Reef fish communities in the central Red Sea show evidence of asymmetrical fishing pressure

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Abstract

In order to assess human impacts and develop rational restoration goals on corals reefs, baseline estimates of fish communities are required. In Saudi Arabian waters of the Red Sea, widespread and unregulated fishing is thought to have been ongoing for decades, but there is little direct evidence of the impact on reef communities. To contextualize this human influence, reef-associated fish assemblages on offshore reefs in Saudi Arabia and Sudan in the central Red Sea were investigated. These reefs have comparable benthic environments, experience similar oceanographic influences, and are separated only by <300 km, offering an ideal comparison to help identify potential anthropogenic impacts such as fishing pressure. This is the first study to assess reef fish biomass in both these regions, providing important baselines estimates. We found that biomass of top predators on offshore Sudanese reefs was on average almost three times that measured on comparable reefs in Saudi Arabia. Biomass values from some of the most remote reefs surveyed in Sudan’s far southern region even approach those previously reported in the Northwest Hawaiian Islands, northern Line Islands, Pitcairn Islands, and other isolated Pacific islands and atolls. The findings suggest fishing pressure has significantly altered the fish community structure of Saudi Arabian Red Sea reefs, most conspicuously in the form of top predator removal. The results point towards the urgent need for enhanced regulation and enforcement of fishing practices in Saudi Arabia while simultaneously making a strong case for protection in the form of no-take marine protected areas to maintain preservation of the relatively intact southern Sudanese Red Sea.
Introduction

The contemporary ocean environment has been drastically altered by human activity over the last few centuries, with changes most directly driven by overexploitation of species at both local and global scales (Jackson 2001; Jackson et al. 2001; Sanderson et al. 2002; Myers and Worm 2003; Pandolfi et al. 2003; Halpern et al. 2008). The ‘shifting baseline’ syndrome (Pauly 1995) suggests that the combined result of the pace of fishing down marine food webs and the relative lack of marine science history impairs one’s ability to determine what is ‘natural’ in ocean ecosystems (Pauly et al. 1998). This poses a major challenge to conservation and restoration efforts worldwide, risks undervaluing marine ecosystem both economically and culturally, and often renders the general public complacent over the rarity of species (Pauly 1995; Knowlton and Jackson 2008; McClenachan 2009; Mora et al. 2011). Because a significant proportion of reef environments have degraded through time (Jackson et al. 2001) and many are projected to continue to decline (Burke et al. 2011), establishing baselines in data-deficient regions is paramount to understanding future changes.

Fortunately there remain select, remote coral reefs that have persisted relatively unchanged by man. Studies conducted in the Northern Line Islands (Sandin et al. 2008), northwest Hawaiian Islands (Friedlander and Demartini 2002), Chagos Archipelago (Graham and McClanahan 2013), Pitcairn Islands (Friedlander et al. 2014), and various islands and atolls across the central and western Pacific (Stevenson et al. 2007; Williams et al. 2011) have reported encouraging results from underwater visual censuses of fish communities on these isolated reef sanctuaries. These ecosystems’ baseline conditions offer invaluable insight into healthy reef dynamics, serving as control sites that provide
the opportunity to measure both direct and indirect effects of human impacts (particularly fishing) on reef fish communities in nearby and physically comparable systems (Knowlton and Jackson 2008). The trademark feature of healthy reefs, as revealed by such studies, is ‘top-heavy’ (inverted) fish biomass pyramids (Sandin et al. 2008). In these unique locations, sharks and other large top predators (jacks, snappers, groupers) overwhelm the reef fish community biomass, supported by lower trophic levels with very high turnover rates (Sandin et al. 2008). Studies of healthy reefs also reveal compelling cascading effects of predator removal on coral reefs under even modest fishing pressure, including changes in the abundance, body condition, length, and reproductive potential of prey species (Ruttenberg et al. 2011; Walsh et al. 2012). Identification of additional near- or relatively-pristine coral reefs in novel biogeographic provinces would do well to advance this field of study and allow for comparison of human impacts across broader spatial scales.

