1   **Depth and habitat are important drivers of abundance for predatory**
2   **reef fish off Pemba Island, Tanzania**
3
4   Authors: Kennedy E. Osuka[1,2], Bryce D. Stewart[1], Melita Samoilys[2], Colin J. McClean[1], Peter
5   Musembi[2], Saleh Yahya[3], Ali R. Hamad[4] and James Mbugua[2]
6   Affiliations
7   [1.] Department of Environment and Geography, University of York, Heslington, York, YO10 5NG,
8   United Kingdom
9   [2.] Coastal Oceans Research and Development – Indian Ocean (CORDIO East Africa). 9 Kibaki
10 Flats P.O. Box 10135-80101, Mombasa, Kenya
11 [3.]Institute of Marine Sciences, University of Dar es Salaam, Zanzibar, Tanzania
12 [4.] Department of Fisheries Development, Zanzibar-Tanzania
13
14 * Corresponding author.
15 E-mail address: koe503@york.ac.uk (K.E. Osuka).
16

Abstract

Coral reefs across the world face significant threats from fishing and climate change, which tends to be most acute in shallower waters. This is the case off Pemba Island, Tanzania, yet the effects of these anthropogenic stressors on the distribution and abundance of economically and ecologically important predatory reef fish, including how they vary with depth and habitat type, is poorly understood. Thus, we deployed 79 baited remote underwater video stations (BRUVs) in variable water depths and habitats off Pemba Island, and modelled the effects of depth and habitat on abundance of predatory reef fish. Predatory reef fish types/taxa were significantly predicted by depth and habitat types. Habitats in relatively deeper waters and dominated by hard and soft corals hosted high species richness and abundance of predatory reef fish types/taxa compared to mixed sandy and rubble habitats. The findings add to the growing evidence that deep waters around coral reefs are important habitats for predatory reef fish. Thus, careful management, through effective area and species protection measures, are needed to prevent further depletion of predatory reef-associated populations and conservation of this biologically important area.

Keywords: Coral reefs, depth refugia, habitat effects, predation, movement behaviour, fisheries, conservation

Introduction

Coral reef predatory fishes - fish that feed on other fish or marine animals - have profound economic and ecological importance (Moberg and Folke, 1999; Hammerschlag *et al.*, 2019). They are an important source of animal protein and contribute significantly to the livelihoods of more than 20 million people living in close proximity to the eastern African coast (Bell *et al.*, 2016). Their large body size makes them desirable and a relatively easy target, but the late maturation and longevity of many species makes them more susceptible to overfishing (de Mitcheson *et al.*, 2020). Fishing pressure on large reef predators has increased significantly in recent decades, causing major declines in many areas around the world (Worm *et al.*, 2013). Overfishing of predatory fish populations can have severe ecological impacts as it often destabilizes food webs leading to community-wide impacts (Bascompte et al., 2005; Worm *et al.*, 2013; Hussey *et al.*, 2014; Sandin and Zgliczynski, 2015). Reef predators structure reef fish communities by directly exerting top-down control of prey organisms (Stewart and Jones, 2001; Baum and Worm, 2009), and indirectly by influencing the behavior of prey assemblages while searching for food (Hixon, 2015; Rasher et al., 2017) or when resting and mating as part of their life history (Green *et al.*, 2015). The role of predatory fishes is therefore multi-faceted, extending from the oceans to the coastal communities.

Predatory fish show preferences for particular habitat types such as forereef ledges (Papastamatiou *et al.*, 2009), outer atolls and shelf areas (Cappo et al., 2007; Skinner *et al.*, 2020) that are associated with abrupt changes in depth. Such habitats are characterised by increased depth that can provide refuge to a wide variety of reef predator populations (Tyler *et al.*, 2009; Stefanoudis *et al.*, 2019). These outer deeper reef habitats or contiguous to deep are nutrient rich hence attract a high abundance of schooling planktivorous species, which are an important food item for the highly mobile predators (Wyatt *et al.*, 2013). Thus, abundance, biomass and diversity of predators often increases from shallower lagoon reefs to deeper seaward reefs (Jennings et al., 1996; Pinheiro *et al.*, 2016). Shallower areas are more vulnerable to climate-induced coral bleaching (Graham et al., 2013; Obura et al., 2017), which can lead to coral mortality and loss of structural complexity. This in turn can cause declines in the prey that predatory reef fish generally consume (Hempson et al., 2017). Recovery of such reefs after bleaching is generally greatest where reefs are structurally complex and in deeper waters (Graham et al., 2015). However, the cover of live coral also declines below a certain depth, due to light limitation (Kahng et al., 2019; Osuka et al, 2021a). Interactions between different predator types (e.g., schooling transient and resident predators) with habitat types and their associated depths remains unclear (Hixon, 2015). Fishing pressure is usually highest

in shallow coral reef areas and can amplify the depth-predator pattern (Tyler *et al.*, 2009). Increasing water depth is anticipated to have positive and negative relationships with abundance of fish predators and fishing pressure, respectively (Tyler *et al.*, 2009; Pinheiro *et al.*, 2016; Stefanoudis *et al.*, 2019). Therefore, the depth distribution of predatory reef fish will be governed by the combined influences of habitat structure, food availability and fishing disturbance, and how they interact with one another.

One area that is thought to support high numbers of predatory coral reef fish, but that is also under pressure from fishing, is the Pemba channel off the coast of Tanzania. The western margins of Pemba Island neighbors a deep channel that averages 300 m and reaches a maximum of 800 m, making the Island a true oceanic Island (Semba et al., 2019). The shallow (<20 m) marine areas of Pemba Island have highly variable coral reef conditions, with some in healthy states with a high cover of hard coral, while others are in degraded states with low hard coral cover (Grimsditch et al., 2009). Reefs with low coral cover have been linked to destructive fishing activities particularly dynamite fishing (Grimsditch *et al.*, 2009; Wells *et al.*, 2010; Slade and Kalangahe, 2015). The mesophotic reef areas (30-150 m) are characterised by ledges, and oceanic steep outer reef slopes forming "staircase" walls in some locations (Osuka *et al.*, 2021a). These seafloor features, together with a deep channel and the remoteness of the island, makes Pemba Island a potential hotspot for large reef predators. Yet, little is understood of the influence of depth and habitat on fish predators in this area.

The Pemba Island fishery is mainly artisanal involving the use of traditional gears (e.g. gillnets, hook and line) and introduced gears (e.g. small purse seines) to target coral associated fish (Rehren et al., 2020). Evidence of overfishing has been reported at several sites. Indeed, a study conducted a decade ago in waters <21 m recorded no sharks, implying high rates of overfishing (Grimsditch *et al.*, 2009). Similarly, other large predatory taxa like groupers and snappers were either rare or of small size. In recent times, surveys on apex predators in Tanzanian waters (western margins of Pemba Channel) suggest that shark populations are "functionally extinct" (MacNeil *et al.*, 2020). Further, biomass projections of commercial species including large reef-associated predators in the Tanzanian Exclusive Economic Zone predict declines of up to 56-69% under increased fishing scenarios by the end of the 21st Century (Wilson et al., 2021). The decline in large reef-associated predator stocks is considered a key driver motivating fishers' migration to other distant fishing grounds as far as Mozambique and Kenya, where depletion of fish stocks has been reported in the host fishing grounds (Wanyonyi *et al.*, 2016).

4

107 Sampling of coral reef fish communities in areas that are inaccessible or challenging for SCUBA

108 divers was traditionally done with traps or nets (Collin, 1990; Bacheler et al., 2017). However,

109 an increasingly popular method is the use of baited remote underwater videos (BRUVs).

110 BRUVs are considered a non-invasive and non-destructive technique, which has been applied

111 to assess occurrences of larger and more mobile species (Harvey *et al.*, 2012; White *et al.*,

112 2013). The method has been widely applied over extensive geographic areas, depth ranges

113 and habitats (Harvey *et al.*, 2013; MacNeil *et al.*, 2020). Surveys with BRUVs ensure fish are

114 not disturbed by divers, species are likely attracted from larger areas by the bait, and a

115 permanent record is produced. Use of BRUVS enhances species ID and allows more detailed

116 analysis of the surrounding habitats and more importantly can be deployed much deeper than

117 SCUBA (Harvey *et al.*, 2012).

118

119 Coral reef communities show clear spatial patterns that vary across a range of fine-scale local

120 habitat conditions (Karisa et al., 2020). The outer reefs of Pemba Island have been little

121 surveyed to date, likely due to logistical challenges associated with sampling deeper reefs with

122 standard SCUBA underwater visual censuses. Indeed, previous ecological fish surveys

123 conducted in Pemba Island were restricted to depths <21m and conducted either on SCUBA

124 (e.g., Daniels et al., 2003; Grimsditch et al., 2009) or snorkel (e.g., Jones et al., 2019). The

125 results from these studies lacked consensus on the diversity of reef predators. Therefore, we

126 considered that BRUVs would be ideal for providing a more complete picture of the predatory

127 reef fish community in this area.

128

129 This study aimed to examine key environmental characteristics that may be driving the

130 abundance, distribution and diversity of predatory reef fish populations around Pemba Island.

131 We hypothesized that predatory reef fish would be more confined to deeper than shallower

132 reefs and would show significant relationships with healthy habitats dominated by hard

133 corals. Further, habitat type (e.g., live coral vs rubble) were expected to be stronger predictors

134 of the occurrence, abundance and diversity of resident predatory species (i.e., those showing

135 strong association with the reef structure), rather than transient species (i.e., schooling and

136 epipelagic species).

