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

2   **pressure**

3

4

5   Alexander Kattan*[1], Darren J. Coker[1], Michael L. Berumen[1]

6

7   [1]Red Sea Research Center, Division of Biological and Environmental Science and

8   Engineering, King Abdullah University of Science and Technology, Thuwal 23955-6900,

9   Saudi Arabia

10

11

12

13   *** Corresponding author**

14   Alexander Kattan:

15   Red Sea Research Center, King Abdullah University of Science and Technology, Thuwal,

16   23955, Saudi Arabia

17   Phone: +1 561-768-2458

18   E-mail: alexander.kattan@gmail.com

19

20

21

24 **Abstract**

25 In order to assess human impacts and develop rational restoration goals on corals reefs,

26 baseline estimates of fish communities are required. In Saudi Arabian waters of the Red

27 Sea, widespread and unregulated fishing is thought to have been ongoing for decades, but

28 there is little direct evidence of the impact on reef communities. To contextualize this

29 human influence, reef-associated fish assemblages on offshore reefs in Saudi Arabia and

30 Sudan in the central Red Sea were investigated. These reefs have comparable benthic

31 environments, experience similar oceanographic influences, and are separated only by <

32 300 km, offering an ideal comparison to help identify potential anthropogenic impacts

33 such as fishing pressure. This is the first study to assess reef fish biomass in both these

34 regions, providing important baselines estimates. We found that biomass of top predators

35 on offshore Sudanese reefs was on average almost three times that measured on

36 comparable reefs in Saudi Arabia. Biomass values from some of the most remote reefs

37 surveyed in Sudan's far southern region even approach those previously reported in the

38 Northwest Hawaiian Islands, northern Line Islands, Pitcairn Islands, and other isolated

39 Pacific islands and atolls. The findings suggest fishing pressure has significantly altered

40 the fish community structure of Saudi Arabian Red Sea reefs, most conspicuously in the

41 form of top predator removal. The results point towards the urgent need for enhanced

42 regulation and enforcement of fishing practices in Saudi Arabia while simultaneously

43 making a strong case for protection in the form of no-take marine protected areas to

44 maintain preservation of the relatively intact southern Sudanese Red Sea.

45

46

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

70   the opportunity to measure both direct and indirect effects of human impacts (particularly

71   fishing) on reef fish communities in nearby and physically comparable systems

72   (Knowlton and Jackson 2008). The trademark feature of healthy reefs, as revealed by

73   such studies, is 'top-heavy' (inverted) fish biomass pyramids (Sandin et al. 2008). In

74   these unique locations, sharks and other large top predators (jacks, snappers, groupers)

75   overwhelm the reef fish community biomass, supported by lower trophic levels with very

76   high turnover rates (Sandin et al. 2008). Studies of healthy reefs also reveal compelling

77   cascading effects of predator removal on coral reefs under even modest fishing pressure,

78   including changes in the abundance, body condition, length, and reproductive potential of

79   prey species (Ruttenberg et al. 2011; Walsh et al. 2012). Identification of additional near-

80   or relatively-pristine coral reefs in novel biogeographic provinces would do well to

81   advance this field of study and allow for comparison of human impacts across broader

82   spatial scales.

83   The Red Sea is a narrow sea harboring high biodiversity (Stehli and Wells 1971),

84   an elevated level of endemism (Ormond and Edwards 1987; DiBattista et al. 2016), and

85   one of the largest reef systems on the planet despite exhibiting relatively extreme

86   environmental conditions (i.e., salinity, temperature) and seasonal fluctuations (Raitsos et

87   al. 2013). Despite its unique environment, the Red Sea remains a scientifically

88   understudied region, a combined result of its remoteness, regional geopolitical situations,

89   complicated visa and permitting regulations, and a lack of marine infrastructure

90   (Berumen et al. 2013). A number of recent studies have revealed that while latitudinal

91   gradients of environmental conditions in the Red Sea do exist (Ngugi et al. 2012; Raitsos

92   et al. 2013; Kürten et al. 2014; Price et al. 2014), species richness and diversity of coral

93   reef fish assemblages change little, if at all, from north to south (Roberts et al. 2015).

94   Moreover, patterns of reef development, benthic composition, and coral cover along the

95   east and west coastlines of the relatively narrow Red Sea appear to mirror one another

96   (Sheppard and Sheppard 1991; Sheppard et al. 1992; DeVantier et al. 2000; Chekchak

97   and Klaus 2013).

98   Baseline data for patterns of Red Sea reef fish biomass, however, are largely

99   missing. This is particularly troublesome as historical and contemporary information of

100   reef fisheries are also lacking for the region as a whole, limiting attempts to measure the

101   extent to which Red Sea reef fish communities have been impacted by human activities.

102   In the central Red Sea, fishing pressure has been noted as high and ongoing for a number

103   of decades along the Saudi Arabian coastline. This is supported by a limited number of

104   scientific publications (e.g., Jin et al. 2012; Tesfamichael and Rossing 2012;

105   Tesfamichael and Pauly 2016) and robust evidence on this impact on reef fish

106   communities remains missing for both east and west coasts. Separated by ~ 300 km and

107   with a deep mid-basin trench (~ 2000 m) keeping adult fish populations separate, the two

108   sides of the Red Sea therefore provide unique circumstances and opportunities to make

109   comparisons and generate hypotheses about the impacts of human influences (e.g.,

110   fishing pressure) on central Red Sea reefs.

111   In the present study, we conducted underwater visual census (UVC) surveys of

112   offshore reefs in Saudi Arabian and Sudanese waters to provide baseline data on reef fish

113   abundance and biomass across different trophic groups in the central Red Sea. Because of

114   the apparent environmental homogeneity in these complementary regions, any significant

115   differences observed may be indicative of varying levels of exploitation. As evidence of

116   shifting environmental baselines have been revealed in the Red Sea (see Price et al. 2014),

117   this study offers a rare and timely assessment of reef fish biomass in this understudied

118   region and allows for comparisons to other global regions to identify the relative

119   condition of reef fish communities throughout the tropics.

120

Materials and Methods

122

Study Sites

124   A total of 34 reefs were surveyed in two spatially close, but opposing regions in the

125   central Red Sea. Reef fish communities were surveyed on 16 reefs along the Sudanese

126   coast and 14 reefs along the southern central coast of Saudi Arabia within 20° and 18°

127   latitude (Fig. 1). All reef sites surveyed were classified as offshore; that is, in proximity

128   to the outer margin of the continental shelf and characterized by steep profiles with

129   occasional plateaus.