The Red Sea is a narrow sea harboring high biodiversity (Stehli and Wells 1971), an elevated level of endemism (Ormond and Edwards 1987; DiBattista et al. 2016), and one of the largest reef systems on the planet despite exhibiting relatively extreme environmental conditions (i.e., salinity, temperature) and seasonal fluctuations (Raitsos et al. 2013). Despite its unique environment, the Red Sea remains a scientifically understudied region, a combined result of its remoteness, regional geopolitical situations, complicated visa and permitting regulations, and a lack of marine infrastructure (Berumen et al. 2013). A number of recent studies have revealed that while latitudinal gradients of environmental conditions in the Red Sea do exist (Ngugi et al. 2012; Raitsos et al. 2013; Kürten et al. 2014; Price et al. 2014), species richness and diversity of coral
reef fish assemblages change little, if at all, from north to south (Roberts et al. 2015).

Moreover, patterns of reef development, benthic composition, and coral cover along the east and west coastlines of the relatively narrow Red Sea appear to mirror one another (Sheppard and Sheppard 1991; Sheppard et al. 1992; DeVantier et al. 2000; Chekchak and Klaus 2013).

Baseline data for patterns of Red Sea reef fish biomass, however, are largely missing. This is particularly troublesome as historical and contemporary information of reef fisheries are also lacking for the region as a whole, limiting attempts to measure the extent to which Red Sea reef fish communities have been impacted by human activities. In the central Red Sea, fishing pressure has been noted as high and ongoing for a number of decades along the Saudi Arabian coastline. This is supported by a limited number of scientific publications (e.g., Jin et al. 2012; Tesfamichael and Rossing 2012; Tesfamichael and Pauly 2016) and robust evidence on this impact on reef fish communities remains missing for both east and west coasts. Separated by ~300 km and with a deep mid-basin trench (~2000 m) keeping adult fish populations separate, the two sides of the Red Sea therefore provide unique circumstances and opportunities to make comparisons and generate hypotheses about the impacts of human influences (e.g., fishing pressure) on central Red Sea reefs.

In the present study, we conducted underwater visual census (UVC) surveys of offshore reefs in Saudi Arabian and Sudanese waters to provide baseline data on reef fish abundance and biomass across different trophic groups in the central Red Sea. Because of the apparent environmental homogeneity in these complementary regions, any significant differences observed may be indicative of varying levels of exploitation. As evidence of
shifting environmental baselines have been revealed in the Red Sea (see Price et al. 2014),
this study offers a rare and timely assessment of reef fish biomass in this understudied
region and allows for comparisons to other global regions to identify the relative
condition of reef fish communities throughout the tropics.

Materials and Methods

Study Sites
A total of 34 reefs were surveyed in two spatially close, but opposing regions in the
central Red Sea. Reef fish communities were surveyed on 16 reefs along the Sudanese
coast and 14 reefs along the southern central coast of Saudi Arabia within 20° and 18°
latitude (Fig. 1). All reef sites surveyed were classified as offshore; that is, in proximity
to the outer margin of the continental shelf and characterized by steep profiles with
occasional plateaus.

Survey Methodology
Underwater visual censuses (UVC) of reef fish communities were conducted using
replicate 25 m belt transects with species-specific widths as described in Sandin et al.
(2008) and utilized in a number of similar peer-reviewed publications (Demartini et al.
2008; Friedlander et al. 2010; Williams et al. 2011; Ruttenberg et al. 2011). A width of 8
m was employed for large-bodied, vagile species greater than 20 cm, while small-bodied,
more site-attached species were surveyed over a 4 m width. These transect dimensions
have been shown to optimize data precision and accuracy, minimize surveyor bias, and
compensate for differences in size and species-specific differences in density for this type of in situ underwater visual census (Mapstone and Ayling 1998). Transects were laid at a depth of 10 m on the side of the reef consistently exposed to wave energy. Transects were replicated three times in Saudi Arabia, however, due to logistical constrains most reefs were only replicated twice in Sudan (see ESM1). All diurnally active reef fishes with total length (TL) > 3 cm were documented to species level or to the lowest reliably identifiable taxon. For each individual, TL was estimated to the nearest cm in situ and later sorted into; TL between 3 and 5 cm, 5 cm size-class bins between TL 5 cm and 60 cm, 10 cm size-class bins between TL 60 cm and 100 cm, and 50 cm size-class bins > TL 100 cm. Size-estimation was regularly practiced prior to and throughout the study period using objects of known length to maintain accuracy. Surveys were conducted by a single diver (AK) to help eliminate bias and provide consistency between surveys and locations.