137

138 **Materials and methods**

139 *Study site*

140 The survey was conducted on the outer reefs of the western margins of Pemba Island (Figure

141 1). Reefs selected for sampling corresponded in part with previous surveys conducted in the

5

142   Greater Pemba Channel within the Pemba Community Conservation Area (PECCA) using
143   SCUBA (Grimsditch *et al.*, 2009; Gudka et al., *in prep*) and autonomous underwater vehicles -
144   AUV (Osuka *et al.*, 2021a). Sites were chosen to be representative of different reef habitats
145   and on the basis of depth (5-47 m) using a real-time depth echo sounder (Figure 1). Stations
146   were largely fore reefs on the western margins of Pemba Island spanning from reefs in the
147   north to the south (Figure 1). The BRUV stations occurring in continuous reef and separated
148   to the next set of stations by a reef pass were pooled together to form a 'sector'. This resulted
149   in three sectors conveniently named as north, central and south. The north and central sectors
150   were separated by a deep channel called the Fundo Gap (Figure 1). Similarly, the central and
151   south sectors were separated by a channel north of Misali Island (Figure 1). The survey was
152   conducted in November 2019 over a five-day period during daytime hours.

153

154   Each sampling involved deployment of a mono-BRUV unit consisting of a video GoPro Hero4
155   camera Silver fixed on a stainless-steel frame, which was attached to a 1.65 m conduit pipe in
156   the field of view of the camera (Appendix 1). A meshed bait bag was mounted on the pipe and
157   filled with bait of ca. 1 kg composed of oily fish from the families Scombridae and Carangidae.
158   The bait was cut into small pieces, which was filled into the bait bags. The BRUV unit was tied
159   with a rope to the top of the frame to facilitate deployment and a buoy on the other end to
160   enable detection and retrieval.

161
162   Each BRUV system was assembled and deployed following the Standard Operating Procedure
163   described in Langlois et al. (2020). The first BRUV unit was deployed close to preset GPS
164   coordinates while subsequent deployments were done approximately 500 m away but along
165   the reef. This distance was selected to minimize the chances of the same fish individuals being
166   documented on neighboring BRUV deployments. If there was insufficient reef in an area to
167   allow this spacing, re-sampling was done at an interval of ~ 250 m but on a different day. The
168   deployment points were geo-referenced using a handheld Global Positioning System (GPS).
169   The time of deployment, depth, visibility, cloud cover, tidal state, currents and GPS readings
170   were recorded during the deployment. Each BRUV unit was retrieved after at least 1-hour of
171   recording.

172

Figure 1: Map showing location of 79 baited remote underwater video (BRUV) stations in Pemba Island deployed in three sectors north, central and south.

Video footage processing

After the BRUV unit was retrieved, visibility, field of view, profile and percentage cover of habitat/substrate types (hard coral, soft coral, sea fans, halimeda, sponges, fleshy and turf algae, rubble and sand) was visually estimated for each video recording. Fish species

182 identification from the video footage focused solely on predatory fish from 14 families at
183 normal play speed. These were: Aulostomidae (trumpetfish), Carangidae (jacks),
184 Carcharhinidae (sharks), Congridae (conger eels), Dasyatidae (whiptail stingrays), Haemulidae
185 (sweetlips), Fistulariidae (cornetfish), Lethrinidae (emperors), Lutjanidae (snappers),
186 Muraenidae (moray eels), Myliobatidae (eagle rays), Scombridae (mackerel), Epinephelidae
187 (groupers), and Sphyraerinidae (barracuda) (Appendix 2). Wherever video footage of
188 individuals was unclear the genus or family was used. Two researchers (KO, PM) reviewed
189 species identification to ensure accuracy. Species identification was done using Lieske and
190 Myers, (1994) and Taquet and Diringer, (2012) and confirmed using Eschmeyer's Catalog of
191 Fishes (Fricke et al., 2021). Species observed were classified according to their association
192 with the reef as either resident or transient (Hixon, 2015; Froese and Pauly, 2020). Resident
193 predators were species showing strong association with the reef structure or seafloor such as
194 groupers, snappers, emperors, sweetlips and eels. Transient predators were fast swimming,
195 schooling and epipelagic species, such as sharks, barracuda, jacks and mackerel (Appendix 2).
196 The conservation status of each species was derived from the International Union for
197 Conservation of Nature (IUCN) Red List website (IUCN, 2021).
198
199 *Data analysis*
200 The maximum number of individuals (MaxN) of each species of predatory reef fish observed
201 at one time from each video with a recording time of 1-hour was quantified. These data were
202 used to derive a summary of the number of individuals and species per reef sector, and a
203 rarefaction curve based on the cumulative number of BRUV deployments (Hammer et al.,
204 2001).
205
206 Nonmetric multidimensional scaling (nMDS) based on Bray–Curtis similarity (Clarke and
207 Warwick 2001), was performed on square root transformed MaxN data (Supplementary
208 material Figure S1) to graphically assess patterns in abundance of reef predators across the
209 three geographic sectors. A one-way SIMPER analysis was used to identify species that
210 contributed the most towards dissimilarity of the sectors.
211
212 Principal components analysis (PCA) was applied to benthic variables to determine key
213 variables contributing greatest to the variation. The loading of the first component was used
214 to differentiate BRUVs stations into two major habitat types: hard coral and soft coral *versus*
215 sand and rubble. An ordinary least squares regression of the first component loadings and
216 depth was thereafter conducted to determine the relationship of habitat variables with depth.

217

218   Three predictor variables of fish abundance: sector, habitat and depths were modeled (Table

219   1) using zero-inflated Poisson (ZIP) model. Generalised linear model (GLM) and zero-inflated

220   Poisson (ZIP) model outputs were first compared using Vuong Non-Nested Hypothesis Test-

221   Statistic (Vuong, 1989; Long and Long, 1997). The test showed ZIP was better than the

222   standard Poisson model. Therefore, ZIP was fitted to MaxN data on pooled predators, resident

223   predators, transient predators, species richness, fish family and species. The ZIP model had

224   two parts: a Poisson regression model to model fish count (MaxN) using predictor variables

225   of Depth and Habitat; and the logit model for predicting the probability of excess zeros in

226   random variables of Sector. The logit model provided the basis for uncovering the excessive

227   absence of reef predators in a sector, an indication of overfishing. To help with the

228   interpretation of the results we assessed the interaction effects between depth and habitat

229   type using GLM.

230

231

232   Table 1. Predictors used in the analysis of predatory fish taxa

Predictor	Abbreviation	Data type	Description
Habitat	Hab	Categorical	Two major habitat-types identified from PCA i.e. Sand and Rubble (SA_RU) and Hard coral and Soft coral (HC_SC).
Sector	Sec	Categorical	Three sectors separated by reef passes i.e. North, Central and South
Depth	Dep	Continuous	Station depth in metres

233

234

235   **Results**

236   *Predatory reef fish abundance and taxonomic richness*

237   A total of 5,767 individuals from 71 species and 14 families were recorded, with 83% of the

238   species occurring in depths > 20 m (Appendix 2). Overall, a majority (89%) of the species

239   sampled were in the Least Concern category under the IUCN Red List of species. Only two

240   species (< 3% of the total) the sky emperor *Lethrinus mahsena* and honeycomb stingray

241   *Himantura uarnak*, were classified as Endangered. Vulnerable species accounted for 4% and

242   included the silvertip shark *Carcharhinus albimarginatus,* spotted eagle ray *Aetobatus*

243   *ocellatus,* brown-marbled grouper *Epinephelus fuscoguttatus*, while only one Near

244   Threatened species, the narrow-barred Spanish mackerel *Scomberomorus commerson* was

245 observed. Two species assessed as Data Deficient were also recorded – Indian mackerel

246 *Rastrelliger kanagurta* and Kuhl's maskray *Neotrygon kuhlii.*

247

248 The species rarefaction curve of the cumulative number of BRUV deployments showed that

249 the curve was flattening suggesting that the predatory reef fish community had been

250 relatively well sampled overall (Figure 2). However, the southern sector was least sampled

251 yielding fewer species compared to the northern and central sectors. The total number of

252 species encountered in the northern and central sectors were 54 and 42 species, respectively,

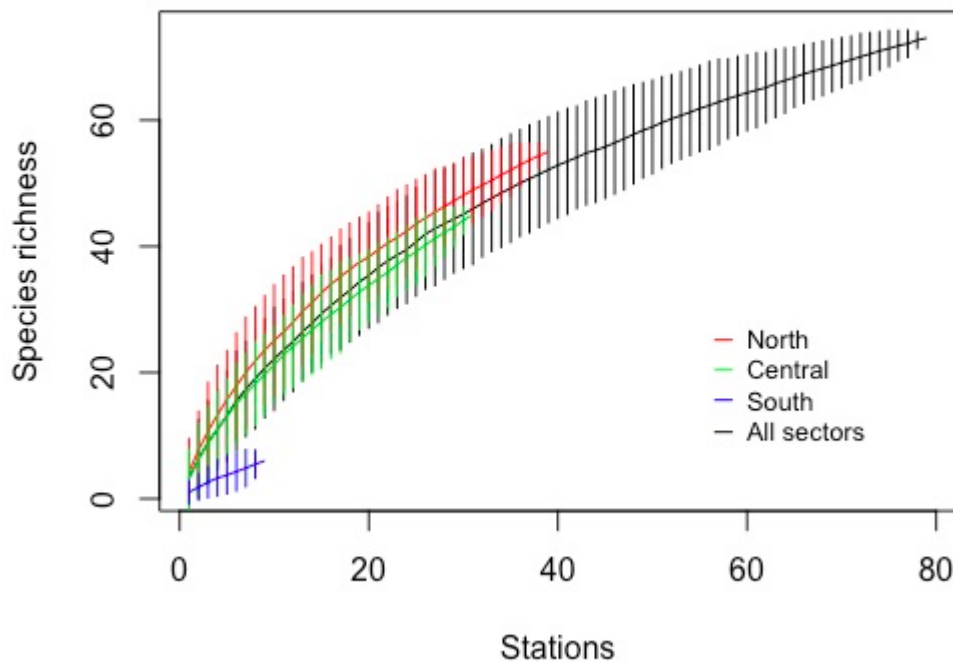253 compared to six in the southern sector.

