Spatial variation in coral reef fish and benthic communities in the central Saudi Arabian Red Sea

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Abstract

Local-scale, ecological information is critical as a sound basis for spatial conservation and management and as support for ongoing research in relatively unstudied areas. We conducted visual surveys of fish and benthic communities on 9 reefs in the Thuwal area of the central Saudi Arabian Red Sea. Fish biomass increased with distance ~~from shore~~offshore, but was generally low compared with~~to~~ relatively ~~untouched~~ protected reefs around the world. All reefs had a herbivore-dominated trophic structure and few predators. Coral cover was considerably lower on inshore reefs, likely due to a 2010 bleaching event. Community analyses showed inshore reefs to be characterized by higher cover of turf algae and~~,~~ slower-growing corals, lower herbivore diversity, and higher ~~ly~~ abundan~~ce~~t of turf-farming damselfishes than offshore reefs. Offshore reefs had more planktivorous fishes, a more diverse herbivore assemblage, and faster-growing corals. All reefs appear to be impacted by overfishing, and inshore reefs seem more vulnerable to thermal bleaching. The spatial variation we describe in biomass and community structure can provide a preliminary basis for future spatial prioritization and subsequent marine protected area design in Thuwal.

Keywords: Community assemblages; Coral cover; Diversity; Fish biomass; Inshore-offshore gradients; Red Sea; Saudi Arabia; Trophic structure

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1. Introduction

Despite the uniqueness of its environment and the fact that it possesses one of the longest coral reef systems in the world, coral reef ecology remains relatively understudied in the Red Sea in comparison ~~remains a relatively understudied~~ to other biogeographical regions ~~of the world with regards to coral reef ecology~~ (Berumen et al. 2013). Detailed information on spatial patterns of fish biomass, fish densities, and structure of benthic and fish community assemblages are available only for some parts of the Red Sea, primarily the Gulf of Aqaba and parts of Egypt (e.g., Bouchon-Navaro and Bouchon 1989; Alwany and Stachowitsch 2007).

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Saudi Arabia has the largest stretch of Red Sea coastline (approximately 1700 km) and is home to a variety of coral reef habitat types (e.g., Sheppard et al. 1992), yet there are relatively few publications available from this region. Ecological information from the Saudi Arabian Red Sea is mostly confined either to reports prepared by collaborating regional and international organizations and published in grey literature (e.g., PERSGA/GEF 2003) or to large-scale studies focused on regional trends and patterns (e.g., Roberts et al. 1992; Price et al. 1998; DeVantier et al. 2000). With the exception of a few recent studies (e.g., Furby et al. 2013), little work has been done to characterize reef communities on small, local scales, which are appropriate for informing local resource-managers and decision makers (Margules and Pressey 2000), and there are even fewer studies using detailed taxonomic resolution ~~survey categories~~ (e.g., fish ~~species~~ or benthic species~~categories~~).

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However, recent expansion of research activity in Saudi Arabia (Mervis 2009) has begun to address questions about the functioning of Red Sea reefs at local scales (e.g., Davis et al. 2011; Jessen et al. 2013; van der Merwe et al. 2014). One example is the thermal bleaching event that occurred in summer 2010 (Furby et al. 2013, Pineda et al. 2013), which raised questions about the potential local impact of overfishing and coastal development on reef resilience in the presence of climate change (Khalil et al. 2013). Ongoing research efforts and eventual conservation planning increasingly highlight the need for detailed assessments of local and regional (e.g., Roberts et al. 2016) reef communities.

This study aimed to characterize the reef communities off the coast of Thuwal in the central Saudi Arabian Red Sea by exploring spatial patterns of ~~the~~ fish biomass, density, and species diversity ~~of reef fishes~~, with focus on important trophic and commercial groups. We also describe the spatial variation in benthic cover and in fish and benthic community assemblages. Finally, we suggest ~~potential~~ explanations for potential ~~what the~~ drivers of some of these spatial patterns ~~may be,~~ based on comparisons with other parts of the world and information available in the literature. Results obtained here may ~~The ultimate aim of the study was to~~ provide a scientific basis for subsequent spatial prioritization and conservation planning (Khalil 2015) by highlighting potential local "hotspots" and "coldspots" of fish diversity or biomass.

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We expected to find a cross-shore gradient of increasing fish biomass and diversity with distance from shore, which is a recurrent pattern found in previous cross-shelf studies in other regions of the world (e.g., Fabricius 2005; Aguilar-Perera and Appeldoorn 2008; Nemth and Appeldoorn 2009; Malcolm et a. 2010) due to typical environmental gradients in reef topography, depth, sedimentation, food availability, and/ or human impact~~, which are recurring patterns found in previously conducted cross-shore analyses around the world (e.g., Fabricius 2005; Aguilar-Perera and Appeldoorn 2008; Nemth and Appeldoorn 2009; Malcolm et a. 2010)~~. We also expected to find clear spatial variation in the structure of fish species ~~richness and~~ assemblages (fish abundance and species richness) co-occurring with ~~any~~ differences in benthic assemblages (Roberts and Ormond 1987; Chabanet et al. 1997; Chong-Seng et al. 2012).

2. Methods

2.1. Study Site

The study area includes 355 patch reefs of varying sizes distributed within an area of about 2200 km^2 along approximately 70 km of the central Saudi Arabian coast (Figure 1). The furthest reef is about 25 km from shore. The study area encompasses two large coastal establishments (the King Abdullah University of Science and Technology (KAUST) and the King Abdullah Economic City (KAEC)) and a small fishing town called Thuwal (22.28° N, 39.10° E). The area suffered from a severe bleaching event in summer 2010, which had the highest impact on reefs closest to shore. Inshore reefs lost most of their adult coral cover up to a depth of 10 meters and experienced a change in coral community assemblage (Furby et al. 2013).

We surveyed 9 reefs at increasing distances from shore (Figure 1). The three offshore reefs (furthest from shore and adjacent to waters deeper than 200 m) were, from north to south, Abu Romah Reef (RR), Nazar Reef (NR), and Abu Madafi Reef (AMR). Midshelf reefs (closer to shore and adjacent to waters that are 50 – 200 m deep) were Al-Fahal Reef (FR), Al-Taweel Reef (TWR), and Abu-Henshan Reef (AHR). Inshore reefs (closest to shore and surrounded by waters around 20 m deep) were Abu Shosha Reef (ASR), Tahla Reef (TR), and East Fsar Reef (EFR). Typical of the region, these reefs are arranged in small clusters, with relatively large elongated reef patches oriented on a north-south axis and surrounded by smaller, rounder, patches and pinnacles. All study reefs have relatively steep walls dropping down to 20 m or deeper and very shallow reef tops, with the exception of inshore reefs which drop to a sloping seabed at 10 – 15 m (Sheppard et al. 1992).