Fish species were allocated into one of four functional trophic guilds (see Sandin et al. 2008) based on Sandin and Williams (2010) and diet information obtained from FishBase (Froese and Pauly 2016). These groupings were: i) top predators (sharks, jacks, large groupers and snappers, as well as any other fish at or near the end of the food chain), ii) carnivores (smaller groupers and snappers, benthic invertivores, corallivores), iii) planktivores, and iv) herbivores (including detritivores) (see ESM2 for a complete list of surveyed species and their trophic allocations). While limitations to trophic allocation (Frisch et al. 2016; Roff et al. 2016) as well as the UVC methodology (Ward-Paige et al. 2010a; Caldwell et al. 2016) may exist, those employed in the current study were selected to enhance comparison of the data to similar investigations.
Data Analysis

To compare reef fish communities between the two regions, fish abundance from each reef was plotted using non-metric multi-dimensional scaling (nMDS) based on Bray-Curtis similarity matrix. Data were square root transformed prior to analysis to reduce the influence of abundant species. Analysis of similarity (ANOSIM) tested differences in community composition between the two regions and similarity percentage routine (SIMPER) provided species contribution to observed differences (Clarke 1993). Analyses were performed in PRIMER and PERMANOVA+ V6.

To calculate biomass, fish lengths were converted using the allometric length-weight conversion $W = aL^b$, where $W$ is weight in kilograms, $L$ is total length in centimeters and $a$ and $b$ are species-specific constants, obtained from FishBase (Froese and Pauly 2016). These converted weights coupled with numerical densities supplied from transects provided the input required for calculating biomass values per study region.

Local fishing pressure is purported to influence fish biomass within the two regions. However, due to political and logistical reasons, quantitative data on fishing levels in the two regions is lacking. To identify if local extraction through fishing is influencing fish communities, we investigated the relationship between overall biomass of each trophic group at each surveyed reef, and the linear distance to the nearest major fishing port (Port Sudan in Sudan, and Al Lith in Saudi Arabia). Due to tight maritime security in the region, we suspect that most of the fishing in the region is by local fishermen and not larger-scale fishing boats from other countries (Jin et al. 2012). In addition, fishing in this region is mainly through small (<10 m) outboard driven boats, so we postulate that fishing pressure would be greatest close to port and decrease with
distance from port. Distances (km) from surveyed reefs to associated ports were estimated through Google Earth and relationships were tested using linear regression models using \textit{lme4} package in R (R Core Team 2016; Bates et al. 2015).

results

Fish communities

Across all survey locations, a total of 130 species were recorded from 27 families, 111 species across Saudi Arabian reefs and 118 from Sudanese reefs (ESM1). While measures of species richness, evenness, and diversity (Shannon’s Diversity $H'$) showed little difference between the two regions, average reef fish abundance (all trophic groups) was 60% greater in Sudan compared to in Saudi Arabia (Table 1).