254

255
256 Figure 2: Species rarefaction curve with their 95% confidence interval separated by sectors:

257 north - red, central - green, south - blue and all sectors - black.

258
259 The mean fish abundance (MaxN) showed no significant differences across the sectors

260 (ANOVA, F = 0.494; p = 0.612), although relatively higher values were found in the northern

261 (8.87 ± 1.49 (se)) and central (9.90 ± 2.98 (se)) sectors compared to the southern sector (5.11

262 ± 3.30 (se)). Proportion of zero counts for species encountered during the survey across three

263 sectors showed predators were more encountered in the north than the central and the south

264 (Figure 3). Resident predators were more encountered in the north and central sectors while

265 transient predators occurred more in the north sector (Figure 3).
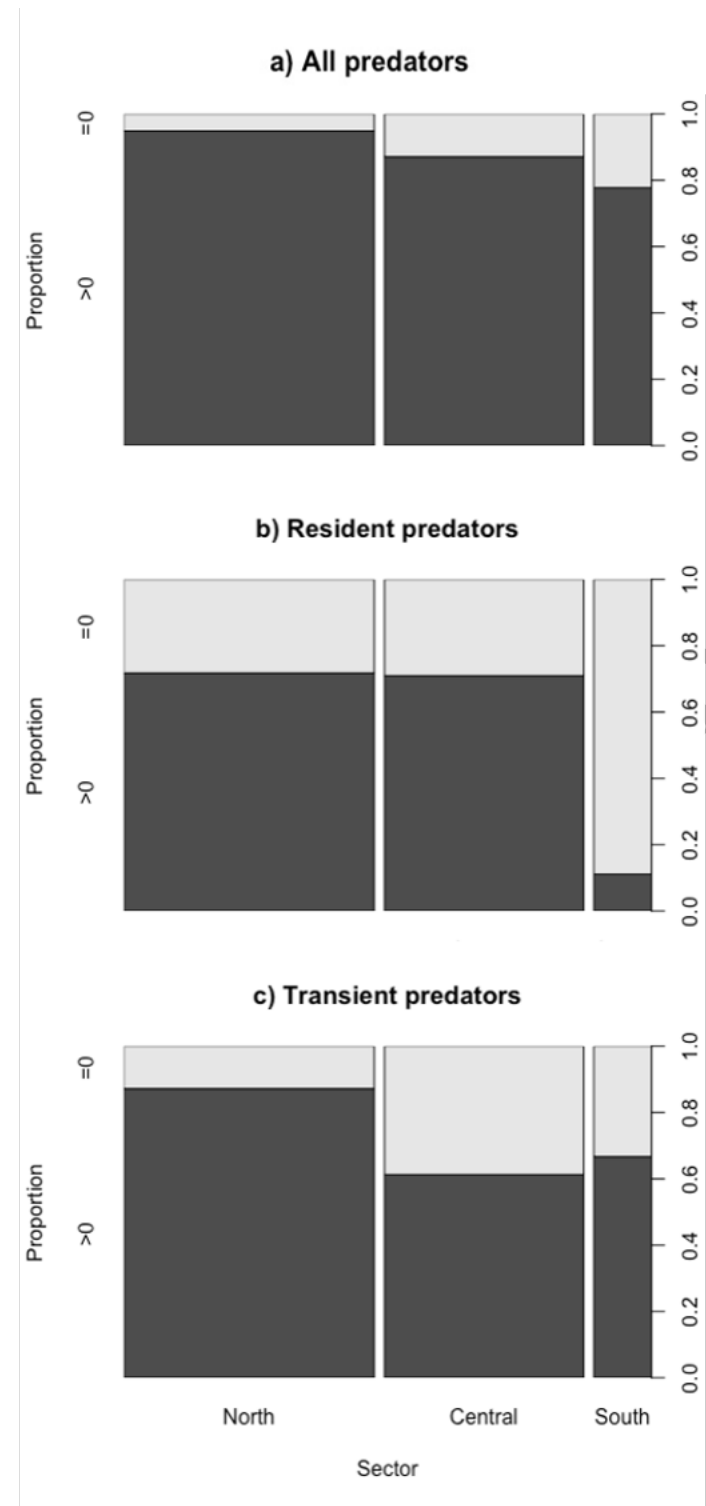

266

267 Figure 3: Proportion of zero counts (light shadings) across three sectors for all predators (a),

268 resident predators (b), and transient predators (c). The widths of the bars show the number

269 of BRUVS per sector North n = 39, Central n = 31 and South n = 9.

270

271

Predator community structure

273 SIMPER analysis revealed that dissimilarity in predatory reef fish between the sectors was

274 generally high (> 90%). The greatest dissimilarity was between North and South (Average

275 dissimilarity = 96.2%) driven by snubnose pompano *Trachinotus blochii,* small-toothed jobfish

276 *Aphareus furca,* green jobfish *Aprion virescens* and Chinese trumpetfish *Aulostomous*

277 *chinensis* (Table 2).

278

279 Table 2: Results of one-way SIMPER analyses of species contributing more than 5% of the

280 dissimilarity in abundance (%) in the three sectors of Pemba Island – North, Central and South.

281 Species are classified according to their association with the reef as either resident (R) or

282 transient (T).

Species	Average abundance		Average dissimilarity	Contribution (%)
Average dissimilarity = 93.2	North	Central		
Aprion virescens (T)	1.3	0.1	8.6	9.3
Aulostomous chinensis (T)	0.6	0.5	6.7	7.2
Lethrinus olivaceus (R)	0.3	0.8	6.3	6.8
Aphareus furca (T)	0.8	0.4	5.9	6.4
Cephalopholis argus (R)	0.2	0.7	5.0	5.4
Average dissimilarity = 94.5	South	Central		
Aphareus furca (T)	1.1	0.4	14.5	15.3
Trachinotus blochii (T)	3.3	0.0	13.3	14.1
Aulostomous chinensis (T)	0.1	0.5	6.4	6.8
Cephalopholis argus (R)	0.0	0.7	6.2	6.6
Lethrinus olivaceus (R)	0.0	0.8	5.8	6.1
Average dissimilarity = 96.2	North	South		
Trachinotus blochii (T)	0.0	3.3	12.5	13.0
Aphareus furca (T)	0.8	1.1	12.3	12.8
Aprion virescens (T)	1.3	0.0	10.4	10.8
Aulostomous chinensis (T)	0.6	0.1	7.4	7.7

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284

285 *Description of benthic structure*

286 On the face value, the cover of benthic variables showed minimal differences between the

287 north and central sectors, but together they differed from the southern sector that had high

288 cover of sand (52%) and fleshy algae (20%) (Supplementary material Figure S2). Hard and soft

289 coral cover averaged around 19% and 9% respectively in the north and central sectors. Overall,

290 sand was dominant in all sectors, although the percent cover was 21% and 30% in central and

291 northern sectors respectively. The cover of rubble was 15%, 10% and 4% in north, central and

292 south sectors respectively.

293
294 The first component (PC1) of the PCA explained 51.53% of variation in habitat composition

295 (Figure 4), showing positive correlation with the cover of sand (r = 0.82) and rubble (r = 0.13),

296 and negative correlations with the cover of hard corals (r = -0.48) and soft corals (r = -0.27).

297 The second PCA explained an additional 19.12% and was positively correlated to sand (0.41)

298 and hard coral (0.39) and negatively correlated to rubble (-0.81). Linear regression of PC1

299 loadings and depth showed sites with high cover of sand and rubble to be in deeper areas