2.2. Fish and Benthic Surveys

Surveys were conducted in May 2013 at two depths (10 m and on the reef crest at 1 – 3 m) at each of the 9 reefs. All transects were located on the west sides of the reefs, exposed to prevailing winds, currents, and waves. Fish surveys were conducted along three belt transects at each depth (a total of 6 transects per reef), where a diver swam along the transects twice, first to record larger vagile fish in 25 x 8 m belts and a second time to record smaller, less mobile fish in 25 x 4 m belts (following Sandin et al. 2008). Individual fishes were counted and their sizes were estimated and placed in categories of total length in cm (0 – 3, 4 – 5, 6 – 10, 11 – 15, 16 –

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20…61 – 70, 71 – 80…101 – 150, 151 – 200 cm). Categories larger than 100 cm were merged as only two species (the moray eel *Gymnothorax javanicus* and the white tip reef shark *Triaenodon obesus*) were observed in these categories, and we were less confident in the accuracy of these size estimates. We did not attempt to count cryptic species (see Table S1 for a list of species observed) as these are poorly described in the Red Sea and require specific sampling methods (e.g., Tornabene et al. 2012).

Benthic surveys to determine live scleractinian (hard) coral cover, coral genus richness, and other benthic categories were conducted on the same transects as the fish surveys using the line-intercept method. Apart from hard coral genera, we recorded the cover of soft corals and zoanthids (to genus level when possible), sponges, crustose coralline algae (CCA), turf algae, and "other" algae. Transects for benthic surveys were 10 m long and located in the middle of each of the 25 m transects used for counting fish, making a total of 6 transects per reef, 3 at each depth. The transect length was chosen for its convenience in the field, to be comparable to previous studies done in this region (Furby et al. 2013), and because it has been previously shown to be adequate for quantitative studies of coral cover (Beenaerts and Berghe 2005). In order to minimize the impact of observer bias, all data were collected by the same divers (JB benthos, MLB fishes).

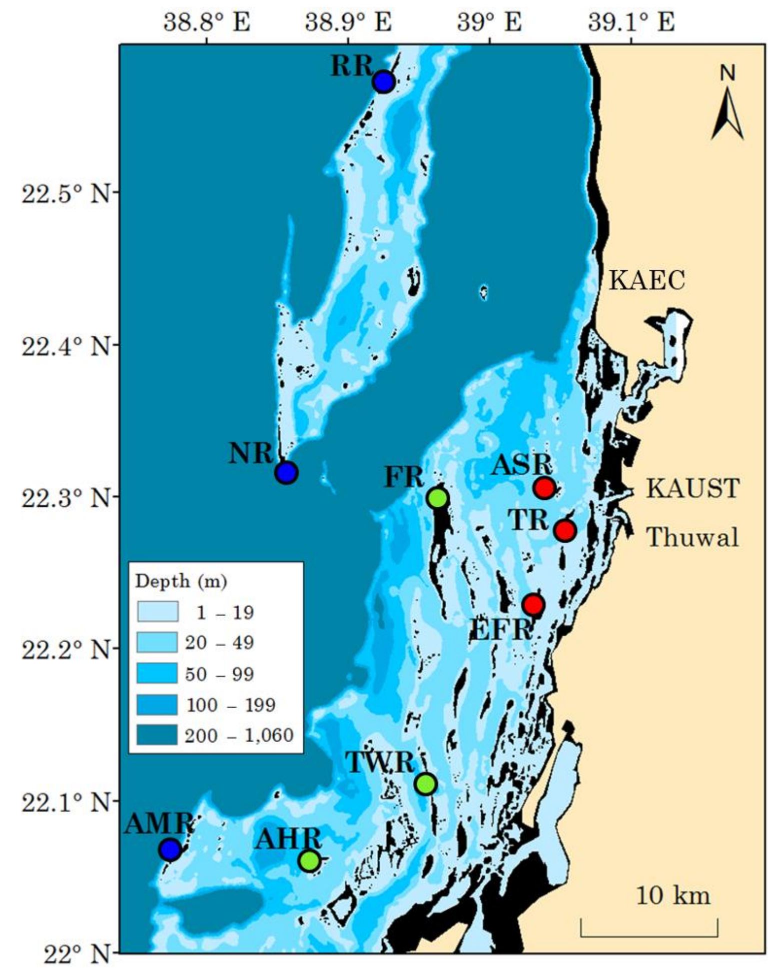

Figure 1. The study area and locations of survey reefs in the central Saudi Arabian Red Sea, near the town of Thuwal, the King Abdullah University of Science and Technology (KAUST), and the King Abdullah Economic City (KAEC). Depth is color coded as noted in the inset key. The black color represents the shallowest portion of reef areas (seasonally intertidal). Reef name abbreviations (see main text) are shown next to their respective, color-coded marker circles: red = inshore reefs; green = midshelf reefs; blue = offshore reefs. Geographic location is indicated by a decimal-degree grid on the left and top margins, and orientation by a north arrow in the top right corner. (Map created by MTK using various mapping sources in ArcMap, version 10.1.)

2.3. Biomass, Abundance, and Diversity Estimations

2.3.1. Fish Biomass and Trophic Composition

Fish biomass was calculated following Friedlander and DeMartini (2002) using the equation: $W = a \times L^b$, where *W* is the weight of the fish in grams, *L* is its total length (TL) in cm and *a* and *b* are species-specific constants obtained from FishBase (2014) (see Table S1 for a list of species-specific constants). For the *L* value, we used the mid-range value of each TL size category. When several values of *a* and *b* were present in the database for a given species, we used an average of the available values, and when values were missing from the database, we used those provided for sister species, the genus, or the family. The average biomass of all species was then calculated in kg/100 m^2 for each reef, and, from these values, we summarized the biomass of four trophic guilds (top predators, carnivores, herbivores, and planktivores) and 3 major groups of commercially targeted fish, which included 25 species in 5 subfamilies: parrotfishes (Scarinae and Sparisomatinae: 10 species), snappers (Lutjaninae: 6 species), and groupers (Serraninae and Epinephelinae: 9 species) (Table S2). ~~We assigned our study species to the most appropriate one of the four t~~Trophic guilds were assigned following ~~defined by~~ Sandin et al. (2008).

2.3.2. Fish and Coral Diversity

The total number of fish species (species richness) per reef was determined (i.e., if an individual was recorded on any one of the six transects per reef). Species richness was then used to calculate Shannon's Diversity Index *(H)*, which was in turn used to calculate species evenness using the equations: $H_{(R)} = -\sum_{i=1}^{S}\left(P_{(i)} \text{ x} \ln P_{(i)}\right)$ and $E_{(R)} = H_{(R)}/\ln S$, where $H_{(R)}$ is Shannon's Diversity Index for a reef *R*, which has *1* → *S* number of species (thus, *S* is species richness), *P* is the proportion of species *i* (number of individuals of the species/total number of individuals of all species), and $E_{(R)}$ is species evenness for reef *R* (Heip et al. 1998). For scleractinian corals, genus richness, which has been shown to be an adequate surrogate for species richness (Balmford et al. 1996; Bett and Narayanaswamy 2013), was recorded on each reef. Species richness was not measured directly for the sake of convenience in the field and due to the high probability of identification errors encountered within many genera present in the Red Sea. Several recent studies in the region have revealed troublesome scleractinian groups and new taxonomic discoveries (e.g., Huang et al. 2014; Terraneo et al. 2014; Arrigoni et al. 2015; Bouwmeester et al. 2015), highlighting the need for caution when working at the species level in this region until coral taxonomy is formally revised.