A comparison of fish community composition associated with all reefs from the two regions revealed that they were not homogenous (ANOSIM, Global $R=0.33$, $P=0.001$). There was separation of reefs based on associated fish communities between the two regions as displayed by nMDS. Here most reefs from Sudan separate from reefs in Saudi Arabia with the exception of Mar Mar and Malathu (Fig. 2). SIMPER analysis revealed that 31 of the 130 species contributed to 90% of the dissimilarity between the two regions (Table 2). Over half of the difference was attributed to two planktivores and both were more abundant on Sudanese reefs: \textit{Pseudanthias squamipinnis} and \textit{Chromis dimidiata} (36% and 17% dissimilarity, respectively). Planktivores encompassed half of the species, with top predators and carnivores making up the majority of the rest (Table
2). Within these two groups, ten out of the twelve species had higher average abundances Sudan reefs compared to Saudi Arabia.

**Biomass**

Biomass estimates at a regional scale was 1.04 tonnes hectare$^{-1}$ higher in Sudan (5.01 ± 0.77 SE) compared to Saudi Arabia (4.05 ± 0.92 SE). Among the four trophic groups, biomass was highest on Sudanese reefs for top predators, carnivores, and herbivores (Table 3). Top predator biomass was nearly three times higher on Sudanese reefs, reflective of a similar increase in overall top predator abundance. Overall carnivore biomass on Sudanese reefs was twice that of Saudi Arabia reefs driven by a 47% increase in mean weight and a 51% increase in abundance. Herbivore biomass was also greater on Sudanese reefs with a two-fold increase and approaching a three-fold increase with respect to abundance. Conversely, planktivores revealed a lower biomass estimate in Sudan of almost a tonne hectare$^{-1}$; while planktivore abundance was higher in Sudan by 170%, mean planktivore weight was higher by 35% in Saudi Arabia (Table 3).

At a reef level, overall mean biomass was highest in Saudi Arabia on Mubarak reef (mean = 12.52, SE = 3.19), and was also the highest overall biomass for the central Red Sea study area (Fig. 3). Habily Lory (mean = 10.30, SE = 1.06) and Dahrat Qab (mean = 9.98, SE = 3.29) contained the highest biomass in Sudan. The lowest overall biomass estimates were observed at Mar Mar (mean = 0.70, SE = 0.34), followed by three other reefs in Saudi Arabia (Belgium Point, Long Reef, and Malathu). Of the 30 reefs included in this study, mean biomass of top predators was greatest at Dahrat Qab (mean = 5.21, SE = 0.49) in Sudan. Nine of the next ten reefs ranked in order of
decreasing top predator biomass were also found in Sudan while only Mubarak in Saudi Arabia contained similar levels of top predator biomass to that in Sudan (Fig. 3). Overall biomass levels of planktivores varied greatly among regions while the top seven reefs with the highest herbivore biomass were from Sudan with Masamarit highest containing 2.37 tonnes hectare\(^{-1}\). Carnivore biomass varied from 0.08 (Long Reef, Saudi Arabia) to 2.13 (Darraka, Sudan) with the top seven reefs all within Sudan (Fig. 3).

The four species that contributed the greatest proportion of biomass for each of the four trophic groups showed a trend where Sudan biomass was greater (Fig. 4). One species of herbivore (*Ctenochaetus striatus*) and one species of planktivore (*Naso hexacanthus*), however, had a higher mean in Saudi Arabia although differences were not statistically significant.

The relationship between biomass and distance from the nearest major fishing port identified a significant positive relationship for top predators (R\(^2\) = 0.45, P < 0.01). There was also a slight tendency for increase of biomass for the other three trophic groups, yet this was not statistically supported (Fig. 5).

**Size demographics**

Sudan had 60% more planktivores in the smallest size class (< 4 cm), while Saudi Arabia had a higher frequency (12-39%) of medium-sized individuals (13-23 cm) (Fig. 6). In Saudi Arabia, the frequency of herbivores peaked at size class 14-18 cm (4 individuals) and then declined to the maximum size of 49 cm. In Sudan, herbivore size class 19-23 cm had the highest frequency (7 individuals) and there was a maximum size of 58 cm. The frequency of individuals in each size class for carnivores were similar for classes < 23 cm,
but Sudan displayed a higher number of individuals between 23 cm and 53 cm. Few top predators below 18 cm were observed in either region, but Saudi Arabia displayed greater frequency of top predators between 48 cm and 65.5 cm.