300 compared to those with high cover of hard corals and soft corals depth (R2 = 0.13; p<0.001;
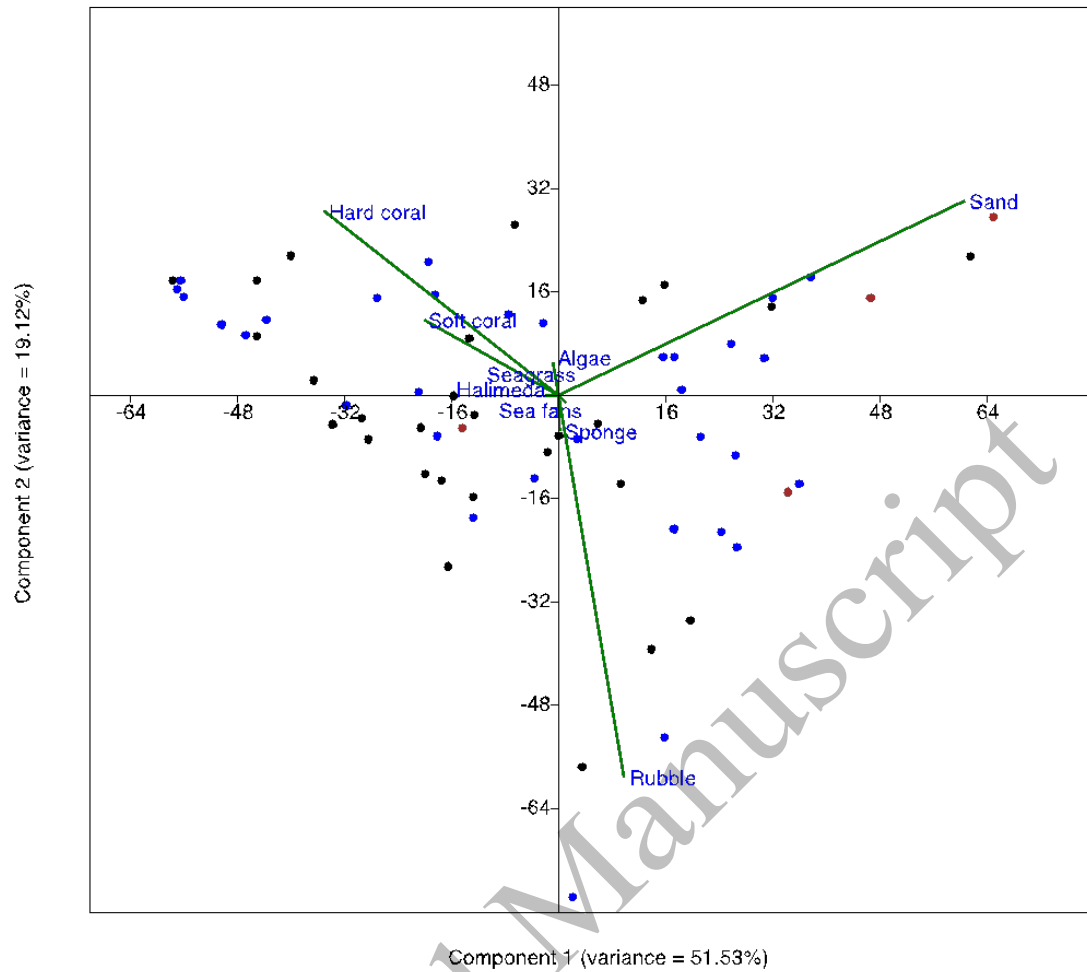
301 Figure 5)

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Figure 4: Principal component analysis plot showing the loadings of stations on the first and second principal components and bi-plots of the benthic variables. North, central and south sectors represented by blue, black and red dots.
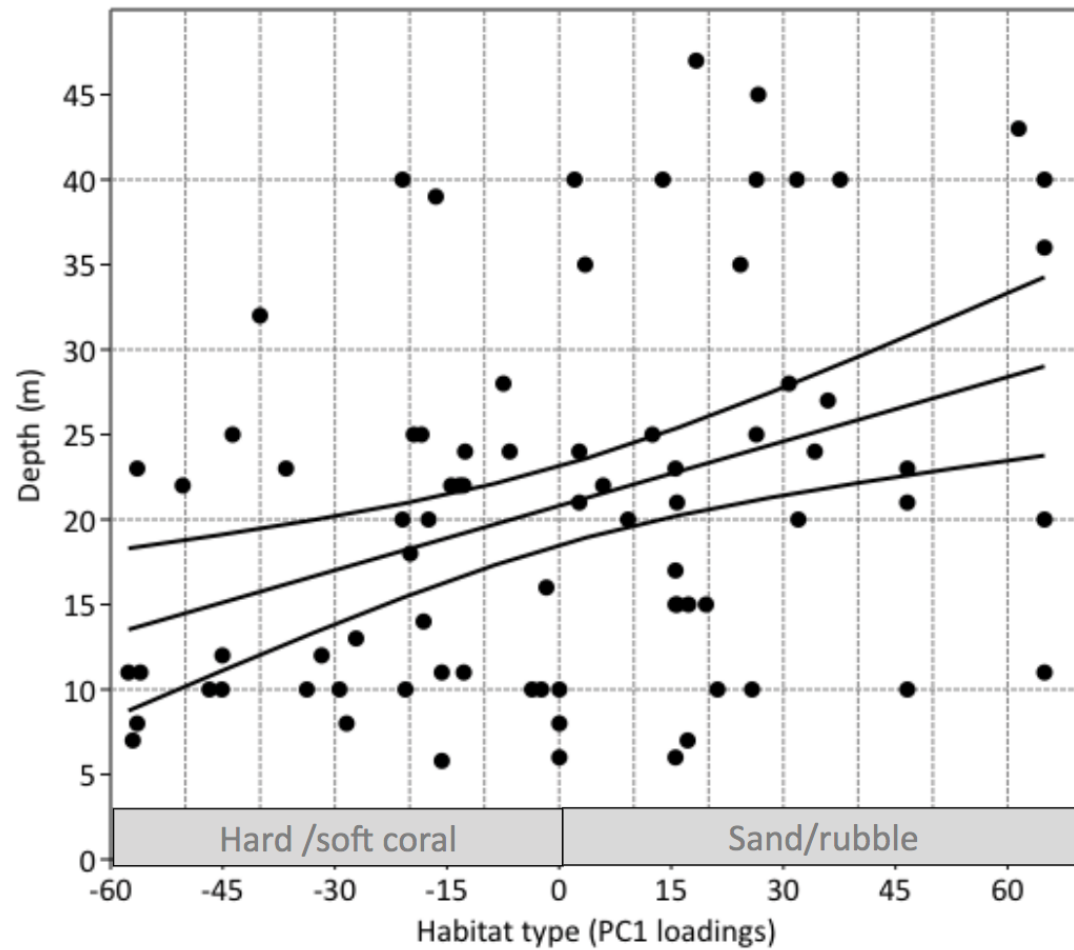
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309   Figure 5: Relationship between first principal component (PC1) habitat loadings and depth.

310   Sites with negative loadings were correlated with high cover of hard and soft coral while

311   those with positive loadings were correlated with sand and rubble cover.

312

313   *Influence of depth and habitat types*

314   Species richness and the abundance of all predators (cumulative MaxN) and resident

315   predators were significantly ($p<0.05$) influenced by depth and habitat type, with higher counts

316   in deeper than in shallower areas as well as in coral habitats than in sandy and rubble habitats

317   (Supplementary material Table S1). The zero-inflation model showed resident predators had

318   significantly excess zeros in the south in comparison to the central sector, while transient

319   predators had significantly excess zeros in the central in comparison to the north sector (Table

320   3a-b). GLM results showed significant interaction between habitat type and depth for all

321   predators, resident and transient predators (Figure 6). In sandy and rubble habitats, every

322   10m increase in depth was associated with an average increase in abundance of 0.3, 0.3 and

323   0.2 individuals for all predators, resident and transient predators respectively.
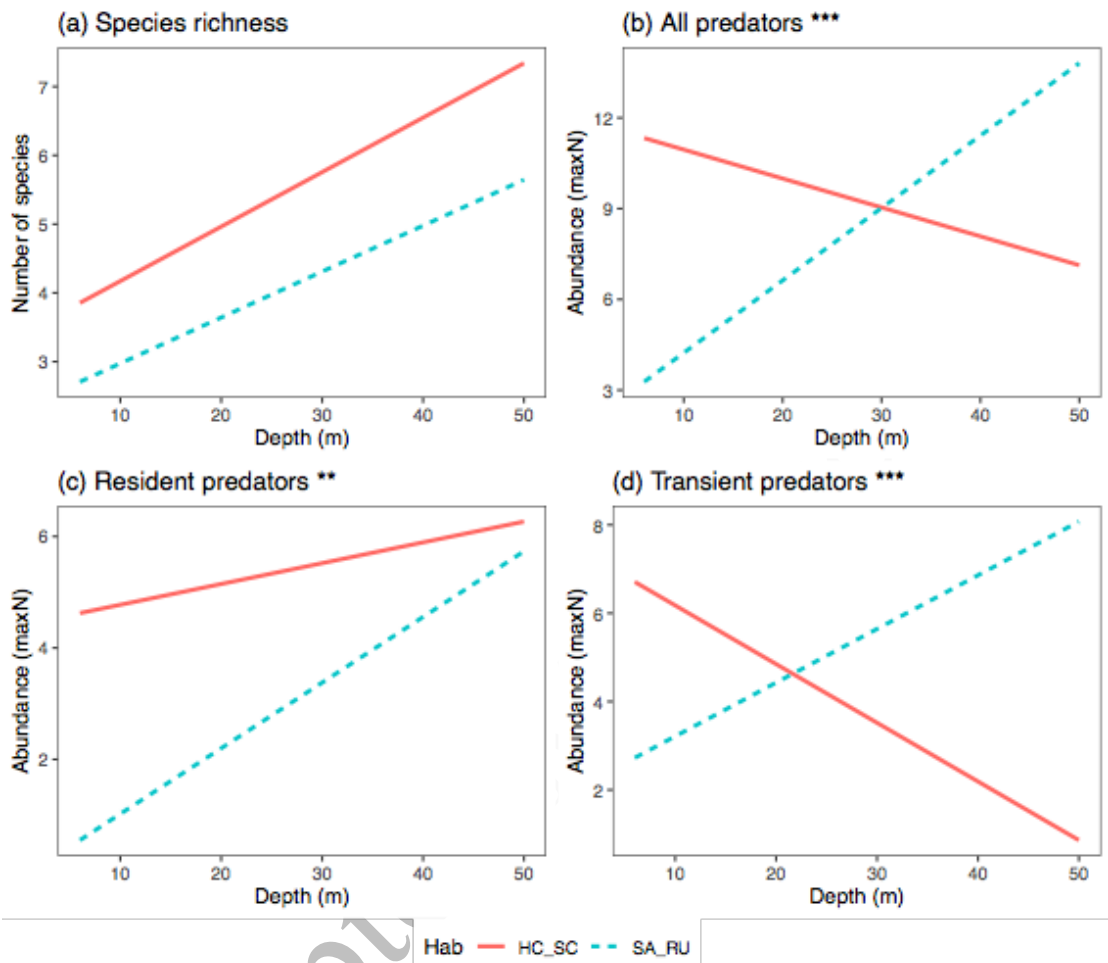
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328   Figure 6: Simple-slope plots of the interaction between depth and habitat type (Hab) in

329   predicting four aggregate abundance metrics. Habitat is represented by Hard coral and Soft

330   coral (HC_SC) and Sand and Rubble (SA_RU). All trend lines indicate significant relationships

331   and asterisks indicate significant interaction with '***' = <0.001, '**' = <0.01, '* = <0.05.