2.4. Spatial Trends and Statistical Analysis

The data collected were examined for cross-shore patterns and differences between reefs using simple regression and Kruskal-Wallis tests (KW) with post-hoc Mann-Whitney U tests (MW). One-way ANOVA tests and post-hoc Tukey's tests were used with datasets that met assumptions of normality. Regression was also used to examine whether coral cover or coral genus richness

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were good predictors of fish biomass or species richness. SPSS Statistics®, version 21, was used for these statistical analyses.

2.5. Fish and Benthic Community Assemblages

In order to identify and analyze patterns of similarity in community assemblages across reefs, we created non-metric multidimensional scaling (NMDS) plots using fish biomass, fish densities, and benthic cover data. All data were log-transformed (Log(x + 1)) to eliminate biases caused by very highly abundant species, and the Bray-Curtis method was used to create all resemblance matrices. As per guidelines provided by Clarke (1993) for ecological data, we considered plots with 2D stress values higher than 0.2 to be poor representations of the data in 2-dimensional space, while stress values lower than 0.1 to be excellent representations. Most analyses were followed up by analyses of similarity (ANOSIM) to test for significant clustering and similarity percentage (SIMPER) analyses to identify the top species or categories contributing to dissimilarity between clusters (Clarke 1993). The software PRIMER, version 6, was used for these analyses (Clarke and Gorley 2006).

3. Results

3.1. Fish Biomass and Trophic Composition

A grand total of 13,792 fish from 136 species and 44 families/sub-families (Table S1) were counted on the surveys. Overall, fish biomass was higher at 2 m depth than at 10 m on most reefs (Figures 2 and 3; Table 1). However, mean fish biomass at 10 m increased significantly with respect to distance from shore (R = 0.800, R^2 = 0.800, p = 0.009), while at 2 m it did not change significantly (Figure 2 b). The grand mean of fish biomass for all Thuwal Reefs, with depths pooled, is 16.4 kg/100 m^2.

Biomass trophic composition on all reefs was dominated by herbivores at both depths with few to no top predators, with the exception of NR, which is the only reef in which top predator biomass was dominant at 10 m (Figure 3). This was due to the observation of two whitetip reef sharks *(Triaenodon obesus)* on one of the 10 m transects on that reef. No sharks were observed on any of the other reefs. Other observed fish that were considered top predators were grouper, snapper, eel, and jack species. The biomass of herbivores increased significantly with distance from shore at 10 m (R = 0.811, R^2 = 0.657, p = 0.008), but not at 2 m (R = 0.487, R^2 = 0.238, p = 0.183). The grand mean biomass of trophic groups on Thuwal reefs are 1.0 ±0.2, 10.8 ±2.6, 2.5 ±0.1, and 2.1 ±1.2 kg/100 m^2 for planktivores, herbivores, carnivores, and top predators, respectively.

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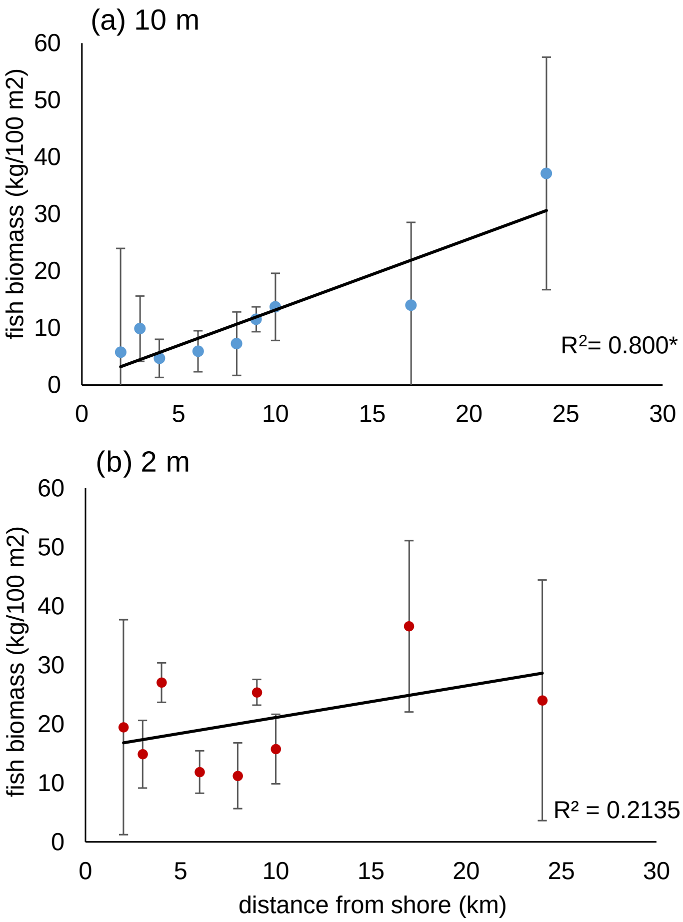

Figure 2. Mean fish biomass in kg/100 m^2 at (a) 10 m and (b) 2 m plotted against nearest straight line distance from shore as calculated in ArcMap to the nearest kilometer. Error bars represent standard error of the mean. R^2 values are shown on each panel and suggest strong correlation at 10 m and poor correlation at 2 m; (*) indicates significant regression ($p = 0.009$). Fish surveys were conducted in May 2013 on 9 reefs in the central Saudi Arabian Red Sea, with 3 replicate 25 x 8 m belt transects at each depth per reef.

Table 1. Mean and total fish biomass from 9 reefs in the central Saudi Arabian Red Sea, expressed as mean kg/100 m^2 (±SE) on each of the surveyed reefs. Each reef was surveyed using six replicate visual belt transects. *Habitat* indicates the location of each reef on the continental shelf, *Reef* is the name of each study reef (see main text for abbreviations). Values are divided into trophic groups (planktivores, herbivores, carnivores, and top predators) and shown as a *Total* for all groups combined.