Discussion

Surveys of conspicuous reef fishes from Sudanese and Saudi Arabian reefs in the central Red Sea revealed notable differences in associated community composition and biomass estimates between the two regions. Reefs within these two regions sit opposite each other in the Red Sea basin and, while they are less than 200-300 km apart, average fish abundance was 62% higher and biomass was 20% higher on Sudanese reefs than on Saudi Arabian reefs. Fish communities in Sudan were also slightly more diverse with an average of six more species per transect. Furthermore, 71% (22/31) of the species that comprised 90% of the disparity in community composition between regions were a result of higher average abundance on Sudanese reefs. Given the close proximity to each other and the consistent differences between the two regions in environmental parameters, it appears fish communities in Saudi Arabia are, in some aspects, degraded.

Planktivores are generally the most numerous trophic group on coral reefs, playing an important role in the transfer of energy from the base of the food web to higher trophic levels (Hobson 1991). In the central Red Sea, this group made up the numerical majority of fishes in both regions and was the largest contributor to overall biomass in Saudi Arabia. Differences in fish community composition between the two regions were greatly driven by species of planktivores, whereby eight species accounted for 73% of the observed discrepancy. A pronounced proportion of the total difference (53%) was a result of higher numbers of Pseudanthias squamipinnis and Chromis
*dimidata* associated with reefs in Sudan. Both of these species are common in the Red Sea and found in large schools close to the reef structure feeding on plankton (Lieske and Myers 2004). Overall mean biomass estimates of planktivores were a third higher on Saudi Arabian reefs although abundance was a third lower. This suggests that Saudi Arabian reefs contain higher abundances of larger bodied species but less small species. Indeed, Saudi Arabian reefs had high levels of all three species of fusiliers: *Caesio lunaris*, *C. suevica*, and *C. striata*. Planktivores are generally dependent on oceanographic parameters for nutrient input and for smaller species, complex reef structure for habitat and shelter (Munday and Jones 1998; Friedlander and Parrish 1998). However, species that displayed the greatest differences between the two regions were not regarded as coral-dependent species and therefore not expected to be influenced by variation in benthic structure (see Cole et al. 2008; Coker et al. 2014). While reefs in similar biogeographic provinces may differ in their capacity to support fish stocks and possess variable trophic compositions (Williams et al. 2015), these regions are reported to have similar reef parameters (e.g., coral cover and composition, reef complexity, reef profile) (Sheppard and Sheppard 1991; Sheppard et al. 1992; DeVantier et al. 2000; Chekchak and Klaus 2013; Hussey et al. 2013). It is probable that the observations between regions concerning planktivores may be a function of predator removal in the form of either reduced predation and/or shifts in the behaviour and movement of these planktivores in the absence of predators.

Large herbivores (e.g., parrotfish) are targeted on both sides of the Red Sea. We hypothesize that we observed lower herbivore biomass in Saudi Arabian waters because of higher fishing pressure. In Saudi Arabian fish markets parrotfishes are regularly
present in high numbers, and they are a staple menu item in local seafood establishments.

Furthermore, the large, annual aggregation of one species, *Hipposcarus harid*, is intensely harvested (Gladstone 1996; Spaet 2013). The herbivore *Naso unicornis* can likewise be found daily in Saudi Arabian markets, typically in large bundles of many individuals. This is a species that was recorded in very large schools on several reefs in southern Sudan. The great disparity in biomass of *N. unicornis* between Saudi Arabia and Sudan (see Fig. 4) further suggests differences in fishing pressure between these two Red Sea nations.