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339 Table 3: Estimated coefficients of zero-inflation model (ZIP) and their standard errors (S.E.) for
340 resident and transient predators and three species. Significant codes: '***' = <0.001, '**' =
341 <0.01, '*' = <0.05. Sec = sector. Reference group for Sec was the Central sector.

	Estimate	Coefficients	S.E
a) Resident predators	Intercept*	-0.92	0.40
	Sec_North	-0.07	0.55
	Sec_South**	2.98	2.63
b) Transient predators	Intercept	-0.46	0.37
	Sec_North*	-1.47	0.61
	Sec_South	-0.24	0.80
c) Species			
Lethrinus harak	Intercept**	2.80	1.05
	Sec_North**	-3.19	1.22
	Sec_South	15.17	5797.15
L. rubrioperculatus	Intercept*	1.47	0.80
	Sec_North*	-0.43	0.95
	Sec_South	15.89	2183.26
Aprion virescens	Intercept***	2.07	0.62
	Sec_North**	-2.08	0.73
	Sec_South	16.33	3994.54

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343
344 The predictor variables showed significant influence on four families (Figure 7; Supplementary
345 material Table S2). The abundance of Haemulidae and Lethrinidae showed significant positive
346 relationships with increasing depth, while only Aulostomidae displayed significant negative
347 relationships. Other families particularly Carcharhinidae, Dasyatidae, Fistulariidae,
348 Muraenidae, Myliobatidae, Epinephalidae and Sphyraerinidae exhibited non-significant
349 relationships. Abundance of Lutjanidae was greater in hard and soft coral habitats compared
350 to sandy and rubble habitats. A contrast observation was found for Carangidae showing higher
351 abundance in sandy and rubble than hard and soft coral habitats.
352
353 The GLM with interaction effects showed significant interaction between habitat type and
354 depth for Lethrinidae, Lutjanidae, Haemulidae, Fistulariidae and Scombridae (Figure 7). Every

355   10m increase in depth within hard coral and soft coral habitats was associated with an average

356   increase in abundance of 0.6, 0.1 and 0.1 individuals for Lethrinidae, Haemulidae and

357   Fistulariidae respectively. In sandy and rubble habitats, every increase in depth was associated

358   with an average increase in abundance of 0.7 and 0.4 individuals for every 10 m for Lutjanidae

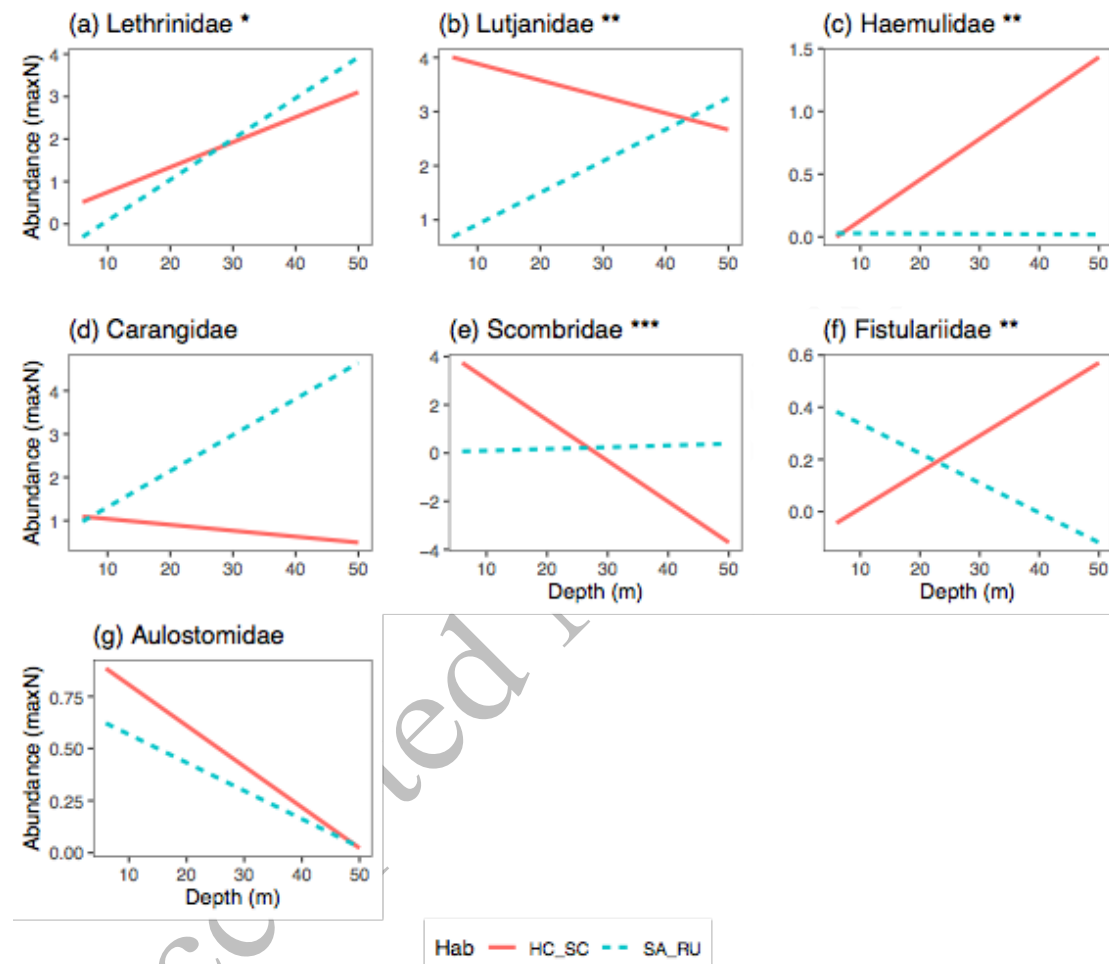359   and Scombridae respectively.

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363   Figure 7: Simple-slope plots of the interaction between depth and habitat type (Hab) in

364   predicting abundance of three resident predator fish families (a-c) and four transient predator

365   fish families (d-g). Habitat is represented by hard coral and soft coral (HC_SC) and sand and

366   rubble (SA_RU). All trend lines indicate significant relationships and asterisks indicate

367   significant interaction with '***' = <0.001, '**' = <0.01, '* = <0.05.

368

369

370   The abundance of *Trachinotus blochii* and spotcheek emperor *Lethrinus rubrioperculatus*

371   increased with increased depth, while for *Aulostomous chinensis,* bluefin trevally *Caranx*

372   *melampygus* and Indian mackerel *Rastrelliger kanagurta* it decreased with depth (Figure 8;

373   Supplementary material Table S3). The abundance of thumbprint emperor *Lethrinus harak*

374   and *Aprion virescens* was higher in hard and soft coral habitats compared to sandy and rubble

375   habitats. This was different for *Aphareus furca* and *Rastrelliger kanagurta,* which had greater

376   abundance in sandy and rubble habitats than hard and soft coral habitats. The zero inflated

377   models showed that excess zeros occurred in central in comparison to the northern sectors

378   for three species: *Lethrinus harak, Lethrinus rubrioperculatus* and *Aprion virescens* (Table 3c)*.*

379   GLM results showed significant interaction between habitat type and depth for *Lethrinus*

380   *olivaceus* (Figure 8), with every 10 m increase in depth within hard coral and soft coral habitats