130

Survey Methodology

132   Underwater visual censuses (UVC) of reef fish communities were conducted using

133   replicate 25 m belt transects with species-specific widths as described in Sandin et al.

134   (2008) and utilized in a number of similar peer-reviewed publications (Demartini et al.

135   2008; Friedlander et al. 2010; Williams et al. 2011; Ruttenberg et al. 2011). A width of 8

136   m was employed for large-bodied, vagile species greater than 20 cm, while small-bodied,

137   more site-attached species were surveyed over a 4 m width. These transect dimensions

138   have been shown to optimize data precision and accuracy, minimize surveyor bias, and

139   compensate for differences in size and species-specific differences in density for this type

140   of *in situ* underwater visual census (Mapstone and Ayling 1998). Transects were laid at a

141   depth of 10 m on the side of the reef consistently exposed to wave energy. Transects were

142   replicated three times in Saudi Arabia, however, due to logistical constrains most reefs

143   were only replicated twice in Sudan (see ESM1). All diurnally active reef fishes with

144   total length (TL) > 3 cm were documented to species level or to the lowest reliably

145   identifiable taxon. For each individual, TL was estimated to the nearest cm *in situ* and

146   later sorted into; TL between 3 and 5 cm, 5 cm size-class bins between TL 5 cm and 60

147   cm, 10 cm size-class bins between TL 60 cm and 100 cm, and 50 cm size-class bins > TL

148   100 cm. Size-estimation was regularly practiced prior to and throughout the study period

149   using objects of known length to maintain accuracy. Surveys were conducted by a single

150   diver (AK) to help eliminate bias and provide consistency between surveys and locations.

151   Fish species were allocated into one of four functional trophic guilds (see Sandin

152   et al. 2008) based on Sandin and Williams (2010) and diet information obtained from

153   FishBase (Froese and Pauly 2016). These groupings were: i) top predators (sharks, jacks,

154   large groupers and snappers, as well as any other fish at or near the end of the food chain),

155   ii) carnivores (smaller groupers and snappers, benthic invertivores, corallivores), iii)

156   planktivores, and iv) herbivores (including detritivores) (see ESM2 for a complete list of

157   surveyed species and their trophic allocations). While limitations to trophic allocation

158   (Frisch et al. 2016; Roff et al. 2016) as well as the UVC methodology (Ward-Paige et al.

159   2010a; Caldwell et al. 2016) may exist, those employed in the current study were selected

160   to enhance comparison of the data to similar investigations.

161

162 **Data Analysis**

163 To compare reef fish communities between the two regions, fish abundance from each

164 reef was plotted using non-metric multi-dimensional scaling (nMDS) based on Bray-

165 Curtis similarity matrix. Data were square root transformed prior to analysis to reduce the

166 influence of abundant species. Analysis of similarity (ANOSIM) tested differences in

167 community composition between the two regions and similarity percentage routine

168 (SIMPER) provided species contribution to observed differences (Clarke 1993). Analyses

169 were performed in PRIMER and PERMANOVA+ V6.

170 To calculate biomass, fish lengths were converted using the allometric length-

171 weight conversion $W = aL^b$, where W is weight in kilograms, L is total length in

172 centimeters and a and b are species-specific constants, obtained from FishBase (Froese

173 and Pauly 2016). These converted weights coupled with numerical densities supplied

174 from transects provided the input required for calculating biomass values per study region.

175 Local fishing pressure is purported to influence fish biomass within the two

176 regions. However, due to political and logistical reasons, quantitative data on fishing

177 levels in the two regions is lacking. To identify if local extraction through fishing is

178 influencing fish communities, we investigated the relationship between overall biomass

179 of each trophic group at each surveyed reef, and the linear distance to the nearest major

180 fishing port (Port Sudan in Sudan, and Al Lith in Saudi Arabia). Due to tight maritime

181 security in the region, we suspect that most of the fishing in the region is by local

182 fishermen and not larger-scale fishing boats from other countries (Jin et al. 2012). In

183 addition, fishing in this region is mainly through small (<10 m) outboard driven boats, so

184 we postulate that fishing pressure would be greatest close to port and decrease with

185   distance from port. Distances (km) from surveyed reefs to associated ports were

186   estimated through Google Earth and relationships were tested using linear regression

187   models using *lme4* package in R (R Core Team 2016; Bates et al. 2015).

188

189   **Results**

190

191   **Fish communities**

192   Across all survey locations, a total of 130 species were recorded from 27 families, 111

193   species across Saudi Arabian reefs and 118 from Sudanese reefs (ESM1). While

194   measures of species richness, evenness, and diversity (Shannon's Diversity *H'*) showed

195   little difference between the two regions, average reef fish abundance (all trophic groups)

196   was 60% greater in Sudan compared to in Saudi Arabia (Table 1).

197   A comparison of fish community composition associated with all reefs from the

198   two regions revealed that they were not homogenous (ANOSIM, Global R=0.33,

199   P=0.001). There was separation of reefs based on associated fish communities between

200   the two regions as displayed by nMDS. Here most reefs from Sudan separate from reefs

201   in Saudi Arabia with the exception of Mar Mar and Malathu (Fig. 2). SIMPER analysis

202   revealed that 31 of the 130 species contributed to 90% of the dissimilarity between the

203   two regions (Table 2). Over half of the difference was attributed to two planktivores and

204   both were more abundant on Sudanese reefs: *Pseudanthias squamipinnis* and *Chromis*

205   *dimidiata* (36% and 17% dissimilarity, respectively). Planktivores encompassed half of

206   the species, with top predators and carnivores making up the majority of the rest (Table

207   2). Within these two groups, ten out of the twelve species had higher average abundances

208   Sudan reefs compared to Saudi Arabia.

209

210   **Biomass**

211   Biomass estimates at a regional scale was 1.04 tonnes hectare^{-1} higher in Sudan (5.01 ±

212   0.77 SE) compared to Saudi Arabia (4.05 ±0.92 SE). Among the four trophic groups,

213   biomass was highest on Sudanese reefs for top predators, carnivores, and herbivores

214   (Table 3). Top predator biomass was nearly three times higher on Sudanese reefs,

215   reflective of a similar increase in overall top predator abundance. Overall carnivore

216   biomass on Sudanese reefs was twice that of Saudi Arabia reefs driven by a 47% increase

217   in mean weight and a 51% increase in abundance. Herbivore biomass was also greater on

218   Sudanese reefs with a two-fold increase and approaching a three-fold increase with

219   respect to abundance. Conversely, planktivores revealed a lower biomass estimate in

220   Sudan of almost a tonne hectare^{-1}; while planktivore abundance was higher in Sudan by

221   170%, mean planktivore weight was higher by 35% in Saudi Arabia (Table 3).