Top predators and carnivores characterize the top of the food chain, are the first group to decline as a result of fishing, and their presence and abundance is indicative of healthy reef systems (Pauly et al. 1998). Seminal studies in remote and ‘pristine’ regions have documented high levels of biomass when compared to regions exposed to anthropogenic impacts and, in particular, prevalent fishing pressure (Friedlander and Demartini 2002; Sandin et al. 2008; Williams et al. 2011). In the central Red Sea, four of the most common top predators and carnivores were all documented in greater abundance on Sudanese reefs along with up to a five-fold increase in biomass levels. The high levels in abundance and biomass of species such as *Lutjanus bohar* are reflective of reefs around the world with lower fishing pressure as these fish groups are the targets of fisheries (Russ and Alcala 1989; Pauly et al. 1998). This also suggests that reefs in Sudan are subjected to lower fishing pressure than those on the Saudi Arabian side.

Very little detailed information is available on fishing in the Red Sea. Based on anecdotal evidence from local fish markets, everything that is caught in the Red Sea is kept and sold. Moreover, fishing methods employed (including hook-and-line, gill nets,
and traps) are similar in both the Saudi Arabian and Sudanese study regions (Tesfamichael and Pauly 2016). Species easily caught with these standard fishing methods are therefore vulnerable to overfishing. The unique biology of some species, however, may contribute to some of our unexpected observations. For example, we found the abundance of the blackfin barracuda (*Sphyraena genie*) to be more than 16 times higher in Saudi Arabia compared to Sudan. This species is known to form large, semi-stationary schools of similarly-sized individuals numbering in the hundreds (Lieske and Myers 2004; Froese and Pauly 2016). As evidenced in our abundance estimates, this species is either present in high numbers or entirely absent. In fact, two large schools of *S. genie* from only two reefs in Saudi Arabia are responsible for the entirety of their abundance for the region. It is therefore suggested that differences observed for some species in this study are most likely driven by occurrences of schools rather than solely fishing pressure.

While the presence of sharks is often considered synonymous with healthy reef ecosystems, populations of many species around the globe have been devastated in recent decades (Myers and Worm 2003; Robbins et al. 2006; Myers et al. 2007; Sandin et al. 2008; Ward-Paige et al. 2010b). Remote regions like Kingman with limited local anthropogenic impacts report UVC-based levels of shark biomass up to 3.3 tonnes hectare\(^{-1}\) (Sandin et al. 2008), a value almost twice as great as the mean biomass of all top predators presently recorded for Sudan. Sadly, across all reefs and replicates of this study only four individuals belonging to one species (*Triaenodon obesus*) were recorded within transect boundaries (Mar Mar, Saudi Arabia), and all of these sharks were located under a single Acropora table. Several species of sharks (*T. obesus, Carcharinus amblyrhynchos*,}
Carcharhinus falciformis, Sphyrna lewini, and even a single Rhincodon typus) were sighted outside transect boundaries or during non-survey portions of dives, but these observations varied greatly in their frequency between the two study regions. Sharks were regularly encountered on Sudanese reefs and were very sparse in Saudi Arabia. These observations corroborate those reported in previous studies for both regions (Hussey et al. 2013; Clarke et al. 2013; Spaet and Berumen 2015) and echo warnings of elasmobranch overexploitation in Saudi Arabia despite a 2008 royal decree prohibiting all shark fishing activities in the country (Jabado et al. 2015; Spaet et al. 2016). Urgent enforcement of this law is needed to avoid ecosystem-wide repercussions of shark removal (Stevens et al. 2000; Baum and Worm 2009; Ferretti et al. 2010; Ruppert et al. 2013).

Declines in biomass and abundance, along with changes in species composition of reef associated fishes, can be influenced by suitable habitat, prey availability, recruitment, environmental parameters, and direct removal through a variety of fishing methods. While little information exists for specific comparisons, personal observations and communications as well as broad-scale descriptions of biotic (Sheppard and Sheppard 1991; Sheppard et al. 1992; DeVantier et al. 2000; Chekchak and Klaus 2013) and abiotic variables (Ngugi et al. 2012; Raitsos et al. 2013) support east-west similarity in the central Red Sea. It therefore seems likely that the observed differences in reef fish communities between Sudan and Saudi Arabia are heavily influenced by human disturbances, particularly exploitation. The high overall and top predator biomass recorded at furthest-offshore Mubarak reef, comparable to that measured on southern Sudanese reefs, lends further evidence that Saudi Arabian reefs are indeed capable of
supporting large fish stocks.

