principle family	$\delta_i$	$\delta_i/SD(\delta_i)$	Avg. abundance <sub>(G1)</sub>	Avg. abundance <sub>(G2)</sub>	Contribution (%)
Spatial pairwise differences	Fall	FSS Vs. FS	0.91	0.029	Nemipteridae	10.83	3.34	1.76	7.41	22.2
		FSS Vs. NS	0.89	0.030	Lutjanidae	7.35	1.65	3.70	0.00	12.26
		FS Vs. NS	0.93	0.030	Nemipteridae	14.67	3.93	7.41	0.56	21.36
	Winter	FSS Vs. FS	0.59	0.087	-	-	-	-	-	-
		FSS Vs. NS	0.96	0.025	Carangidae	13.65	2.63	3.65	6.77	16.79
		FS Vs. NS	0.87	0.59	-	-	-	-	-	-
	Spring	FSS Vs. FS	0.95	0.11	-	-	-	-	-	-
		FSS Vs. NS	0.88	0.028	Lutjanidae	11.49	2.12	5.68	0.00	17.01
		FS Vs. NS	0.58	0.17	-	-	-	-	-	-
	Summer	FSS Vs. FS	0.76	0.060	-	-	-	-	-	-
		FSS Vs. NS	0.94	0.029	Nemipteridae	6.96	1.53	2.29	5.98	16.77
		FS Vs. NS	0.92	0.10	-	-	-	-	-	-
Seasonal pairwise differences	FSS	Fall Vs. Winter	0.84	0.056	-	-	-	-	-	-
		Fall Vs. Spring	0.59	0.11	-	-	-	-	-	-
		Fall Vs. Summer	0.76	0.027	Lethrinidae	5.82	2.74	3.24	0.00	13.57
		Winter Vs. Spring	0.70	0.16	-	-	-	-	-	-
		Winter Vs. Summer	0.33	0.62	-	-	-	-	-	-
		Spring Vs. Summer	0.54	0.14	-	-	-	-	-	-
	FS	Fall Vs. Winter	0.42	0.19	-	-	-	-	-	-
		Fall Vs. Spring	0.98	0.089	-	-	-	-	-	-
		Fall Vs. Summer	0.93	0.029	Nemipteridae	9.96	4.98	7.41	2.13	21.83
		Winter Vs. Spring	0.68	0.11	-	-	-	-	-	-
		Winter Vs. Summer	0.58	0.056	-	-	-	-	-	-
		Spring Vs. Summer	0.94	0.10	-	-	-	-	-	-
	NS	Fall Vs. Winter	0.84	0.028	Carangidae	13.51	2.74	4.66	6.77	19.31
		Fall Vs. Spring	0.69	0.029	Labridae	8.35	1.93	0.0	3.71	15.57
		Fall Vs. Summer	0.85	0.032	Nemipteridae	11.22	4.21	0.56	5.98	18.70
		Winter Vs. Spring	0.94	0.060	-	-	-	-	-	-
		Winter Vs. Summer	0.76	0.059	-	-	-	-	-	-
		Spring Vs. Summer	0.84	0.026	Carangidae	9.88	2.66	5.45	0.58	17.03

Fig 1

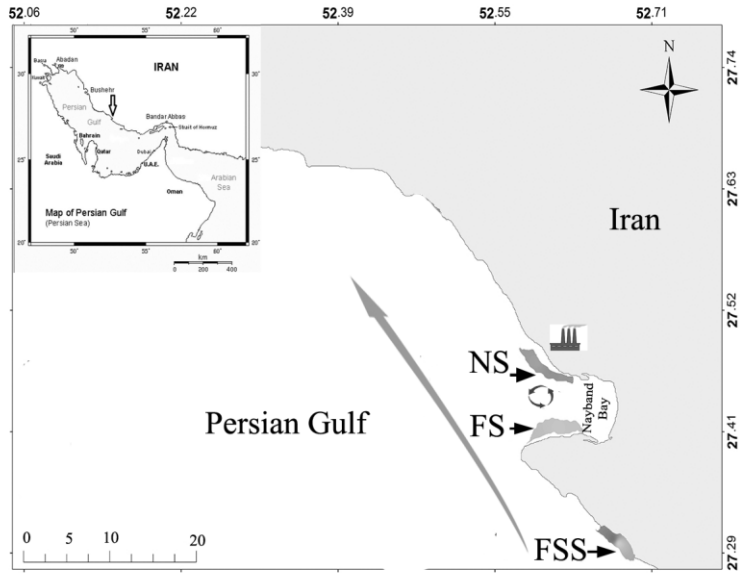


Fig 2.