381   being associated with an average increase in abundance of 1.3 individuals.
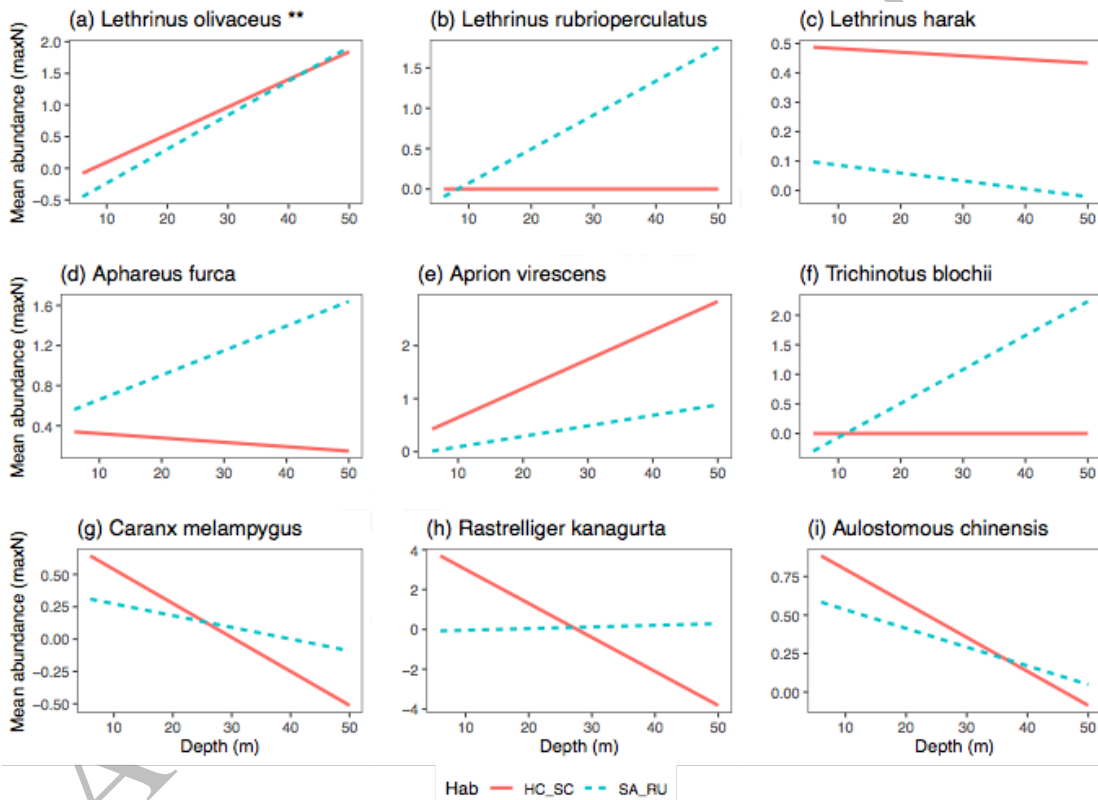
382
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385
386   Figure 8: Simple-slope plots of the interaction between depth and habitat type (Hab) in

387   predicting fish abundance of three resident predator species (a-c) and six transient predator

388   species. Habitat is represented by hard coral and soft coral (HC_SC) and sand and rubble

389   (SA_RU). All trend lines indicate significant relationships and asterisks indicate significant

390   interaction with '***' = <0.001, '**' = <0.01, '*' = <0.05.

391

392   **Discussion**

393   *General observations and novelty of the study*

19

394 Predatory reef fish have excessively been targeted around the world and latest studies show

395 that many of these species are increasingly becoming absent in regions such as the western

396 Indian Ocean (WIO) (de Mitcheson *et al.*, 2020; MacNeil *et al.*, 2020). The present study, one

397 of the first reef surveys to sample the west coast of Pemba Island, showed 83% of the 71

398 predator species encountered were present in depths greater than 20 m. This provides strong

399 evidence of the importance of deeper waters for predatory reef fish. Habitat types were also

400 found to influence abundance of predatory fish types in varying ways. Thus, habitat and depth

401 have a profound influence on predator abundance, although these factors often interact

402 (Pinheiro *et al.*, 2016; Skinner *et al.*, 2020). In our study, the abundance of all reef-associated

403 predators in the shallow areas was high in the hard and soft coral habitats, but in relatively

404 deeper areas of up to 47m, high levels of abundance were seen in the sandy and rubble

405 habitats. While the interaction between depth and habitat may indicate fishing effects on

406 predatory reef fishes (Tyler, et al., 2009), a more plausible ecological cause of the observed

407 pattern is changing habitat use of fishes with depth, for example due to ontogenetic shifts

408 (Green *et al.*, 2015; Nash *et al.*, 2015)*.* This imply that shallow coral reefs areas in relatively

409 healthy state play an important role in hosting predatory fishes. However, ontogenetic shifts

410 coupled with the high fishing pressure that is prevalent in shallow areas such as around Pemba

411 Island (Grimsditch et al., 2009) appears to be leading to a shift in the distribution of predatory

412 fishes into the deep areas where sandy habitats dominate. This study therefore provides both

413 a valuable baseline for the study area, and findings that are likely to be of wider interest to

414 coastal communities and managers in coral reef areas around the world.

415

416 *Transient and resident predators -habitat and depth associations*

417 The abundance of predatory reef types with different movement behaviours (transient *versus*

418 resident) was influenced by habitat types and depth in a non-random manner (Hixon, 2015;

419 Filous *et al.*, 2017; Paxton *et al.*, 2020). Resident predators presented strong positive

420 relationships with hard and soft coral habitat and increasing depth. This habitat association

421 was expected since resident predators show high degrees of site fidelity and are usually

422 confined to 'home' reefs', which offer both shelter and food resources (Stewart and Jones,

423 2001; Dance et al., 2011). Contrastingly, transient predators are highly mobile epipelagic

424 species that generally show the weakest relationships with coral habitat types, except when

425 the abundance of target prey species is above certain thresholds or the habitat is structurally

426 complex with an extensive vertical relief (Paxton *et al.*, 2020). Interestingly, the depth effect

427 was observed in all habitat types for resident predators but only in sandy and rubble habitats

428 for transient predators. This suggests preferences of particular habitat and depth by different
429 types of predatory fish, which could in turn be targeted by local fisheries (Tyler, et al., 2009;
430 Bongaerts et al., 2010). Certainly, predatory reef fish are attracted to areas of high prey fish
431 density that tend to occur in areas of live coral and high structural complexity (Stewart and
432 Jones 2001; Chong-Seng et al., 2012). Therefore, the influence of habitat and depth on the
433 abundance of reef fish was clearer in resident predators but more complex for transient
434 predators.

435

436 Incorporation of depth and habitat information into management strategies for resident and
437 transient predatory fish is likely to benefit the fisheries of Pemba Island. This will certainly
438 require information comparing the effects of depth and habitat in fished areas versus un-
439 fished areas. Indeed, such information is critical in selecting management measures geared
440 towards promoting the attainment and maintenance of thresholds of prey and predatory fish
441 densities (McClanahan et al., 2011; Hill et al., 2020). To ensure the sustainability of predatory
442 reef fish in areas like Pemba Island, where human population is growing (NBS 2018) and
443 fishing effort is increasing (Jacquet and Zeller, 2007; Rehren et al., 2020), it will be important
444 to manage both the fisheries and protect the habitats that their prey fish rely upon.

445

446 *Species driving the pattern*
447 We found three to six key species within the resident and transient predator types were the
448 most responsible for the patterns in the habitat and depth relationships. Within the resident
449 predators, significant interaction between habitat and depth was only apparent in longface
450 emperor, *Lethrinus olivaceus,* highlighting increased abundance in deeper areas but more so
451 for those individuals occurring in sandy and rubble habitats. A positive depth effect was
452 evident in spotcheek emperor, *Lethrinus rubrioperculatus,* while coral habitat effects were
453 detected in thumbprint emperor, *Lethrinus harak*. In general, emperors are linked to sandy
454 habitats where they feed by hunting less mobile prey (Kulbicki et al., 2005). Spotcheek
455 emperors prefer outer reef slopes in waters greater than 10 m (Sommer et al., 1996; Fricke et
456 al., 2011) thus it was not surprising that their abundance increased with increasing depth.
457 Similar studies in the Maldives have shown coral habitats to host more thumbprint emperors
458 (Skinner *et al.*, 2020). The species move either in small schools or solitary and can traverse
459 different habitats including shallow sandy and hard coral habitats (Carpenter and Allen, 1989).
460 We therefore postulate that emperor species respond to habitat and depth effects in varying
461 ways.

462

We observed habitat and depth effects with no interaction effects within the transient predators. Green jobfish, *Aprion virescens,* showed significant association with hard coral and soft coral in contrast to small-toothed jobfish *Aphareus furca*, which were more affiliated to sandy and rubble habitats. The opposing patterns in these closely related species is likely related to their biology and movement patterns. The adults of green job fish inhabit seaward reefs, while those of small-toothed jobfish prefer inshore coral and sandy habitats (Anderson and Allen, 2001). Positive depth effects were evident in snubnose pompano, *Trachinotus blochii,* while negative relationships with depth were found for Chinese trumpetfish, *Aulostomous chinensis,* and schooling species of bluefin trevally, *Caranx melampygus,* and Indian mackerel, *Rastrelliger kanagurta*. These associations are coherent with ontogenetic shifts and feeding behaviour that involve various depths and habitat types (Green *et al.*, 2015; Nash *et al.*, 2015). For example, the juveniles of snubnose pompano occur in shallow sandy habitats and later move to adjacent relatively deeper coral reef habitats as they grow (Fischer et al., 1990). This suggests the individuals surveyed in sandy habitats were all sub-adults. Chinese trumpetfish utilise multiple habitat types such as seagrass lagoons, coral and rocky reefs in the shallow areas and caves reaching 200 m in the deep areas (Bowen *et al.*, 2001; McGratten and Pollom, 2015). The species is not fished which makes it ubiquitous in shallow water depths. Bluefin trevally and Indian mackerel are mobile predators and often hunt in shallow waters (Sancho, 2000), where their food items are generally most abundant, and they may exhibit high residency in such depths (Filous *et al.*, 2017). Taken together, these findings indicate that schooling transient predator species are least dependent on healthy coral habitat types and therefore, less likely to be affected by changes in habitat conditions.