222   At a reef level, overall mean biomass was highest in Saudi Arabia on Mubarak

223   reef (mean = 12.52, SE = 3.19), and was also the highest overall biomass for the central

224   Red Sea study area (Fig. 3). Habily Lory (mean = 10.30, SE = 1.06) and Dahrat Qab

225   (mean = 9.98, SE = 3.29) contained the highest biomass in Sudan. The lowest overall

226   biomass estimates were observed at Mar Mar (mean = 0.70, SE = 0.34), followed by

227   three other reefs in Saudi Arabia (Belgium Point, Long Reef, and Malathu). Of the 30

228   reefs included in this study, mean biomass of top predators was greatest at Dahrat Qab

229   (mean = 5.21, SE = 0.49) in Sudan. Nine of the next ten reefs ranked in order of

230   decreasing top predator biomass were also found in Sudan while only Mubarak in Saudi

231   Arabia contained similar levels of top predator biomass to that in Sudan (Fig. 3). Overall

232   biomass levels of planktivores varied greatly among regions while the top seven reefs

233   with the highest herbivore biomass were from Sudan with Masamarit highest containing

234   2.37 tonnes hectare^{-1}. Carnivore biomass varied from 0.08 (Long Reef, Saudi Arabia) to

235   2.13 (Darraka, Sudan) with the top seven reefs all within Sudan (Fig. 3).

236   The four species that contributed the greatest proportion of biomass for each of

237   the four trophic groups showed a trend where Sudan biomass was greater (Fig. 4). One

238   species of herbivore (*Ctenochaetus striatus*) and one species of planktivore (*Naso*

239   *hexacanthus*), however, had a higher mean in Saudi Arabia although differences were not

240   statistically significant.

241   The relationship between biomass and distance from the nearest major fishing

242   port identified a significant positive relationship for top predators ($R^2 = 0.45$, P < 0.01).

243   There was also a slight tendency for increase of biomass for the other three trophic

244   groups, yet this was not statistically supported (Fig. 5).

245

246   **Size demographics**

247   Sudan had 60% more planktivores in the smallest size class (< 4 cm), while Saudi Arabia

248   had a higher frequency (12-39%) of medium-sized individuals (13-23 cm) (Fig. 6). In

249   Saudi Arabia, the frequency of herbivores peaked at size class 14-18 cm (4 individuals)

250   and then declined to the maximum size of 49 cm. In Sudan, herbivore size class 19-23 cm

251   had the highest frequency (7 individuals) and there was a maximum size of 58 cm. The

252   frequency of individuals in each size class for carnivores were similar for classes < 23 cm,

253 but Sudan displayed a higher number of individuals between 23 cm and 53 cm. Few top

254 predators below 18 cm were observed in either region, but Saudi Arabia displayed greater

255 frequency of top predators between 48 cm and 65.5 cm.

256 **Discussion**

257   Surveys of conspicuous reef fishes from Sudanese and Saudi Arabian reefs in the

258 central Red Sea revealed notable differences in associated community composition and

259 biomass estimates between the two regions. Reefs within these two regions sit opposite

260 each other in the Red Sea basin and, while they are less than 200-300 km apart, average

261 fish abundance was 62% higher and biomass was 20% higher on Sudanese reefs than on

262 Saudi Arabian reefs. Fish communities in Sudan were also slightly more diverse with an

263 average of six more species per transect. Furthermore, 71% (22/31) of the species that

264 comprised 90% of the disparity in community composition between regions were a result

265 of higher average abundance on Sudanese reefs. Given the close proximity to each other

266 and the consistent differences between the two regions in environmental parameters, it

267 appears fish communities in Saudi Arabia are, in some aspects, degraded.

268   Planktivores are generally the most numerous trophic group on coral reefs,

269 playing an important role in the transfer of energy from the base of the food web to

270 higher trophic levels (Hobson 1991). In the central Red Sea, this group made up the

271 numerical majority of fishes in both regions and was the largest contributor to overall

272 biomass in Saudi Arabia. Differences in fish community composition between the two

273 regions were greatly driven by species of planktivores, whereby eight species accounted

274 for 73% of the observed discrepancy. A pronounced proportion of the total difference

275 (53%) was a result of higher numbers of *Pseudanthias squamipinnis* and *Chromis*

276   *dimidata* associated with reefs in Sudan. Both of these species are common in the Red

277   Sea and found in large schools close to the reef structure feeding on plankton (Lieske and

278   Myers 2004). Overall mean biomass estimates of planktivores were a third higher on

279   Saudi Arabian reefs although abundance was a third lower. This suggests that Saudi

280   Arabian reefs contain higher abundances of larger bodied species but less small species.

281   Indeed, Saudi Arabian reefs had high levels of all three species of fusiliers: *Caesio*

282   *lunaris*, *C. suevica*, and *C. striata.* Planktivores are generally dependent on

283   oceanographic parameters for nutrient input and for smaller species, complex reef

284   structure for habitat and shelter (Munday and Jones 1998; Friedlander and Parrish 1998).

285   However, species that displayed the greatest differences between the two regions were

286   not regarded as coral-dependent species and therefore not expected to be influenced by

287   variation in benthic structure (see Cole et al. 2008; Coker et al. 2014). While reefs in

288   similar biogeographic provinces may differ in their capacity to support fish stocks and

289   possess variable trophic compositions (Williams et al. 2015), these regions are reported to

290   have similar reef parameters (e.g., coral cover and composition, reef complexity, reef

291   profile) (Sheppard and Sheppard 1991; Sheppard et al. 1992; DeVantier et al. 2000;

292   Chekchak and Klaus 2013; Hussey et al. 2013). It is probable that the observations

293   between regions concerning planktivores may be a function of predator removal in the

294   form of either reduced predation and/or shifts in the behaviour and movement of these

295   planktivores in the absence of predators.

296   Large herbivores (e.g., parrotfish) are targeted on both sides of the Red Sea. We

297   hypothesize that we observed lower herbivore biomass in Saudi Arabian waters because

298   of higher fishing pressure. In Saudi Arabian fish markets parrotfishes are regularly

299 present in high numbers, and they are a staple menu item in local seafood establishments.