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habitat	reef	mean biomass kg/100m² (±SE)									
		planktivores		herbivores		carnivores		top predators		all fish	
		10 m	2 m	10 m	2 m	10 m	2 m	10 m	2 m	10 m	2 m
offshore	RR	1.07 (±0.5)	1.94 (±0.1)	7.12 (±5.3)	11.01 (±3.4)	3.32 (±0.4)	1.04 (±0.2)	2.21 (±0.9)	1.75 (±0.9)	13.71 (±5.9)	15.74 (±14.6)
	NR	2.12 (±0.9)	0.08 (±0.1)	8.57 (±3.0)	21.73 (±16.5)	3.32 (±0.4)	1.71 (±0.7)	23.31 (±17.9)	0.49 (±0.3)	37.13 (±20.4)	24.01 (±10.1)
	AMR	2.78 (±0.5)	2.12 (±0.7)	9.63 (±5.3)	30.95 (±5.8)	3.32 (±0.4)	3.20 (±0.7)	0.38 (±0.3)	0.28 (±0.1)	14.02 (±14.5)	36.56 (±3.6)
midshore	FR	0.67 (±0.1)	0.50 (±0.2)	1.87 (±0.7)	7.64 (±3.4)	3.32 (±0.4)	2.50 (±0.7)	2.06 (±1.5)	0.59 (±0.6)	7.26 (±5.6)	11.22 (±1.4)
	TWR	0.96 (±0.8)	0.20 (±0.2)	2.46 (±0.9)	8.24 (±1.0)	3.32 (±0.4)	2.80 (±1.3)	0.23 (±0.2)	0.61 (±0.5)	5.93 (±3.6)	11.85 (±5.6)
	AHR	1.78 (±0.6)	0.84 (±0.2)	2.61 (±0.8)	21.52 (±2.3)	3.32 (±0.4)	2.40 (±0.7)	2.92 (±2.8)	0.61 (±0.4)	11.54 (±2.2)	25.37 (±1.1)
inshore	ASR	0.49 (±0.1)	0.09 (±0.1)	2.93 (±18.1)	22.65 (±18.1)	3.32 (±0.4)	4.07 (±1.5)	0.00 (±0.1)	0.20 (±0.1)	4.68 (±3.3)	27.01 (±18.6)
	TR	2.65 (±1.1)	0.01 (±1.1)	3.51 (±1.2)	11.96 (±2.4)	3.32 (±0.4)	2.18 (±0.8)	0.55 (±0.1)	0.71 (±0.1)	9.89 (±5.7)	14.86 (±6.1)
	EFR	0.03 (±0.0)	0.00 (±0.0)	3.07 (±1.8)	16.27 (±3.6)	3.32 (±0.4)	2.61 (±1.2)	0.91 (±0.9)	0.57 (±0.5)	5.75 (±18.2)	19.45 (±4)

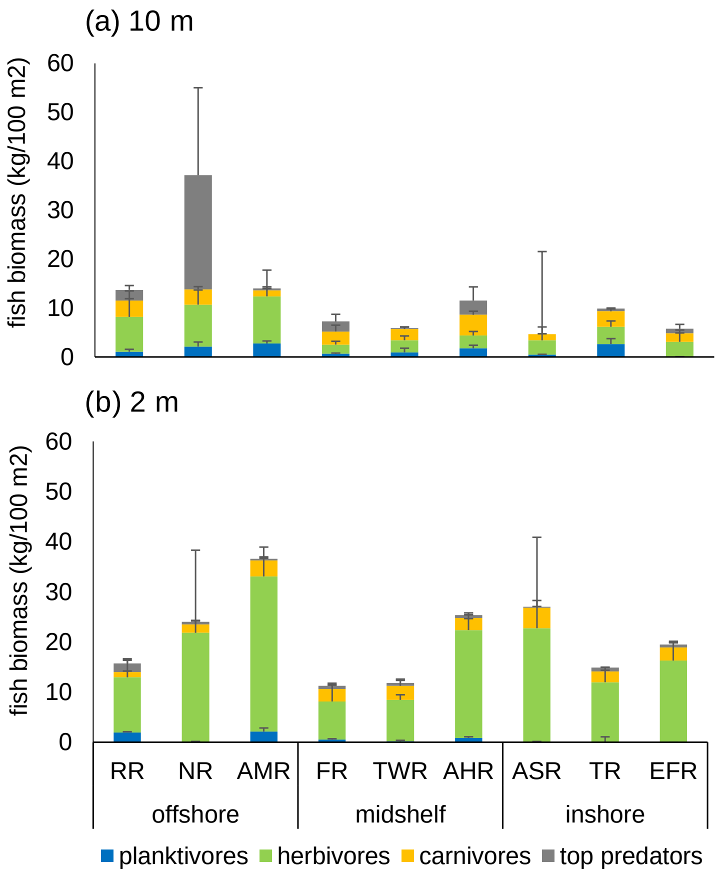

Figure 3. Mean fish biomass in kg/100 m^2 for each of the 9 study reefs at (a) 10 m, and (b) 2 m depth, color-coded according to stacked trophic group as per the inset key (planktivores, herbivores, carnivores, or top predators). Reef name abbreviations are presented on the x-axis (see main text for full names) and separated according to distance from shore into offshore, midshelf, and inshore reefs. All data were collected in May 2013 from the central Saudi Red Sea.

3.2. Commercial Fish

The reefs RR (offshore) and TR (inshore) had the highest biomass of parrotfish and groupers, respectively (depths pooled), and RR had the highest overall mean biomass of the three commercial fish groups combined with 3.1 ±0.9 kg/100 m^2 (Figure 4). However, none of these observations were statistically significant (KW, $p > 0.05$ for all tests).

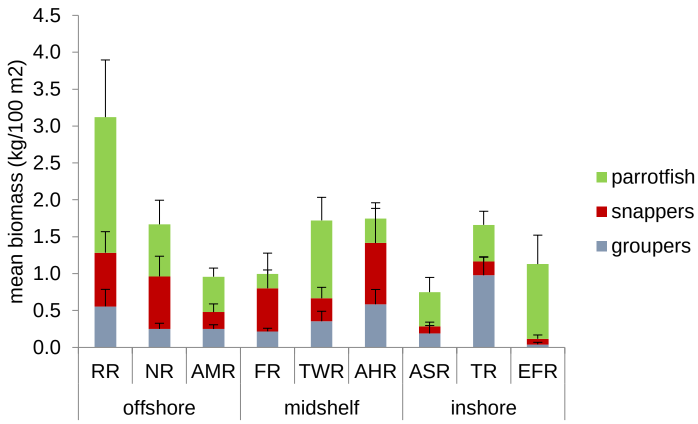

Figure 4. Mean biomass from the 9 study reefs of the 3 most targeted commercial fish groups: parrotfish, snappers, and groupers, color-coded as indicated by the inset key. Bars represent standard error, and reef name abbreviations are presented on the x-axis and separated according to distance from shore into offshore, midshelf, and inshore reefs. All data were collected in May 2013 in the central Saudi Red Sea, and mean values were calculated from six visual belt transects per reef; 3 at 10 m and 3 at 2 m.

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3.3. Coral and Algal Cover

We recorded a total of 38 benthic categories, including 25 genera of scleractinian corals (listed in Table S3). Mean percent coral cover ranged from 8.35 % (±3.3) on inshore reef ASR to 30.70 % (±3.7) on midshelf reef TWR (Table 2). There was no strong correlation between coral cover and distance from shore (R = 0.470-, R^2 = 0.221, p = 0.202). However, one-way ANOVA tests showed significant difference between individual reefs (F = 16.7, $p = 3 \times 10^{-6}$), and post-hoc tests showed that coral cover on inshore reefs was significantly lower than that of midshelf reefs ($p_{Tukey} = 2 \times 10^{-5}$) and offshore reefs ($p_{Tukey} = 7 \times 10^{-6}$). Coral cover also did not correlate strongly with fish species richness or with fish biomass (R^2 = 0.10 and 0.01, respectively). As for mean algal cover, there was a moderate negative correlation with distance from shore (R = -0.659, R^2 = 0.433, p = 0.054), which co-occurred with the aforementioned positive correlation of herbivorous fish biomass.