Quantitative data detailing fishing pressure is limited for both regions; however, this study reveals that for top predators a positive relationship exists between biomass and distance to the closest major fishing port. This supports the theory that extraction by local fishermen is responsible for declines in stocks and concurs with studies in other locations that show a negative association with human population and the distribution of large-bodied fishes (Stallings 2009; Cinner et al. 2012; Williams et al. 2015). While the region as a whole lacks reliable fisheries records, a number of studies support this notion of asymmetrical fishing pressure in the Red Sea (Gladstone 2002; Hariri et al. 2002; Tesfamichael and Pauly 2016). Reports suggest that aggregate traditional fisheries in Saudi Arabia have been overexploited since the early 1990s (Jin et al. 2012; Tesfamichael and Rossing 2012) and Sudan uses their marine resources the least of any Red Sea nation (Tesfamichael and Pitcher 2006; Jin et al. 2012). This has been attributed to Sudan’s small and ill-equipped fishing fleet (e.g., lack of ice limits the distance fishing vessels venture) as well as the nation’s low consumption of fish, the least of any Red Sea country (Sanders and Morgan 1989). While the fish trade in Sudan is still in a primitive stage (Tesfamichael and Elawad 2012), demand for reef-associated Red Sea products in Saudi Arabia remains high. The disparity in sustainability status between Sudan and Saudi Arabia may extend in general to the entire eastern and western Red Sea (Tesfamichael and Pitcher 2006).

If reefs in Sudan are taken as benchmarks for Saudi Arabia, our results suggest that a number of management actions could be taken to restore Saudi Arabian reefs to under-exploited states and to ensure that Sudanese marine resources avoid depletion.
Such measures are critical to promote the overall health of these coral reef systems and their resilience in the face of ongoing climate change (Sala 2006; Brand 2009). Enforcement of existing regulations in Saudi Arabia, including the aforementioned royal decree prohibiting shark fishing, would be an important first step. Moreover, new regulations to protect highly-prized top predators (e.g., *L. bohar*) as well as large carnivores (e.g., *Cheilinus undulatus*) and herbivores (e.g., *Scarus* spp.) may be needed. Both species-specific actions (e.g., size restrictions, seasonal closures, moratoriums) and ecosystem-wide approaches should be considered. Although a large number of studies have demonstrated the efficacy of marine protected areas (MPAs) for restoring large predators (e.g., Russ and Alcala 1996; Russ and Alcala 2004; Aburto-Oropeza et al. 2011), the recovery of reefs with altered fish composition has been estimated to take up to 60 years (MacNeil et al. 2015). MPA implementation should therefore be considered a high priority in Saudi Arabia’s Red Sea management plan. While reefs in Sudan herein appear to be relatively healthy, large MPA creation and enforcement as well as full protection of elasmobranch species should still be considered important for Sudan as exploitation, particularly of sharks, appears to be on the rise (L. Segalini, pers. comm.).

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**Figure captions**

Fig. 1. Map of the central Red Sea showing locations of surveyed reefs. Insert illustrates the location of surveyed reefs with respect to the Red Sea. Identifying numbers in red (1-16) represent sites in Sudan. Identifying numbers in green (1-14) represent sites in Saudi Arabia. See Appendix A for complete site details.

Fig. 2. nMDS illustrating all reefs in 2-dimentional space based on fish abundance data associated with each reef from Saudi Arabia (green) and Sudan (red).

Fig. 3. Average biomass (tonnes hectare$^{-1}$ ±SE) for each trophic group for each reef surveyed in Saudi Arabia and Sudan. Reefs are organized latitudinal from north (left) to south (right) for both regions.

Fig. 4. Grand mean biomass of the top four taxa by weight of each trophic guild in Sudan (red) and corresponding values for these taxa in Saudi Arabia (green). a = top predators, b = carnivores, c = herbivores, d = planktivores. Error bars are standard error of the mean.