300 Furthermore, the large, annual aggregation of one species, *Hipposcarus harid*, is

301 intensely harvested (Gladstone 1996; Spaet 2013). The herbivore *Naso unicornis* can

302 likewise be found daily in Saudi Arabian markets, typically in large bundles of many

303 individuals. This is a species that was recorded in very large schools on several reefs in

304 southern Sudan. The great disparity in biomass of *N. unicornis* between Saudi Arabia and

305 Sudan (see Fig. 4) further suggests differences in fishing pressure between these two Red

306 Sea nations.

307   Top predators and carnivores characterize the top of the food chain, are the first

308 group to decline as a result of fishing, and their presence and abundance is indicative of

309 healthy reef systems (Pauly et al. 1998). Seminal studies in remote and 'pristine' regions

310 have documented high levels of biomass when compared to regions exposed to

311 anthropogenic impacts and, in particular, prevalent fishing pressure (Friedlander and

312 Demartini 2002; Sandin et al. 2008; Williams et al. 2011). In the central Red Sea, four of

313 the most common top predators and carnivores were all documented in greater abundance

314 on Sudanese reefs along with up to a five-fold increase in biomass levels. The high levels

315 in abundance and biomass of species such as *Lutjanus bohar* are reflective of reefs

316 around the world with lower fishing pressure as these fish groups are the targets of

317 fisheries (Russ and Alcala 1989; Pauly et al. 1998). This also suggests that reefs in Sudan

318 are subjected to lower fishing pressure than those on the Saudi Arabian side.

319   Very little detailed information is available on fishing in the Red Sea. Based on

320 anecdotal evidence from local fish markets, everything that is caught in the Red Sea is

321 kept and sold. Moreover, fishing methods employed (including hook-and-line, gill nets,

322   and traps) are similar in both the Saudi Arabian and Sudanese study regions

323   (Tesfamichael and Pauly 2016). Species easily caught with these standard fishing

324   methods are therefore vulnerable to overfishing. The unique biology of some species,

325   however, may contribute to some of our unexpected observations. For example, we found

326   the abundance of the blackfin barracuda (*Sphyraena qenie*) to be more than 16 times

327   higher in Saudi Arabia compared to Sudan. This species is known to form large, semi-

328   stationary schools of similarly-sized individuals numbering in the hundreds (Lieske and

329   Myers 2004; Froese and Pauly 2016). As evidenced in our abundance estimates, this

330   species is either present in high numbers or entirely absent. In fact, two large schools of *S.*

331   *qenie* from only two reefs in Saudi Arabia are responsible for the entirety of their

332   abundance for the region. It is therefore suggested that differences observed for some

333   species in this study are most likely driven by occurrences of schools rather than solely

334   fishing pressure.

335   While the presence of sharks is often considered synonymous with healthy reef

336   ecosystems, populations of many species around the globe have been devastated in recent

337   decades (Myers and Worm 2003; Robbins et al. 2006; Myers et al. 2007; Sandin et al.

338   2008; Ward-Paige et al. 2010b). Remote regions like Kingman with limited local

339   anthropogenic impacts report UVC-based levels of shark biomass up to 3.3 tonnes

340   hectare^{-1} (Sandin et al. 2008), a value almost twice as great as the mean biomass of all top

341   predators presently recorded for Sudan. Sadly, across all reefs and replicates of this study

342   only four individuals belonging to one species (*Triaenodon obesus*) were recorded within

343   transect boundaries (Mar Mar, Saudi Arabia), and all of these sharks were located under a

344   single *Acropora* table. Several species of sharks (*T. obesus, Carcharinus amblyrhynchos,*

345   *Carcharhinus falciformis, Sphyrna lewini,* and even a single *Rhincodon typus*) were

346   sighted outside transect boundaries or during non-survey portions of dives, but these

347   observations varied greatly in their frequency between the two study regions. Sharks

348   were regularly encountered on Sudanese reefs and were very sparse in Saudi Arabia.

349   These observations corroborate those reported in previous studies for both regions

350   (Hussey et al. 2013; Clarke et al. 2013; Spaet and Berumen 2015) and echo warnings of

351   elasmobranch overexploitation in Saudi Arabia despite a 2008 royal decree prohibiting

352   all shark fishing activities in the country (Jabado et al. 2015; Spaet et al. 2016). Urgent

353   enforcement of this law is needed to avoid ecosystem-wide repercussions of shark

354   removal (Stevens et al. 2000; Baum and Worm 2009; Ferretti et al. 2010; Ruppert et al.

355   2013).

356   Declines in biomass and abundance, along with changes in species composition of

357   reef associated fishes, can be influenced by suitable habitat, prey availability, recruitment,

358   environmental parameters, and direct removal through a variety of fishing methods.

359   While little information exists for specific comparisons, personal observations and

360   communications as well as broad-scale descriptions of biotic (Sheppard and Sheppard

361   1991; Sheppard et al. 1992; DeVantier et al. 2000; Chekchak and Klaus 2013) and abiotic

362   variables (Ngugi et al. 2012; Raitsos et al. 2013) support east-west similarity in the

363   central Red Sea. It therefore seems likely that the observed differences in reef fish

364   communities between Sudan and Saudi Arabia are heavily influenced by human

365   disturbances, particularly exploitation. The high overall and top predator biomass

366   recorded at furthest-offshore Mubarak reef, comparable to that measured on southern

367   Sudanese reefs, lends further evidence that Saudi Arabian reefs are indeed capable of

368   supporting large fish stocks.

369   Quantitative data detailing fishing pressure is limited for both regions; however,

370   this study reveals that for top predators a positive relationship exists between biomass

371   and distance to the closest major fishing port. This supports the theory that extraction by

372   local fishermen is responsible for declines in stocks and concurs with studies in other

373   locations that show a negative association with human population and the distribution of

374   large-bodied fishes (Stallings 2009; Cinner et al. 2012; Williams et al. 2015). While the

375   region as a whole lacks reliable fisheries records, a number of studies support this notion

376   of asymmetrical fishing pressure in the Red Sea (Gladstone 2002; Hariri et al. 2002;

377   Tesfamichael and Pauly 2016). Reports suggest that aggregate traditional fisheries in

378   Saudi Arabia have been overexploited since the early 1990s (Jin et al. 2012;

379   Tesfamichael and Rossing 2012) and Sudan uses their marine resources the least of any

380   Red Sea nation (Tesfamichael and Pitcher 2006; Jin et al. 2012). This has been attributed

381   to Sudan's small and ill-equipped fishing fleet (e.g., lack of ice limits the distance fishing

382   vessels venture) as well as the nation's low consumption of fish, the least of any Red Sea

383   country (Sanders and Morgan 1989). While the fish trade in Sudan is still in a primitive

384   stage (Tesfamichael and Elawad 2012), demand for reef-associated Red Sea products in

385   Saudi Arabia remains high. The disparity in sustainability status between Sudan and

386   Saudi Arabia may extend in general to the entire eastern and western Red Sea

387   (Tesfamichael and Pitcher 2006).