Family patterns

Resident fish families like Haemulidae and Lethrinidae increased in abundance with increasing depth, particularly in hard and soft coral habitats. This finding may be explained by the idea that during the day, coral heads on the reef offer shelter to nocturnal species. For example, at night haemulids forage on diets composed of small fish, invertebrates and dead animals in seagrass beds but during the day shift to coral associated habitats to escape predation from meso-predators (Burkepile and Hay, 2008). A contrasting result was found for Lutjanidae. While Lutjanidae also rest during the day in reef ledges and feed during the night (Nagelkerken et al., 2000), it is possible that the pattern observed was due to the bait plume from our BRUVs (Harvey et al., 2012; Espinoza et al., 2014) attracting them during the day (Bacheler et al., 2021) and especially in the open sandy and rubble habitats.

497

498 A non-significant influence of habitat type and depth was found on resident predators of the

499 subfamily Epinephelinae. This could reflect high abundance or diversity within this group,

500 which can influence the ability to detect relationships (Gerrodette, 1987). Nonetheless, the

501 non-significant results are in contrast to a previous study in the Maldives that showed deep

502 outer reefs had greater abundance of Epinephelinae than shallow lagoonal reefs (Skinner *et*

503 *al.*, 2020). However, the depth preferences of different species within the Epinephelinae

504 (Froese and Pauly, 2020), could be masking the relationships with depth.

505

506 Among the transient predators, there was evidence of habitat effects for the family

507 Carangidae and interaction effects for Scombridae and Fistularidae. Fish belonging to the

508 families Carangidae and Scombridae generally move in schools, often at speed, and therefore

509 can quickly respond to temporal and spatial fluctuations in prey fish density (Stewart and

510 Jones, 2001). As for Fistularidae, members of this family are generalist, usually very broad

511 ranging inhabiting shallow reef habitats to sandy habitats in depths reaching up to 100 m

512 (Watson and Sandknop, 1996).

513

514 *The north, central and south differences*

515 Coral reefs in the western Indian Ocean have shown declines in coral cover due to climate

516 change causing coral bleaching and subsequent coral mortality, and are predicted to decrease

517 further (Obura *et al.*, 2017; McClanahan *et al.*, 2020). Critically, healthy coral habitats are

518 essential for different groups of predatory fish. Therefore, future habitat loss through

519 destructive fishing activities like dynamite fishing, which has previously been reported in

520 Pemba Island (Slade and Kalangahe, 2015), will adversely affect the abundance of predatory

521 species. Dynamite fishing and bleaching damage create accumulation of rubble, which could

522 hamper recruitment and re-growth of coral. The cover of rubble can be used to disentangle

523 these effects, particularly if one driver like dynamite fishing is localised and the other like

524 bleaching is widespread. In our study the cover of rubble was relatively high in the north (15%)

525 and central (10%) sectors compared to the south (4%). However, the low cover in the south is

526 potentially due to artefacts of sampling, which was hindered by logistical constraints of rough

527 sea conditions. Alternatively, the differences between the north and south sectors could be

528 due to effects of historical dynamite fishing (Slade and Kalangahe, 2015).

529

530   Excessive absence of predators is an indication of widespread overfishing (Myers and Worms,

531   2003). The relatively high proportion of zero counts in the southern and central reef sectors

532   of Pemba Island may therefore indicate overfishing, particularly for emperor reef species:

533   *Lethrinus harak,* and *L. rubrioperculatus.* Previous studies in the southern sector (i.e., Misali

534   Island) point to relatively healthy habitats and fish diversity but a disproportionately

535   decreased abundance and diversity of large reef-associated predators (Grimsditch et al., 2009;

536   Jones et al., 2019; Osuka *et al.*, 2021a). Indeed, in 2017, estimates of species richness drawn

537   from six families: Carangidae, Epinephelinae, Lethrinidae, Lutjanidae, Carcharhinidae and

538   Sphyraenidae at Misali stood at 15 species, down from 46 species in 2004 (Daniels et al., 2004;

539   Jones et al., 2019). In combination these studies suggest overfishing may have worsened in

540   recent decades.

541

542   The central sector was the only sector where Vulnerable (silvertip shark, *Carcharhinus*

543   *albimarginatus,* brown-marbled grouper, *Epinephelus fuscoguttatus)* IUCN Red Listed species

544   were recorded. Also recorded in the central and southern sectors was the Vulnerable spotted

545   eagle ray *Aetobatus ocellatus*. The appearance of these species in the central sector could be

546   an indication of relatively high habitat quality (Harborne et al., 2011), which is critical in

547   maintaining the remaining populations of threatened species (Root 1998; Friedlander et al.,

548   2007). While there were no clear differences in live hard coral cover, a proxy of habitat quality,

549   between central and northern sectors, it is important to highlight the presence of a

550   continuous forereef area in the central sector, making the area ideal for reef predators like

551   sharks and groupers (Papastamatiou et al., 2018; Skinner et al., 2020). Further, the sector's

552   isolation from the main island through an extensive inner reef likely results in lower fishing

553   pressure and implies that future species and area protection measures would certainly be

554   beneficial.

555

556   *Using BRUVs to survey predatory coral reef fish*

557   This study joins a growing number illustrating the utility of BRUVs for gaining unique insights

558   into coral reef fish communities across a range of depths and environments*.* However, it is

559   appropriate to recognize limitations of the method. Our study deployed mono-BRUVs and

560   thus it was not possible to estimate fish size and subsequently fish biomass (Bernard et al.,

561   2014; Langlois et al., 2020). Fish size is an important indicator used to determine reef

562   productivity (Shin et al., 2005; Osuka et al., 2021b). Thus, application of mono-BRUVS has the

563   tendency of missing the opportunity to derive reef-associated variables like biomass and

564 productivity, which would be possible when stereo-BRUVS are applied (Langlois et al., 2020).
565 That said, mono-BRUVS compared to stereo-BRUVS are: easy to assemble as they do not
566 require calibration of the stereo-video streams that enable accurate measurement of length
567 and range (Boutros et al., 2015), relatively cheaper in cost due to use of one camera per BRUV
568 unit and not necessarily requiring specialised software to annotate and measure fish from
569 stereo-video (Gomes-Pereira et al., 2016). An important, but unanswered, question is how
570 biomass of reef-associated predators would change across the sectors. Despite the limitation
571 of mono-BRUVS, we are confident that the central sector had a higher biomass than the other
572 sectors. This is due to the presence of large-sized reef predators including sharks, rays,
573 groupers and trevally in that area. The rarefaction curves showed that our BRUVs surveys
574 were reasonably adequate to estimate the species richness of predatory reef fish of the outer
575 reefs of Pemba Island. However, the asymptote of the curve had not yet been fully reached
576 suggesting that the observed species richness was somewhat underestimated. As such, it is
577 possible that our sampling might have missed observing some of the rarer, cryptic and more
578 wary reef predators (Asher et al., 2017; Skinner et al., 2020).
579
580 The addition of Misali Island (see Figure 1) as a study site would be informative, as this area is
581 known to support high coral cover (Grimsditch et al., 2009) and a potential hotspot for
582 mesophotic coral ecosystem composed of corals, algae, invertebrate and fish (Osuka et al.,
583 2021a). Thus, in future it would be useful to extend the reef studies using BRUVs by examining
584 predators at Misali Island. But perhaps research using stereo-BRUVs (Langlois et al., 2020)
585 complemented by transect based approaches such as mini-ROV (remote operated vehicle)
586 would provide further insight into spatial and depth related variations in predatory reef fish
587 biomass. Of particular relevance would be the mid-water stereo BRUVs (Santana-Garcon et
588 al., 2014), which may be appropriate for the outer reefs with ledges and walls that make it
589 difficult for BRUV units to settle. Future work especially in the outer reefs of Pemba Island
590 would also benefit from application of complementary coral reef survey methods able to
591 survey shallow and mesophotic depths (e.g., AUVs, Osuka et al., 2021a). AUVs have the ability
592 to follow a pre-determined track, map deep areas down to 500 m and beyond, and collect
593 high-resolution data including photos and videos of both the water column and benthic
594 community. Such an effort would provide a much comprehensive insight into the drivers of
595 the diversity, distribution, density and biomass of higher trophic level predatory reef fish in
596 the area.
597

598 Predatory reef fish populations are facing immense pressures worldwide, leading to alarming
599 losses in abundance and diversity. The present study has shed light on the abundance and
600 distribution of predatory reef fish populations off the under-researched oceanic island of
601 Pemba Island. Clearly, different types of predators are discordantly predicted by depth and
602 habitat type with three to six key species within the resident and transient predator categories
603 being responsible for the patterns we observed. Habitats dominated by hard and soft corals,
604 and in relatively deeper waters, hosted high species richness and abundance of reef-
605 associated predators. Our findings add to the growing evidence that deep waters around coral
606 reefs provide important habitats for fish predators and corals. Thus, careful management,
607 through effective area and species protection measures, are needed to prevent further
608 impending reductions in their populations.