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Table 2. Mean cover (±SE) of benthic categories recorded on the 9 study reefs in the central Saudi Arabian Red Sea in May 2013. Reef names are shown as abbreviations in column headers and separated according to distance from shore. Data were collected on 10 m long transects at 10 m and 2 m depths using the line-intercept method. The category *Hard corals* summarizes values for 25 scleractinian coral genera that were observed (listed in table S3); *Soft corals* summarize at least 6 genera; *Hydrozoans* contained only the genus *Millepora;* and the remaining categories were recorded as shown in the table.

Benthic category	Mean percent cover (±SE)								
	offshore			midshore			inshore		
	RR	NR	AMR	FR	TWR	AHR	ASR	TR	EFR
Hard corals	26.4 (±4.6)	21.3 (±2.5)	28.6 (±2.0)	26.3 (±4.3)	24.8 (±4.9)	30.7 (±3.7)	8.4 (±3.3)	14.9 (±2.8)	13.2 (±1.8)
Soft corals and zoanthids	0.3 (±0.3)	15.7 (±2.0)	8.2 (±2.8)	16.7 (±5.1)	5.4 (±0.9)	5.8 (±2.3)	3 (±1.4)	7.6 (±3.5)	3.7 (±2.6)
Hydrozoans	1.5 (±1.2)	0.3 (±0.2)	1.8 (±1.2)	1.7 (±1.7)	0.0 (±0.0)	0.6 (±0.3)	0.0 (±0.0)	0.2 (±0.2)	0.0 (±0.0)
Sponges	0.6 (±0.6)	0.2 (±0.2)	0.7 (±0.4)	0.5 (±0.5)	3.8 (±2.5)	1.6 (±0.5)	0.9 (±0.5)	0.3 (±0.3)	2.6 (±1.5)
CCA	21.9 (±9.7)	9.4 (±2.1)	29.3 (±6.5)	8.1 (±3.9)	2.5 (±1.5)	26.1 (±8.2)	9.7 (±5.0)	9.8 (±3.7)	0.2 (±0.2)
Turf algae	0.0 (±0.0)	0.0 (±0.0)	0.3 (±0.3)	1.8 (±1.8)	3.7 (±0.8)	7.9 (±5.1)	2.4 (±1.1)	11.7 (±5.1)	14.3 (±6.5)
Other algae	0.0 (±0.0)	0.0 (±0.0)	0.2 (±0.2)	0.1 (±0.1)	0.3 (±0.3)	0.4 (±0.4)	0.0 (±0.0)	0.2 (±0.2)	0.0 (±0.0)
Rock	35.5 (±4.0)	52.8 (±2.3)	30.5 (±7.0)	31.3 (±6.0)	36.6 (±5.7)	26.9 (±7.6)	40.9 (±7.6)	43.4 (±3.6)	50.2 (±5.3)
Rubble	14 (±7.6)	0.4 (±0.3)	0.5 (±0.5)	6.9 (±5.4)	13.1 (±2.4)	0.0 (±0.0)	12.6 (±4.6)	8.6 (±3.6)	2.8 (±0.9)
Sand	0.0 (±0.0)	0.0 (±0.0)	0.0 (±0.0)	6.5 (±3.5)	9.8 (±6.2)	0.0 (±0.0)	22.2 (±9.9)	3.3 (±2.0)	13 (±7.3)

3.4. Fish and Coral Diversity

A total of 136 species of fish were recorded in our surveys (Table S1). Fish species richness ranged from 54 on ASR (an inshore reef) to 70 species in TR (inshore) and TWR (midshelf), and species evenness, which was calculated from Shannon's Index for each reef, ranged narrowly from 0.59 to 0.77, indicating a fairly even number of individuals per species on all reefs (Table 3). Species richness was highest on average on midshelf reefs, but no statistical significance was found (One-way ANOVA, $F = 2.461$, $p = 0.166$).

A midshelf reef, FR, had the highest number of hard coral genera (23), while an inshore reef, ASR, had the lowest (10 genera). MW tests showed ASR to have significantly lower coral genus richness than all other reefs ($p_{MW} < 0.005$) except NR and TR. Coral genus richness was also a poor predictor of fish species richness ($R = 0.224$, $R^2 = 0.050$, $p = 0.562$) and fish biomass ($R = 0.096$, $R^2 = 0.009$, $p = 0.806$).

Comentado [RFF18]: I suggest replace this table by a graph

Comentado [RFF19]: Why pooling soft corals and zoanthids? These groups are very different morphologically and ecologically

Comentado [RFF20]: Explain acronyms

Table 3. A summary of fish and hard coral diversity indices for each of the 9 study reefs in the central Saudi Arabian Red Sea. For coral genus and fish species richness, the numbers shown are the maximum numbers of genera and species found on each reef, respectively. Fish species evenness was calculated from Shannon's Diversity Index for each reef which was based on the reported species richness. Each reef was surveyed using six replicate visual belt transects. *Habitat* indicates the location of each reef on the continental shelf, *Reef* is the abbreviated name of each study reef.

Habitat	Reef	Hard coral genus richness	Fish species richness	Fish species evenness
offshore	RR	14	60	0.68
	NR	16	59	0.76
	AMR	20	55	0.59
midshelf	FR	23	69	0.62
	TWR	18	70	0.66
	AHR	20	64	0.61
inshore	ASR	10	54	0.77
	TR	18	70	0.72
	EFR	20	55	0.59

3.5. Fish and Benthic Community Assemblages

A number of iterations were attempted to identify any significant differences in fish and benthic assemblages between the reefs and between the two depths at which the data were collected. These analyses used fish biomass, fish densities, benthic cover, and a combination of fish biomass and benthic cover. Here, we present the most significant results, while a more complete list of NMDS, ANOSIM, and SIMPER analyses and their results can be found in supplementary material (Table S4).

Preliminary analyses including all replicates consistently showed a slight (2D stress > 0.2 for fish and 0.17 for benthos) yet significant (ANOSIM significance 0.1 %) separation of 10 m assemblages from 2 m assemblages. These preliminary analyses also showed a great reduction in 2D stress (< 0.1) when mean values, rather than all replicates, were used.

Comentado [RFF21]: Combining fish biomass and benthic cover in a single NMDS analysis is meaningless

Comentado [RFF22]: Instead of trying different data combinations, I suggest using the more abundant taxa only (e.g. those >0.5% of total abundance and present in more than 5 samples).