388   If reefs in Sudan are taken as benchmarks for Saudi Arabia, our results suggest

389   that a number of management actions could be taken to restore Saudi Arabian reefs to

390   under-exploited states and to ensure that Sudanese marine resources avoid depletion.

391   Such measures are critical to promote the overall health of these coral reef systems and

392   their resilience in the face of ongoing climate change (Sala 2006; Brand 2009).

393   Enforcement of existing regulations in Saudi Arabia, including the aforementioned royal

394   decree prohibiting shark fishing, would be an important first step. Moreover, new

395   regulations to protect highly-prized top predators (e.g., *L. bohar*) as well as large

396   carnivores (e.g., *Cheilinus undulatus*) and herbivores (e.g., *Scarus* spp.) may be needed.

397   Both species-specific actions (e.g., size restrictions, seasonal closures, moratoriums) and

398   ecosystem-wide approaches should be considered. Although a large number of studies

399   have demonstrated the efficacy of marine protected areas (MPAs) for restoring large

400   predators (e.g., Russ and Alcala 1996; Russ and Alcala 2004; Aburto-Oropeza et al.

401   2011), the recovery of reefs with altered fish composition has been estimated to take up

402   to 60 years (MacNeil et al. 2015). MPA implementation should therefore be considered a

403   high priority in Saudi Arabia's Red Sea management plan. While reefs in Sudan herein

404   appear to be relatively healthy, large MPA creation and enforcement as well as full

405   protection of elasmobranch species should still be considered important for Sudan as

406   exploitation, particularly of sharks, appears to be on the rise (L. Segalini, pers. comm.).

407

416

417 **References**

418   Aburto-Oropeza O, Erisman B, Galland GR, Mascarenas-Osorio I, Sala E, Ezcurra E

419   (2011) Large recovery of fish biomass in a no-take marine reserve. Plos One 6(8):1-

420   7

421   Bates D, Maechler M, Bolker B, Walker S (2015). Fitting linear mixed-effects models

422   using lme4. J Stat Softw 67(1):1-48

423   Baum JK, Worm B (2009) Cascading top-down effects of changing oceanic predator

424   abundances. J Anim Ecol 28:699-714

425   Berumen ML, Hoey AS, Bass WH, Bouwmeester J, Catania D, Cochran JEM, Khalil MT,

426   Miyake S, Mughal MR, Spaet JLY, Saenz-Agudelo P (2013) The status of coral reef

427   ecology research in the Red Sea. Coral Reefs 32(3):1-12

428   Brand F (2009) Critical natural capital revisited: ecological resilience and sustainable

429   development. Ecol Econ 68(3):605-612

430   Burke L, Reytar K, Spalding M, Perry A (2011) Reefs at risk revisited. World Resources

431   Institute, Washington, DC

432   Caldwell ZR, Zgliczynski BJ, Williams GJ, Sandin SA (2016) Reef fish survey

433   techniques: assessing the potential for standardizing methodologies. Plos One

434   11(4):1-14

435   Chekchak T, Klaus R (2013) Toward a sustainable future for the Red Sea coast of Sudan:

436   part 1. Coastal and marine habitats survey. Cousteau Society, New York

437   Cinner JE, Graham NAJ, Huchery C, Macneil MA (2012) Global effects of local human

438   population density and distance to markets on the condition of coral reef fisheries.

439   Conserv Bio 27(3):453-458

440   Clarke CR, Lea JSE, Ormond RFG (2013) Changing relative abundance and behaviour of

441   silky and grey reef sharks baited over 12 years on a Red Sea reef. Mar Freshwater

442   Res 64(10):909-919

443   Clarke KR (1993) Non-parametric multivariate analyses of changes in community

444   structure. Aus J Ecol 18(1):117-143

445   Coker DJ, Wilson SK, Pratchett MS (2014) Importance of live coral habitat for reef

446   fishes. Rev Fish Biol Fish 24(1):89-126

447   Cole AJ, Pratchett MS, Jones GP (2008) Diversity and functional importance of coral-

448   feeding fishes on tropical coral reefs. Fish Fish 9:1-22

449   Demartini EE, Friedlander AM, Sandin SA, Sala E (2008) Differences in fish-assemblage

450   structure between fished and unfished atolls in the northern Line Islands, Central

451   Pacific. Mar Ecol Progr Ser 365:199-215

452   DeVantier L, Turak E, Al-Shaikh K, De'ath G (2000) Coral communities of the central-

453   northern Saudi Arabian Red Sea. Fauna of Arabia 18:23-66

454   DiBattista JD, Roberts MB, Bouwmeester J, Bowen BW, Coker DJ et al (2016) A review

455   of contemporary patterns of endemism for shallow water reef fauna in the Red Sea. J

456   Biogeogr 43(3):423-439

457   Ferretti F, Worm B, Britten GL, Heithaus MR, Lotze HK (2010) Patterns and ecosystem

458   consequences of shark declines in the ocean. Ecol Lett 13:1055-1071

459   Friedlander AM, Caselle JE, Ballesteros E, Brown EK, Turchik A, Sala E (2014) The real

460   bounty: marine biodiversity in the Pitcairn Islands. Plos One 9(6):1-11

461   Friedlander AM, Demartini EE (2002) Contrasts in density, size, and biomass of reef

462   fishes between the northwestern and the main Hawaiian Islands: the effects of

463   fishing down apex predators. Mar Ecol Progr Ser 230:253-264

464   Friedlander AM, Parrish JD (1998) Habitat characteristics affecting fish assemblages on a

465   Hawaiian coral reef. J Exp Mar Biol Ecol 224:1-30

466   Friedlander AM, Sandin SA, Demartini EE, Sala E (2010) Spatial patterns of the

467   structure of reef fish assemblages at a pristine atoll in the central Pacific. Mar Ecol

468   Progr Ser 410:219-231

469   Frisch AJ, Ireland M, Rizzari JR, Lonnstedt O, Magenat KA, Mirbach CE, Hobbs J

470   (2016) Reassessing the trophic role of reef sharks as apex predators on coral reefs.