609

610 **Acknowledgements**

618
619

620 Appendix 1: Image of a BRUV unit being deployed off the coast of Pemba Island.

621
622
623
624

625 Appendix 2: Species list and their behaviour, IUCN Red List Categories and minimum and maximum depths sampled. EN = Endangered; VU = Vulnerable; NT
626 = Near Threatened; LC = Least Concern; DD = Data Deficient.
627

Family	Species	Predator type	Reference (in FishBase)	IUCN Red List Category	Min depth (m)	Max depth (m)
Carcharhinidae	*Carcharhinus albimarginatus (Rüppell, 1837)*	Transient	Compagno, 1984	VU	39.0	39.0
Carcharhinidae	*Carcharhinus sp*	Transient	Compagno, 1984	VU	10.0	40.0
Dasyatidae	*Neotrygon kuhlii (Muller & Henle 1841)*	Resident	Michael, 1993	DD	23.0	23.0
Dasyatidae	*Himantura uarnak (Gmelin 1789)*	Resident	Compagno et al., 1989	EN	40.0	40.0
Myliobatidae	*Aetobatus ocellatus (Kuhl 1823)*	Transient	Kapoor et al., 2002	VU	20.0	22.0
Muraenidae	*Gymnothorax buroensis (Bleeker 1857)*	Resident	Lieske and Myers, 1994	LC	22.0	28.0
Muraenidae	*Gymnothorax eurostus (Abbott 1860)*	Resident	Mundy, 2005	LC	23.0	23.0
Muraenidae	*Gymnothorax favagineus Bloch & Schneider 1801*	Resident	Lieske and Myers, 1994	LC	16.0	40.0
Muraenidae	*Gymnothorax fimbriatus (Bennett 1832)*	Resident	Kuiter, 1998	LC	35.0	35.0
Muraenidae	*Gymnothorax flavimarginatus (Rüppell 1830)*	Resident	Mundy, 2005	LC	10.0	15.0
Muraenidae	*Gymnothorax javanicus (Bleeker 1859)*	Resident	Mundy, 2005	LC	10.0	45.0
Muraenidae	*Gymnothorax meleagris (Shaw 1795)*	Resident	Mundy, 2005	LC	10.0	23.0
Muraenidae	*Gymnothorax nudivomer (Günther 1867)*	Resident	Mundy, 2005	LC	40.0	40.0
Muraenidae	*Gymnothorax undulatus (Lacepède 1803)*	Resident	Mundy, 2005	LC	25.0	25.0
Muraenidae	*Gymnothorax griseus (Lacepède 1803)*	Resident	Sommer et al., 1996	LC	10.0	21.0
Congridae	*Heteroconger hassi (Klausewitz & Eibl-Eibesfeldt 1959)*	Resident	Bacchet et al., 2006	LC	20.0	32.0
Aulostomidae	*Aulostomus chinensis (Linnaeus, 1766)*	Transient	Mundy, 2005	LC	5.8	35.0
Echeneidae	*Echeneis naucrates Linnaeus 1758*	Transient	Smith, 1997	LC	11.0	20.0

Fistulariidae	*Fistularia commersonii Ruppell 1838*	Transient	Mundy, 2005	LC	7.0	28.0
Epinephelinae	*Aethaloperca rogaa (Fabricius 1775)*	Resident	Kuiter and Tonozuka 2001	LC	7.0	32.0
Epinephelinae	*Cephalopholis argus Schneider 1801*	Resident	Mundy, 2005	LC	5.8	32.0
Epinephelinae	*Cephalopholis cyanostigma (Valenciennes 1828)*	Resident	Lieske and Myers, 1994	LC	20.0	20.0
Epinephelinae	*Cephalopholis boenak (Bloch 1790)*	Resident	Kuiter and Tonozuka 2001	LC	10.0	40.0
Epinephelinae	*Epinephelus caeruleopunctatus (Bloch 1790)*	Resident	Craig et al., 2011	LC	23.0	23.0
Epinephelinae	*Epinephelus fuscoguttatus (Forsskal 1775)*	Resident	Lieske and Myers, 1994	VU	32.0	32.0
Epinephelinae	*Epinephelus sp.*	Resident	Lieske and Myers, 1994	LC	25.0	39.0
Epinephelinae	*Epinephelus tukula Morgans 1959*	Resident	Kuiter and Tonozuka 2001	LC	47.0	47.0
Epinephelinae	*Plectropomus laevis (Lacepede 1801)*	Resident	Kailola et al., 1993	LC	23.0	23.0
Epinephelinae	*Variola albimarginata Baissac 1953*	Resident	Lieske and Myers, 1994	LC	10.0	45.0
Epinephelinae	*Variola louti (Fabricius 1775)*	Resident	Lieske and Myers, 1994	LC	15.0	28.0
Carangidae	*Carangoides dinema Bleeker, 1851*	Transient	Allen and Erdmann 2012	LC	25.0	25.0
Carangidae	*Carangoides ferdau (Forsskål, 1775)*	Transient	Sommer et al., 1996	LC	12.0	40.0
Carangidae	*Carangoides fulvoguttatus (Forsskål, 1775)*	Transient	Sommer et al., 1996	LC	40.0	40.0
Carangidae	*Carangoides gymnostethus (Cuvier, 1833)*	Transient	Lieske and Myers, 1994	LC	28.0	28.0
Carangidae	*Carangoides orthogrammus (Jordan & Gilbert, 1882)*	Transient	Mundy, 2005	LC	10.0	40.0
Carangidae	*Carangoides sp.*	Transient	Mundy, 2005	LC	21.0	45.0
Carangidae	*Caranx ignobilis (Forsskål, 1775)*	Transient	Mundy, 2005	LC	10.0	15.0
Carangidae	*Caranx melampygus Cuvier, 1833*	Transient	Mundy, 2005	LC	10.0	22.0
Carangidae	*Caranx sexfasciatus Quoy & Gaimard, 1825*	Transient	Mundy, 2005	LC	5.8	40.0
Carangidae	*Caranx sp*	Transient	Mundy, 2005	LC	17.0	22.0
Carangidae	*Caranx tille Cuvier, 1833*	Transient	Paxton et al, 1989	LC	8.0	35.0

2

Carangidae	*Trachinotus blochii (Lacepède, 1801)*	Transient	Fischer et al., 1990	LC	11.0	40.0
Lutjanidae	*Macolor niger (Forsskal 1775)*	Resident	Lieske and Myers, 1994	LC	10.0	27.0
Lutjanidae	*Aphareus furca (Lacepède 1801)*	Transient	Mundy, 2005	LC	6.0	43.0
Lutjanidae	*Aprion virescens Valenciennes 1830*	Transient	Mundy, 2005	LC	7.0	47.0
Lutjanidae	*Lutjanus bohar (Fabricius 1775)*	Transient	Sommer et al., 1996	LC	10.0	40.0
Lutjanidae	*Lutjanus gibbus (Forsskal 1775)*	Resident	Kuiter and Tonozuka 2001	LC	23.0	25.0
Lutjanidae	*Lutjanus kasmira (Fabricius 1775)*	Resident	Mundy, 2005	LC	10.0	16.0
Lutjanidae	*Lutjanus monostigma (Cuvier 1828)*	Resident	Allen, 1985	LC	16.0	16.0
Lutjanidae	*Lutjanus quinquelineatus (Bloch 1790)*	Resident	Allen, 1985	LC	16.0	16.0
Lutjanidae	*Lutjanus rivulatus (Cuvier 1828)*	Resident	Sommer et al., 1996	LC	10.0	10.0
Lutjanidae	*Lutjanus russellii (Bleeker 1849)*	Resident	Sommer et al., 1996	LC	40.0	40.0
Lutjanidae	*Lutjanus vitta (Quoy & Gaimard 1824)*	Resident	Allen, 1985	LC	40.0	40.0
Haemulidae	*Plectorhinchus gaterinus Fabricius 1775*	Resident	Bianchi, 1985	LC	22.0	25.0
Haemulidae	*Plectorhinchus vittatus (Linnaeus 1758)*	Resident	Sommer et al., 1996	LC	23.0	23.0
Lethrinidae	*Lethrinus erythropterus Valenciennes 1830*	Resident	Carpenter and Allen, 1989	LC	40.0	40.0
Lethrinidae	*Lethrinus harak (Fabricius 1775)*	Resident	Carpenter and Allen, 1989	LC	7.0	28.0
Lethrinidae	*Lethrinus mahsena (Fabricius 1775)*	Resident	Sommer et al., 1996	EN	25.0	25.0
Lethrinidae	*Lethrinus microdon Valenciennes 1830*	Resident	Sommer et al., 1996	LC	14.0	14.0
Lethrinidae	*Lethrinus nebulosus (Forsskal 1775)*	Resident	Carpenter and Allen, 1989	LC	28.0	28.0
Lethrinidae	*Lethrinus obsoletus (Forsskal 1775)*	Resident	Carpenter and Allen, 1989	LC	7.0	7.0
Lethrinidae	*Lethrinus olivaceus Valenciennes 1830*	Resident	Sommer et al., 1996	LC	10.0	45.0
Lethrinidae	*Lethrinus rubrioperculatus Sato 1978*	Resident	Sommer et al., 1996	LC	7.0	45.0
Lethrinidae	*Lethrinus sp*	Resident	Sommer et al., 1996	LC	25.0	25.0

3

Lethrinidae	*Lethrinus xanthochilus Klunzinger 1870*	Resident	Carpenter and Allen, 1989	LC	22.0	35.0
Lethrinidae	*Monotaxis grandoculis (Forsskal 1775)*	Resident	Carpenter and Allen, 1989	LC	11.0	40.0
Sphyraenidae	*Sphyraena barracuda (Edwards 1771)*	Transient	De Sylva, 1990	LC	40.0	40.0
Sphyraenidae	*Sphyraena forsteri Cuvier 1829*	Transient	Senou, 2001	LC	15.0	15.0
Scombridae	*Gymnosarda unicolor (Rüppell 1836)*	Transient	Collette and Nauen, 1983	LC	15.0	25.0
Scombridae	*Rastrelliger kanagurta (Cuvier 1816)*	Transient	Collette and Nauen, 1983	DD	10.0	40.0
Scombridae	*Scomberomorus commerson (Lacepède 1800)*	Transient	Collette and Nauen, 1983	NT	12.0	12.0

628

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