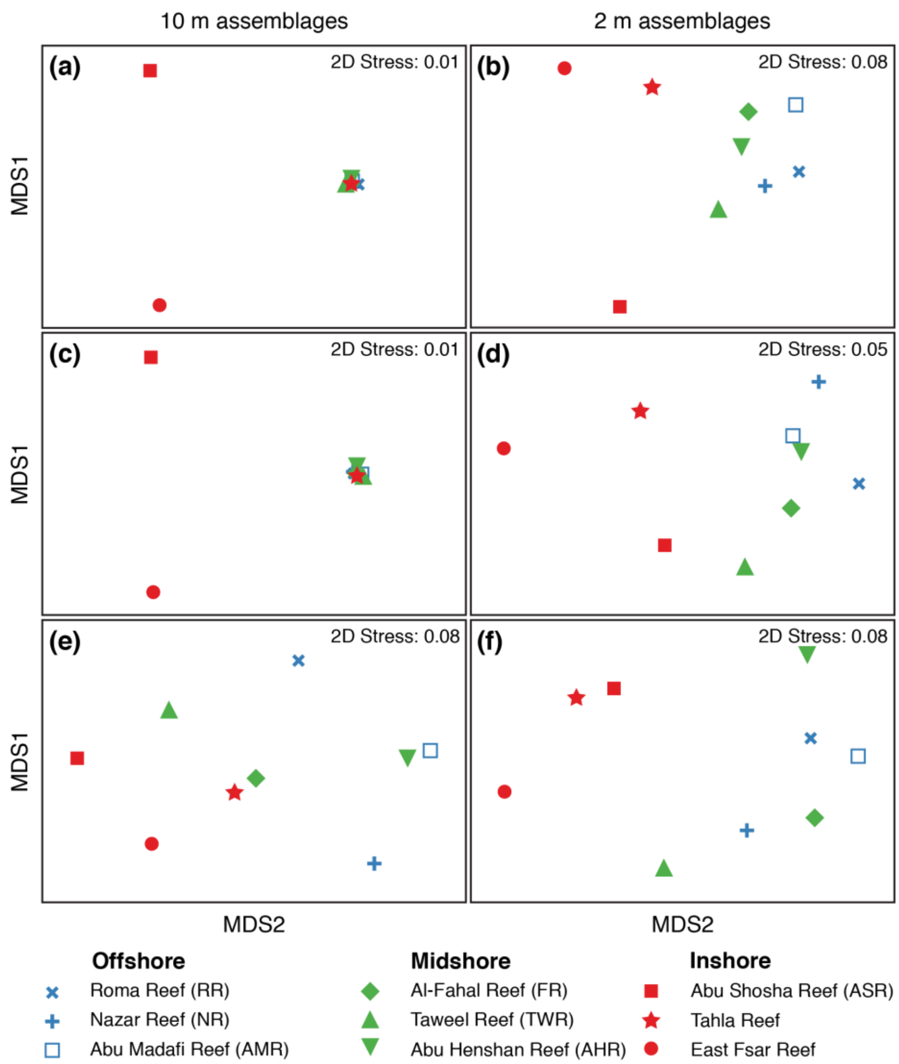

Figure 5. NMDS plots from Bray-Curtis resemblance matrices based on log (x+1)-transformed reef averages for fish biomass (a and b), fish densities (c and d), and benthic cover (e and f); the left column of panels shows 10 m assemblages, while the right column shows 2m assemblages. X-axes represent NMDS1 and y-axes represent NMDS2. Reef name abbreviations are shown in the inset key next to their representative symbols, and the 9 reefs are color-coded according to distance from shore as shown by the key. 2D stress values are shown in the upper right corner of each plot. All data were averaged across the relevant replicates for each reef. Fish and benthic data were collected together on the same transects (6 per reef in total) from the central Saudi Arabian Red Sea.

The most significant NMDS plots produced, all of which have very low 2D stress values, are shown in Figure 5. The NMDS plots for fish biomass and densities at 10 m (Figure 5 a and c) are very similar to each other with a very clear and tight clustering of all reefs in one cluster except for two inshore reefs (ASR and EFR), which separated from the other reefs but did not cluster closely together. This shows very high similarity (ANOSIM *R* = 0.9, sig. 2.8) at 10 m depth in fish assemblages (by biomass as well as densities) among all reefs except ASR and EFR. In terms of biomass, *Caesio lunaris* contributed the most to the dissimilarity (SIMPER dissimilarity contribution (hereafter Contrib.) = 7.9 %), being more abundant in the group containing offshore reefs, midshelf reefs, and TR.

Comentado [RFF23]: This is odd. Separate NMDS should be used for fish and benthos, but not for depth strata/distance offshore.

However, looking at fish assemblages at 2 m (Figure 5 b and d), we find all inshore reefs separating (including TR) from all other reefs, which clustered together (ANOSIM sig. 1.2 % for both biomass and densities). However, the offshore cluster was less tight than it was at 10 m, indicating more dissimilarity within the shallow fish communities. The farming *Stegastes nigricans* contributed highly to the dissimilarity between inshore and offshore communities in terms of both biomass and numerical density (Contrib. 14.6 and 6.8 %, respectively), being abundant on inshore reefs and nearly absent on other reefs. Another damselfish, *Chromis dimidiata*, also contributed by being more abundant on midshelf and offshore reefs (Contrib. 4.3 %).

As for benthic assemblages at 10 m (Figure 5 e), inshore reefs in addition to two midshelf reefs (TWR and FR) separated from the remaining four reefs (ANOSIM *R* = 0.78, sig. 0.8 %), with sand and rubble (collective Contrib. 32.0 %) and CCA (9.2 %) contributing the most to the separation. Sand and rubble were more abundant in the group containing the inshore reefs, while CCA was more abundant in the group containing the offshore reefs. However, at 2 m (Figure 5 f), there was a clearer separation again between inshore reefs and all other reefs (ANOSIM *R* = 0.82, sig. 1.8 %). Turf algae (Contrib. 14.6 %), rock (10.4 %), and *Porites* (10.0 %) were more abundant on inshore reefs, contributing highly to the dissimilarity, while *Pocillopora* (14.3 %), CCA (13.5 %), and xeniid soft corals (9.6 %) were more abundant on offshore and midshelf reefs (Table S4).

4. Discussion

Comentado [RFF24]: Discussion may change with new data analyses

We present here a description of the spatial variation in fish and benthic communities on a group of central Saudi Arabian Red Sea reefs, with particular focus on changes in community assemblages along a cross-shelf gradient. Our results show that fish biomass increases moderately with distance from shore in Thuwal. Results also indicate that fish communities are dominated by herbivorous fishes at all sites. Benthic communities are fairly homogenous with the exception of the shallow parts of inshore sites, which seem to still be showing the impacts of a major bleaching event three years prior to our surveys. As very little detailed ecological data is available for this region, ~~this~~ data from this study ~~will~~ may be of use in future conservation planning efforts, particularly in informing spatial prioritization.

Comentado [RFF25]: Include citation supporting this statement

4.1. Fish Biomass, Trophic Composition, and Commercial Fish

It is likely that the increase in mean fish biomass with distance from shore, which was mostly evident at 10 m depth, is merely due to the change in surrounding water depth (Figure 1). Inshore reefs slope to a sandy bottom at much shallower depths (between 12 – 20 m) than the offshore reefs (Figure 1), and so offshore reefs may simply be able to support the occurrence of higher biomass than inshore reefs. Our results showed that this increase in biomass could not be explained by coral cover or coral genus diversity.