471   Coral Reefs 35(2):459-472

472   Froese R, Pauly D (2016) FishBase. http://fishbase.org. Accessed 27 January 2017

473   Gladstone W (1996) Unique annual aggregation of longnose parrotfish (Hipposcarus

474   harid) at Farasan Island (Saudi Arabia, Red Sea). Copeia 1996:483-485

475   Gladstone W (2002) Fisheries of the Farasan Islands (Red Sea). In: Bell J (ed) Naga, the

476   WorldFish Center Quarterly, vol 25, no 3-4. WorldFish, Penang, pp 30-34

477   Graham NAJ, McClanahan TR (2013) The last call for marine wilderness? Bioscience

478   63(5):397–402

479   Halpern BS, Walbridge S, Selkoe KA, Kappel CV, Micheli F et al (2008) A global map

480   of human impact on marine ecosystems. Science 319(5865):948-952

481   Hariri KI, Nichols P, Krupp F, Mishrigi S, Barrania A, Ali AF, Kedidi SM (2002) Status

482   of the living marine resources in the Red Sea and Gulf of Aden and their

483   management. Strategic Action Programme for the Red Sea and Gulf of Aden,

484   Regional Organisation for the Conservation of the Environment of the Red Sea and

485   Gulf of Aden (PERSGA). The World Bank, Washington, DC

486 Hobson ES (1991) Trophic relationships of fishes specialized to feed on zooplankters

487   above coral reefs. In: Sale PF (ed) The ecology of fishes on coral reefs. Academic

488   Press, Inc., San Diego, pp 69-95

489 Hussey NE, Stroh N, Klaus R, Chekchak T, Kessel ST (2013) SCUBA diver observations

490   and placard tags to monitor grey reef sharks, *Carcharhinus amblyrhynchos*, at

491   Sha'ab Rumi, the Sudan: assessment and future directions. J Mar Biol Assoc UK

492   93(2):299-308

493 Jabado RW, Al-Ghais SM, Hamza W, Henderson AC, Spaet JLY, Shivji MS, Hanner RH

494   (2015) The trade in sharks and their products in the United Arab Emirates. Biol

495   Conserv 181(C):190-198

496 Jackson JBC (2001) What was natural in the coastal oceans? Proc Natl Acad Sci USA

497   98(10):5411-5418

498 Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW et al (2001) Historical

499   overfishing and the recent collapse of coastal ecosystems. Science 293(5530):629-

500   637

501 Jin D, Kite-Powell H, Hoagland P, Solow A (2012) A bioeconomic analysis of traditional

502   fisheries in the Red Sea. Mar Resour Econ 27(2):137-148

503 Knowlton N, Jackson JBC (2008) Shifting baselines, local impacts, and global change on

504   coral reefs. Plos Biol 6(2):215-220

505 Kürten B, Al-Aidaroos AM, Struck U, Khomayis HS, Gharbawi WY, Sommer U (2014)

506   Influence of environmental gradients on C and N stable isotope ratios in coral reef

507   biota of the Red Sea, Saudi Arabia. J Sea Res 85:379-394

508 Lieske M, Myers R (2004) Coral reef guide Red Sea. Collins, London

509 MacNeil MA, Graham NAJ, Cinner JE, Wilson SK, Williams ID, Maina J, Newman S,

510   Friedlander AM, Jupiter S, Polunin NVC, McClanahan TR (2015) Recovery

511   potential of the world's coral reef fishes. Nature 520:341-344

512 Mapstone BD, Ayling AM (1998) An investigation of optimum methods and unit sizes

513   for the visual estimation of abundances of some coral reef organisms. Great Barrier

514   Reef Marine Park Authority. http://hdl.handle.net/11017/310. Accessed 21 June

515   2016

516 McClenachan L (2009) Documenting loss of large trophy fish from the Florida Keys with

517   historical photographs. Conserv Biol 23(3):636-643

518 Mora C, Aburto-Oropeza O, Bocos AA, Ayotte PM, Banks S et al (2011) Global human

519   footprint on the linkage between biodiversity and ecosystem functioning in reef

520   fishes. Plos Biol 9(4):1-9

521 Munday PL, Jones GP (1998) The ecological implications of small body size among

522   coral-reef fishes. Oceanogr Mar Biol 36:373-411

523 Myers RA, Baum JK, Shepherd TD, Powers SP, Peterson CH (2007) Cascading effects

524   of the loss of apex predatory sharks from a coastal ocean. Science 315(5820):1846-

525   1850

526 Myers RA, Worm B (2003) Rapid worldwide depletion of predatory fish communities.

527   Nature 423:280-283

528 Ngugi DK, Antunes A, Brune A, Stingl U (2012) Biogeography of pelagic

529   bacterioplankton across an antagonistic temperature-salinity gradient in the Red Sea.

530   Mol Ecol 21(2):388-405

531   Ormond RFG, Edwards AJ (1987) Red sea fishes. In: Edwards AJ, Heads SM (eds) Key

532   environments: Red Sea. Pergamon Press, Oxford, pp 251-287

533   Pandolfi JM, Bradbury RH, Sala E, Hughes TP, Bjorndal KA, Cooke RG, McArdle D,

534   McClenachan L, Newman MJH, Paredes G, Warner RR, Jackson JBC (2003) Global

535   trajectories of the long-term decline of coral reef ecosystems. Science

536   301(5635):955-958

537   Pauly D (1995) Anecdotes and the shifting baseline syndrome of fisheries. Trends Ecol

538   and Evol 10(10):430

539   Pauly D, Christensen V, Dalsgaard J, Froese R, Torres F Jr (1998) Fishing Down Marine

540   Food Webs. Science 279(5352):860-863

541   Price ARG, Ghazi SJ, Tkaczynski PJ, Venkatachalam AJ, Santillan A, Pancho T,

542   Metcalfe R, Saunders J (2014) Shifting environmental baselines in the Red Sea. Mar

543   Poll Bull 78(1-2):96-101

544   R Core Team (2016) R: a language and environment for statistical computer. R

545   Foundation for Statistical Computing. http://www.R-project.org/. Accessed 21 June

546   2016

547   Raitsos DE, Pradhan Y, Brewin RJW, Stenchikov G, Hoteit I (2013) Remote sensing the

548   phytoplankton seasonal succession of the Red Sea. Plos One 8(6):1-9

549   Robbins WD, Hisano M, Connolly SR, Choat JH (2006) Ongoing collapse of coral-reef

550   shark populations. Curr Biol 16(23):2314-2319

551   Roberts MB, Jones GP, McCormick MI, Munday PL, Neale S, Thorrold S, Robitzch

552   VSN, Berumen ML (2015) Homogeneity of coral reef communities across 8 degrees

553   of latitude in the Saudi Arabian Red Sea. Mar Poll Bull 105(2):558-565

554 Roff G, Doropoulos D, Rogers A, Bozec Y, Krueck NC, Aurellado E, Priest M, Birrell C,

555   Mumby PJ (2016) The ecological role of sharks on coral reefs. Trends Ecol Evol

556   31(5):395-407

557 Ruppert JLW, Travers MJ, Smith LL, Fortin M, Meekan MG (2013) Caught in the

558   middle: combined impacts of shark removal and coral loss on the fish communities