Fig. 5. Relationship between biomass (tonnes hectares$^{-1}$) for each trophic group and distance (km) from the nearest major fishing port. Data points represent each reef from Saudi Arabia and Sudan.
Fig. 6. Mean body size class frequency for each trophic guild in Saudi Arabia and Sudan.

Error bars are standard error of the mean.
Table 1. Average (per transect ± SE) reef fish community indices for Saudi Arabia and Sudan.

<table>
<thead>
<tr>
<th>Region</th>
<th>Abundance</th>
<th>Richness</th>
<th>Evenness</th>
<th>Diversity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Saudi Arabia</td>
<td>543 ±39</td>
<td>27 ±0.6</td>
<td>0.46 ±0.02</td>
<td>1.52 ±0.07</td>
</tr>
<tr>
<td>Sudan</td>
<td>885 ±100</td>
<td>33 ±1.8</td>
<td>0.47 ±0.03</td>
<td>1.64 ±0.13</td>
</tr>
</tbody>
</table>
Table 2. Species that contributed >90% of the observed differences between Saudi Arabia and Sudan fish communities (SIMPER analysis). Shading illustrates a higher average abundance in Sudan than Saudi Arabia.

<table>
<thead>
<tr>
<th>Species</th>
<th>Trophic Guild</th>
<th>Saudi Arabia</th>
<th>Sudan</th>
<th>Av.Diss</th>
<th>Diss/SD</th>
<th>Contrib%</th>
<th>Cum%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pseudanthias squamipinnis</td>
<td>Planktivore</td>
<td>196.07</td>
<td>408.42</td>
<td>18.39</td>
<td>1.43</td>
<td>35.99</td>
<td>35</td>
</tr>
<tr>
<td>Chromis dimidiata</td>
<td>Planktivore</td>
<td>171.19</td>
<td>198.65</td>
<td>8.66</td>
<td>1.27</td>
<td>16.94</td>
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<td>Caranx melampygus</td>
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<td>3.96</td>
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<td>0.15</td>
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Table 3. Comparison of biomass density (tons hectare$^{-1}$), numerical density (number hectare$^{-1}$), and mean weight of individuals (g) between surveyed reefs in Sudan and Saudi Arabia. Values are grand means (± SE). n = 16 for Sudan and n = 14 for Saudi Arabia.

<table>
<thead>
<tr>
<th></th>
<th>Sudan</th>
<th>Saudi Arabia</th>
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<td><strong>Biomass</strong></td>
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<tr>
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<td>1.76 (0.42)</td>
<td>0.61 (0.30)</td>
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<tr>
<td>Carnivore</td>
<td>0.69 (0.12)</td>
<td>0.29 (0.04)</td>
</tr>
<tr>
<td>Planktivore</td>
<td>1.78 (0.43)</td>
<td>2.81 (0.69)</td>
</tr>
<tr>
<td>Herbivore</td>
<td>0.78 (0.15)</td>
<td>0.37 (0.06)</td>
</tr>
<tr>
<td><strong>Number</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Top predator</td>
<td>1296 (245)</td>
<td>445 (224)</td>
</tr>
<tr>
<td>Carnivore</td>
<td>4120 (574)</td>
<td>2587 (232)</td>
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<tr>
<td>Planktivore</td>
<td>64027 (7241)</td>
<td>42535 (3508)</td>
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<tr>
<td>Herbivore</td>
<td>5002 (2259)</td>
<td>1854 (257)</td>
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<tr>
<td><strong>Mean Weight</strong></td>
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<tr>
<td>Top Predator</td>
<td>1321 (173)</td>
<td>1597 (290)</td>
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<tr>
<td>Carnivore</td>
<td>171 (20)</td>
<td>116 (12)</td>
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<td>78 (26)</td>
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<tr>
<td>Herbivore</td>
<td>259 (45)</td>
<td>220 (32)</td>
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</table>