Moreover, as a general trend, fish biomass on Thuwal reefs appears to be relatively low with particularly low proportions of top predators. Compared to relatively remote and nominally pristine locations around the world, including sites in the central Pacific (Sandin et al. 2008; Williams et al. 2011; Friedlander et al. 2014), the North-Western Hawaiian Islands (Friedlander and DeMartini 2002; Williams et al. 2011), and even some relatively remote and unfished parts of the Red Sea (Kattan 2014; Spaet et al. 2016), Thuwal reefs had very low fish biomass. Only Nazar Reef (NR) and Abu Madafi Reef (AMR), which had the highest mean biomass values in this study (Figure 3), had values comparable to, and sometimes higher than these sites (Table 5). However, even when mean biomass on NR exceeded that of other sites, it is important to note that the percentage of top predators in all other sites far exceeded NR's 39 % (most of which was contributed by two whitetip reef sharks – the only sharks observed in our study). In fact, the trophic composition of all locations listed in Table 5, including the Sudanese Red Sea site, was that of an inverted, top-heavy, pyramid with most of the biomass contributed by top predators, as opposed to Thuwal reefs where the bulk of the biomass was attributed to herbivores (Figure 3).

Comentado [RFF26]: For this comparison, I suggest including fish biomass data for other regions such the Caribbean, Brazil and Kenya

Our survey design (using relatively short belt transects for visual census and having only 6 replicates per reef) might not be adequate for accurately capturing the abundances of large mobile predators such as sharks, trevallies, and barracudas, which are typically surveyed using much longer and wider transects or using baited cameras (e.g., Robbins et al. 2005; Goetze and Fullwood 2013; Spaet et al. 2016), among other techniques. Nevertheless, we used the same method that was applied by Kattan (2014) in the Sudanese Red Sea, where much higher abundances of top predators were still recorded despite the shortness of transects and small number of replicates. Some of the other studies listed in Table 5 also used a similar transect length (e.g., Sandin 2008) and captured much higher abundances of top predators. Therefore, it is more likely that the absence of top predators in our study reflects actual low abundances rather than a mere drawback of methodology. This is also confirmed by recent studies that specifically aimed to quantify shark abundances in the Red Sea and found evidence of extremely low abundances and severe fishing pressure (Spaet and Berumen 2015; Spaet et al. 2016).

Comentado [RFF27]: Transects used here are enormous (both, in length and width, in comparison with other studies, so this statement is unsubstantiated.

Table 45. A comparison of mean fish biomass and top predator composition between Thuwal reefs and reefs considered pristine in studies in other *regions*. The comparison includes the mean biomass on Nazar reef as the *reef* with the highest mean biomass in this study as well as the grand mean biomass of all nine Thuwal reefs. *Biomass* indicates the mean fish biomass (standardized to kg/100 m^2) from each site, while *Top predator composition* indicates the percentage of top predator biomass compared to total fish biomass. There were no major differences in the way in which top predators were defined across the studies.

Site	Region	Mean fish biomass (kg/100 m^2)	Top predator composition (%)	Study
Kingman Reef	Pacific	53	81	Sandin et al. 2008
Pearl & Hermes Atoll	North-Western Hawaiian Islands	47	81	Friedlander and DeMartini 2002
Kure Atoll	North-Western Hawaiian Islands	35	66	Williams et al. 2011
Jarvis Reef	Pacific	25	68	Williams et al. 2011
French Frigate Shoals	North-Western Hawaiian Islands	26	62	Friedlander and DeMartini 2002
Palmyra Atoll	Pacific	25	64	Sandin et al. 2008
Ducie Island	Pacific	16	63	Friedlander et al. 2014
Deep South	Red Sea, Sudan	43	67	Kattan (2014)
Nazar Reef	Red Sea, Saudi Arabia	31	39	This study
All Thuwal Reefs	Red Sea, Saudi Arabia	16	13	This study

Top predators such as sharks, jacks, and groupers are critical in forming and maintaining the structure of reef communities, and overfishing these groups can lead to trophic cascades and overall loss of diversity (Friedlander and DeMartini 2002; Sandin et al. 2008; Salomon et al. 2010; Houk and Musburger 2013). Thus, the trophic structure on Thuwal reefs suggests potentially poor resilience and points to a possible overfishing problem. Currently, there is substantial and growing evidence of severe overfishing in the Saudi Arabian Red Sea. Jin et al.

Comentado [RFF28]: Greater herbivores biomass is generally used as a sign of high reef resilience, but not low abundance of piscivores.

(2012) have shown in a study based on several decades of fishing data that Saudi Arabian fisheries have been operating beyond sustainable levels since the 1990s, and Spaet and Berumen (2015) have shown evidence of unsustainable elasmobranch fisheries based on two years of fish market surveys. The trophic structure observed on Thuwal reefs in our study, therefore, could be a result of overfishing.

Herbivores are an essential functional group for maintaining the resilience of reefs, as they assist coral recruitment and recovery from disturbances by keeping macroalgae under control (Williams and Polunin 2001; Hughes et al. 2007; Ledlie et al. 2007). The increase in herbivore biomass with increasing distance from shore in Thuwal indicates that offshore reefs may be relatively more resilient to disturbances than inshore reefs. However, it is unknown whether the biomass of herbivores on Thuwal reefs is sufficient to maintain reef resilience.

4.2. Coral and Algal Cover

Coral cover differed significantly between inshore reefs as a group and other reefs, which is likely due to the impact of the 2010 bleaching event (Furby et al. 2013; Pineda et al. 2013). It appears that these inshore reefs have not yet recovered their coral cover in the top 10 meters in the ~3 years that passed between the bleaching event and the commencement of data collection for this study. Studies from other locations, such as the Great Barrier Reef, have also found that coral cover on inshore reefs tended to decline more severely than on offshore reefs following disturbances (e.g., Sweatman et al. 2007). However, recovery time was found to be highly variable; while some studies reported relatively rapid recovery of coral cover following disturbance (e.g., ~2.5 years reported by Hughes et al. (2007)), others reported that, even after six years, many inshore reefs hardly recovered any lost coral cover (Sweatman et al. 2011). Moreover, in Moorea, several decades following repeated disturbances, considerable coral cover was recovered; however, there were long-term changes in coral community structure that indicated lowered resilience (Pratchett et al. 2011). During the summer of 2015, Red Sea reefs (including Thuwal) were impacted yet again by thermal bleaching (Lozano- Cortés et al. 2016), potentially further deteriorating these inshore reefs (Monroe et al. in review).

At the same time, inshore reefs in this study have higher coverage of turf algae, which correlates with the high abundance of the damselfish species that farms it, *Stegastes nigricans* (see section 4.4), accompanied by generally lower herbivore biomass and diversity. This supports the previous speculation that offshore reefs in the Thuwal area may be more resilient relative to inshore reefs, since high abundances of turf algae and *S. nigricans* are often considered indicators of a degraded habitat (White and O'Donnell 2010). Continued monitoring of the reefs and larger datasets may allow stronger inferences about the level of reef resilience in Thuwal to be made in the future (e.g., Bellwood et al. 2004; Pratchett et al. 2011).