559   of coral reefs. Plos One 8(9):1-9

560 Russ GR, Alcala AC (1989) Effects of intense fishing pressure on an assemblage of coral

561   reef fishes. Mar Ecol Progr Ser 56:13-27

562 Russ GR, Alcala AC (1996) Marine reserves: rates and patterns of recovery and decline

563   of large predatory fish. Ecol Appl 6(3):947-961

564 Russ GR, Alcala AC (2004) Marine reserves: long-term protection is required for full

565   recovery of predatory fish populations. Oecologia 138(4)622-627

566 Ruttenberg BI, Hamilton SL, Walsh SM, Donovan MK, Friedlander AM, Demartini EE,

567   Sala E, Sandin SA (2011) Predator-induced demographic shifts in coral reef fish

568   assemblages. Plos One 6(6):1-9

569 Sala E (2006) Top predators provide insurance against climate change. Trends Ecol Evol

570   21(9):479-480

571 Sanders MJ, Morgan GR (1989) Review of the fisheries resources of the Red Sea and

572   Gulf of Aden. FAO, Rome

573 Sanderson EW, Jaiteh M, Levy MA, Redford KH, Wannebo AV, Woolmer G (2002) The

574   human footprint and the last of the wild. Bioscience 52(10):891-904

575   Sandin SA, Smith JE, Demartini EE, Dinsdale EA, Donner SD et al (2008) Baselines and

576   degradation of coral reefs in the Northern Line Islands. Plos One 3(2):1-11

577   Sandin SA, Williams I (2010) Trophic classifications of reef fishes from the tropical U.S.

578   Pacific (Version 1.0). Scripps Institution of Oceongraphy Technical Report.

579   http://escholarship.org/uc/item/5394f7m3. Accessed 21 June 2016

580   Sheppard CRC, Price ARG, Roberts CM (1992) Marine ecology of the Arabian region.

581   Academic Press, San Diego

582   Sheppard CRC, Sheppard ALS (1991) Corals and coral communities of Arabia. In:

583   Buttiker W, Krupp F (eds) Fauna of Saudi Arabia, vol 12. National Commission for

584   Wildlife Conservation and Development, Riyadh, pp 3-170

585   Spaet JLY (2013) Predictable annual aggregation of longnose parrotfish (Hipposcarus

586   harid) in the Red Sea. Marin Biodivers 43(3):179-180

587   Spaet JLY, Berumen ML (2015) Fish market surveys indicate unsustainable

588   elasmobranch fisheries in the Saudi Arabian Red Sea. Fish Res 161:356–64

589   Spaet JLY, Nanninga GB, Berumen ML (2016) Ongoing decline of shark populations in

590   the eastern Red Sea. Biol Conserv 201:20-28

591   Stallings CD (2009) Fishery-independent data reveal negative effect of human population

592   density on Caribbean predatory fish communities. Plos One 4(5):1-9

593   Stehli FG, Wells JW (1971) Diversity and age patterns in hermatypic corals. Syst Biol

594   20(2):115-126

595   Stevens JD, Bonfil R, Dulvy NK, Walker PA (2000) The effects of fishing on sharks,

596   rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems.

597   J Mar Sci 57(3):476-494

598   Stevenson C, Katz LS, Micheli F, Block B, Heiman KW, Perle C, Weng K, Dunbar R,

599   Witting J (2007) High apex predator biomass on remote Pacific islands. Coral Reefs

600   26(1):47-51

601   Tesfamichael D, Elawad AN (2012) Reconstructing Red Sea fisheries of Sudan: foreign

602   aid and fisheries. In: Tesfamichael D, Pauly D (eds) Catch reconstruction for the

603   Red Sea large marine ecosystem by countries (1950-2010). Fisheries Centre

604   Research Reports, Vancouver, pp 51-70

605   Tesfamichael D, Pauly D (2016) The Red Sea Ecosystem and Fisheries. Springer, New

606   York

607   Tesfamichael D, Pitcher TJ (2006) Multidisciplinary evalution of the sustainability of

608   Red Sea fisheries using Rapfish. Fish Res 78(2-3):227-235

609   Tesfamichael D, Rossing P (2012) Reconstructing Red Sea fisheries catches of Saudi

610   Arabia: national wealth and fisheries transformation. In: Tesfamichael D, Pauly D

611   (eds) Catch reconstruction for the Red Sea large marine ecosystem by countries

612   (1950-2010). Fisheries Centre Research Reports, Vancouver, pp 153-178

613   Walsh SM, Hamilton SL, Ruttenberg BI, Donovan MK, Sandin SA (2012) Fishing top

614   predators indirectly affects condition and reproduction in a reef-fish community. J

615   Fish Biol 80(3):519–537

616   Ward-Paige CA, Flemming JM, Lotze HK (2010a) Overestimating fish counts by non-

617   instantaneous visual censuses: consequences for population and community

618   descriptions. Plos One 5(7):1-9

619   Ward-Paige CA, Mora C, Lotze HK, Pattengill-Semmens C, McClenachan L, Arias-

620   Castro E, Myers RA (2010b) Large-scale absence of sharks on reefs in the greater-

621   Caribbean: a footprint of human pressures. Plos One 5(8):1-10

622   Williams GJ, Gove JM, Eynaud Y, Zgliczynski BJ, Sandin SA (2015) Local human

623   impacts decouple natural biophysical relationships on Pacific coral reefs. Ecography

624   38(8):751-761

625   Williams ID, Richards BL, Sandin SA, Baum JK, Schroeder RE, Nadon MO, Zgliczynski

626   BJ, Craig P, McIlwain JL, Brainard RE (2011) Differences in reef fish assemblages

627   between populated and remote reefs spanning multiple archipelagos across the

628   central and western Pacific. J Mar Biol 2011:1-14

629

630   **Figure captions**

631

632   **Fig. 1.** Map of the central Red Sea showing locations of surveyed reefs. Insert illustrates

633   the location of surveyed reefs with respect to the Red Sea. Identifying numbers in red (1-

634   16) represent sites in Sudan. Identifying numbers in green (1-14) represent sites in Saudi

635   Arabia. See Appendix A for complete site details.

636

637   **Fig. 2.** nMDS illustrating all reefs in 2-dimentinal space based on fish abundance data

638   associated with each reef from Saudi Arabia (green) and Sudan (red).