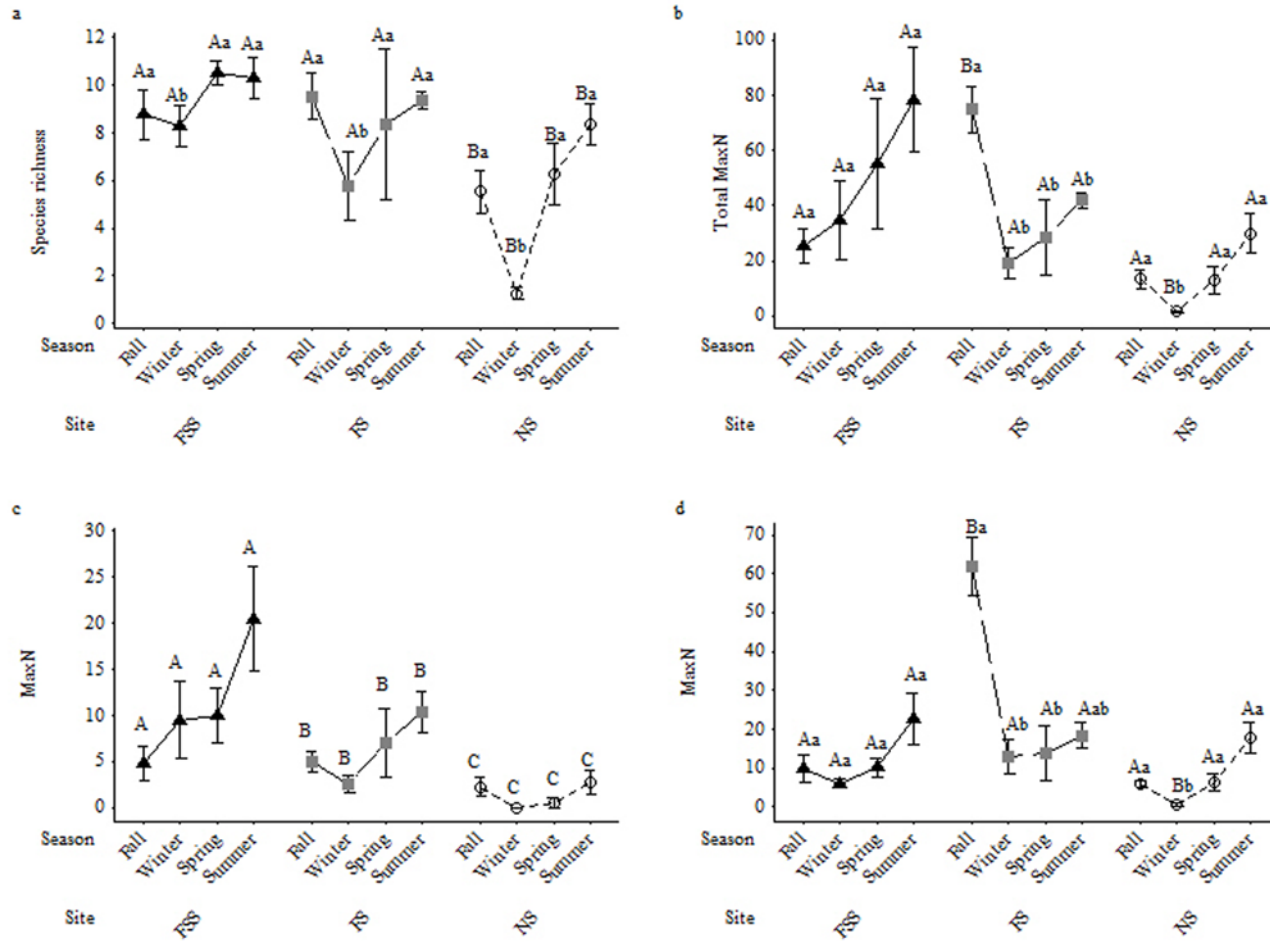


Fig 3

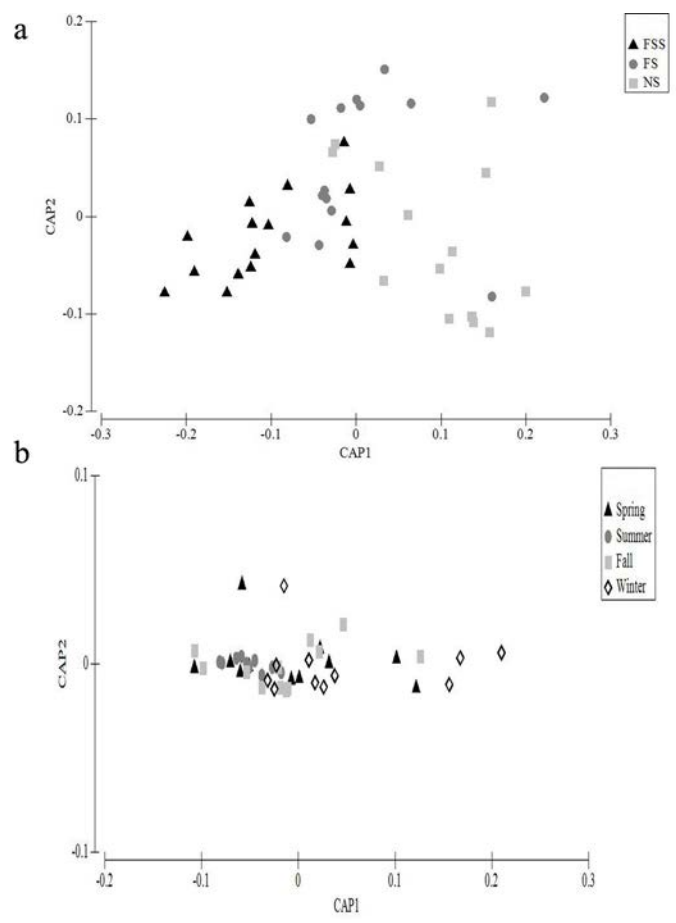


Fig 4

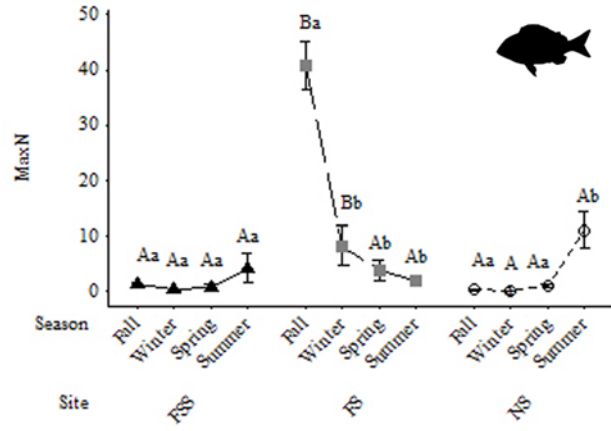


Figure 1. Map of the northern Persian Gulf showing the three sampling sites. Arrows indicate direction of main water currents

Figure 2. Spatial and seasonal changes in mean( $\pm$ SE) (a) species richness (b) total abundance (total MaxN) (c) MaxN of herbivores and (d) MaxN of Planktivores/invertivores. FSS, farthest site (Zahedeh Bay); FS, far site (Sothern Nayband Bay); NS, near site (Assaluyeh Port)

Note: different upper case letters indicate significant differences ( $p < 0.01$  for species richness and  $p < 0.05$  for other data) between study sites and different lower case letter indicate significant differences between seasons.

Figure 3. Canonical analysis of principal coordinates (CAP) ordination plots indicating separation of (a) study sites and (b) seasons based on differences in coral reef fish assemblage composition. FSS, farthest site; FS, far site; NS, near site.

Fig 4. Spatiotemporal changes in mean ( $\pm$ SE) abundance of the family Nemipteridae. FSS, farthest site; FS, far site; NS, near site.

Note: different upper case letters indicate significant differences ( $p < 0.05$ ) between study sites and different lower case letter indicate significant differences between seasons.