Comentado [RFF29]: Turf algae is the most abundant category in most studies, particularly in inshore reefs. The same is true for herbivorous damselfish. Other alternative hypotheses could be given here.

4.3. Diversity

Although previous studies have found benthic cover, diversity, and complexity to be correlated with fish species richness and functional diversity (e.g., Roberts and Ormond 1987; Chabanet et al. 1997; Chong-Seng et al. 2012), we found no such patterns on Thuwal reefs neither with coral cover nor genus richness. This could be due to different stresses impacting the fish and benthic communities in different ways. Indeed, fishing pressure, when present, has less direct impact on benthic communities and a bleaching event has less direct impact on fish communities. Alternatively, the lack of correlation between fish and benthic diversity here could be due to the sampling design and the size of the dataset, which may not be adequate to investigate such correlations. For example, although regular survey methods such as LIT are commonly used to assess coral cover, they have been shown to be less effective in assessing coral richness or diversity unless sampling effort is highly intensified (Leujak and Ormond 2007; Roberts et al. 2016). Therefore, for this study, the relationship between fish and benthic diversity may be observable only on the level of qualitative assemblages rather than total quantitative richness.

Comentado [RFF30]: Please, apply more robust analyses. Other option is to use non-linear fit, such as GAM.

4.4. Fish and Benthic Community Assemblages

It appears that, especially in the shallow depths, inshore reefs are markedly different in fish and benthic community assemblage from other reefs in the area, and it is likely that the change in the benthic community brought about by the bleaching event of 2010 is the main driver of these differences.

Comentado [RFF31]: I think that depth per se may drive this difference, so please include this latter, and other explanatory variables, in tha analyses.

Furby et al. (2013) had found that, prior to bleaching, coral assemblages (genus level abundances and coral cover) were similar on inshore and offshore Thuwal reefs, and that the post-bleaching differences were mostly caused by a decline in acroporids and pocilloporids on inshore reefs, which are faster-growing corals that tend to be more susceptible to bleaching (Marshall and Baird 2000). Very similar trends were also reported in other locations, for example in Moorea by Berumen and Pratchett (2006). Our study supports these findings and also shows turf algae to be one of the main contributors to the dissimilarity between inshore and offshore shallow communities. Similarly, we also found the slow-growing genus *Porites* to be a more characteristic community component on inshore reefs, while *Acropora*, *Pocillopora*, and *Stylophora* were important components of distinguishing assemblages only on midshelf and offshore shallow communities. As for the higher abundance of sand and rubble observed at 10 m inshore assemblages, this is due to the difference in the surrounding bathymetry between inshore and offshore reefs; at 10 m, inshore reefs are closer to the bottom of the slope where there is more sedimentation, while offshore reefs are surrounded by deeper water.

Comentado [RFF32]: This could be used as an explanatory variable too

Herbivore assemblages are commonly recognized as a key functional component of coral reef communities (Lewis 1986; Hughes et al. 2007; Adam et al. 2011). On Thuwal reefs, we found very similar herbivore assemblages on all reefs except the inshore reefs. Offshore communities were characterized by the surgeonfishes *Acanthurus sohal*, *Naso unicornis*, *Ctenochaetus striatus*, and *A. nigrofuscus,* while inshore communities were dominated mostly by the farming damselfish *Stegastes nigricans.* This coincides with the higher abundance of turf algae inshore and presents a potential difficulty for the recovery process of inshore reefs. These territorial damselfish promote the mono-cultural growth of algae on reef flats and crests, subsequently preventing settlement by corals and other invertebrates (e.g., White and O'Donnell 2010), whereas other types of grazers, such as surgeonfishes and parrotfishes, tend to remove algae and promote invertebrate settlement (Vine 1974; Jones et al. 2006). Thus, the poor herbivore diversity on inshore reefs indicates potentially poor resilience.

On our deeper transects, fish assemblages were very similar across all reefs except for two of the inshore reefs. With regards to both biomass and numerical density (Figure 5), the offshore communities seem to be dominated by planktivorous fishes, such as *Caesio lunaris*, *Chromis dimidiata*, *Chromis flavaxilla*, and *Pseudanthias squamipinnis*; these contributed the most to the similarity within the offshore reef cluster. This may be due to a higher influx of zooplankton on more exposed reefs.

Comentado [RFF33]: Please, provide citations to the several studies with similar findings.

5. Conclusions

We presented a description of the spatial variation of fish biomass and fish and benthic communities on Thuwal reefs in the central Saudi Arabian Red Sea. Our findings can be summarized as follows:

1) Offshore Thuwal reefs seem to support higher fish biomass than inshore reefs. But fish biomass in Thuwal in general is quite low compared to other reef systems around the world and in the Red Sea that are considered “healthy”.
2) Trophic structure on all Thuwal reefs is bottom-heavy with most biomass attributed to herbivores; top-predators are few or nearly absent.
3) Commercially valuable fish are in very low abundance throughout the area.
4) There are a few dissimilarities in benthic and fish assemblages which are mostly found between inshore reefs as a group and all other reefs:
    a. Inshore benthic communities are characterized by having more turf algae and slow-growing corals compared to offshore reefs.
    b. Farming damselfish dominate shallow inshore herbivore communities compared to more diverse herbivore communities on offshore reefs.
5) The separation of inshore assemblages from other reefs is probably a result of the 2010 bleaching event, from which inshore reefs have not yet recovered.

It seems that, apart from the bleaching event that altered inshore communities, Thuwal reef communities are fairly spatially homogeneous, although expanding the dataset to include more replicates may allow subtle spatial differences to be revealed. However, the vulnerability of inshore reefs to thermal bleaching was most likely due to exposure and water current patterns (Furby et al. 2013), which may be the most significant environmental drivers in this area. Our results suggest that inshore reefs may be generally less healthy and more vulnerable to disturbances than offshore reefs, and this provides some basis for future spatial prioritization and planning. Whether the more or the less vulnerable reefs will be prioritized would be dependent on conservation goals (Game et al. 2008). Our analysis also identified individual species that characterize inshore and offshore reefs, and these species, together with a selection of commercial species, could now be used to set quantitative conservation goals and as habitat surrogates, depending on ultimate conservation objectives (e.g.. Schmiing et al. 2014).

Our findings also support existing evidence that Thuwal reefs may be heavily overfished, as indicated by trophic structure and low biomass. Intense fishing affects communities on many levels, from species' life-history traits to population fitness and community structure, in ways that generally lower diversity and reef resilience (Robertson et al. 2005; Salomon et al. 2010). The status of both sharks (Spaet et al. 2012; Spaet and Berumen 2015) and groupers (DesRosiers 2011) are particularly alarming in the Saudi Arabian Red Sea, even compared to other parts of the Red Sea (Kattan 2014; Spaet et al. 2016), and fishing regulations as well as other forms of protection may be urgently needed to halt the collapse of fisheries.

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