639

640   **Fig. 3.** Average biomass (tonnes hectare $^{-1}$ ±SE) for each trophic group for each reef

641   surveyed in Saudi Arabia and Sudan. Reefs are organized latitudinal from north (left) to

642   south (right) for both regions.

643

644   **Fig. 4.** Grand mean biomass of the top four taxa by weight of each trophic guild in Sudan

645   (red) and corresponding values for these taxa in Saudi Arabia (green). a = top predators, b

646   = carnivores, c = herbivores, d = planktivores. Error bars are standard error of the mean.

647

648   **Fig. 5.** Relationship between biomass (tonnes hectares^{-1}) for each trophic group and

649   distance (km) from the nearest major fishing port. Data points represent each reef from

650   Saudi Arabia and Sudan.

651

652   **Fig. 6**. Mean body size class frequency for each trophic guild in Saudi Arabia and Sudan.

653   Error bars are standard error of the mean.

654 **Tables**

655

656 **Table 1.** Average (per transect ± SE) reef fish community indices for Saudi Arabia and

657 Sudan.

Region	Abundance	Richness	Evenness	Diversity
Saudi Arabia	543 ±39	27 ±0.6	0.46 ±0.02	1.52 ±0.07
Sudan	885 ±100	33 ±1.8	0.47 ±0.03	1.64 ±0.13

658

659

660   **Table 2.** Species that contributed >90% of the observed differences between Saudi

661   Arabia and Sudan fish communities (SIMPER analysis). Shading illustrates a higher

662   average abundance in Sudan than Saudi Arabia

Species	Trophic Guild	Saudi Arabia Av.Abund	Sudan Av.Abund	Av.Diss	Diss/SD	Contrib%	Cu
Pseudanthias squamipinnis	Planktivore	196.07	408.42	18.39	1.43	35.99	35
Chromis dimidiata	Planktivore	171.19	198.65	8.66	1.27	16.94	52
Caesio lunaris	Planktivore	46.19	5.66	3.19	1.1	6.24	59
Chromis flavaxilla	Planktivore	9.76	37.33	2.06	1.08	4.03	63
Naso hexacanthus	Planktivore	24.85	22.24	1.78	1.09	3.49	66
Caesio suevica	Planktivore	26.79	4.28	1.75	0.57	3.42	70
Naso unicornis	Herbivore	2.29	18.31	1.34	0.76	2.63	72
Caesio striata	Planktivore	9.54	3.13	0.8	0.61	1.57	74
Macolor niger	Planktivore	4.18	10.47	0.77	0.82	1.5	75
Lutjanus bohar	Top Predator	1	9.94	0.71	0.79	1.39	77
Sphyraena qenie	Top Predator	11.46	0.69	0.67	0.32	1.31	78
Caranx sexfasciatus	Top Predator	1.64	7.19	0.51	0.76	1	79
Chromis pembae	Planktivore	5.4	2.88	0.48	0.7	0.93	80
Kyphosus cinerascens	Herbivore	4.39	2.97	0.45	0.66	0.88	81
Lutjanus ehrenbergii	Carnivore	1.63	5	0.45	0.51	0.88	82
Naso elegans	Herbivore	2.14	5.34	0.39	0.46	0.76	82
Lutjanus kasmira	Carnivore	3.01	4	0.39	0.54	0.76	83
Carangoides bajad	Top Predator	2.21	4.9	0.37	0.52	0.72	84
Ctenochaetus striatus	Herbivore	6.98	7.21	0.33	1.24	0.65	85
Cephalopholis miniata	Carnivore	3.79	7.21	0.33	1.31	0.64	85
Abudefduf vaigiensis	Planktivore	0	3.94	0.27	0.59	0.54	86
Acanthurus gahhm	Herbivore	3.15	2.91	0.24	0.78	0.47	86
Plectorhinchus gaterinus	Carnivore	0.21	3.81	0.23	0.43	0.46	87
Monotaxis grandoculis	Carnivore	3.33	1.66	0.23	0.88	0.46	87
Caranx melampygus	Top Predator	1.04	3.96	0.21	0.79	0.42	88
Chromis viridis	Planktivore	0	3	0.2	0.32	0.39	88
Lutjanus gibbus	Carnivore	0.36	2.72	0.19	0.41	0.38	88
Odonus niger	Planktivore	0.5	2.41	0.17	0.65	0.34	89
Plectroglyphidodon lacrymatus	Planktivore	1.44	1.53	0.17	0.86	0.33	89
Acanthurus nigrofuscus	Herbivore	1.11	2.88	0.16	0.94	0.32	89
Pomacentrus sulfureus	Planktivore	1	2.16	0.15	0.86	0.3	90

663

664

665   **Table 3.** Comparison of biomass density (tons hectare^{-1}), numerical density (number

666   hectare^{-1}), and mean weight of individuals (g) between surveyed reefs in Sudan and Saudi

667   Arabia. Values are grand means (± SE). n = 16 for Sudan and n = 14 for Saudi Arabia.

	Sudan	Saudi Arabia
Biomass		
Top predator	1.76 (0.42)	0.61 (0.30)
Carnivore	0.69 (0.12)	0.29 (0.04)
Planktivore	1.78 (0.43)	2.81 (0.69)
Herbivore	0.78 (0.15)	0.37 (0.06)
Number		
Top predator	1296 (245)	445 (224)
Carnivore	4120 (574)	2587 (232)
Planktivore	64027 (7241)	42535 (3508)
Herbivore	5002 (2259)	1854 (257)
Mean Weight		
Top Predator	1321 (173)	1597 (290)
Carnivore	171 (20)	116 (12)
Planktivore	27 (5)	78 (26)
Herbivore	259 (45)	220 (32)

668
669