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1   **Coral reef pinnacles act as ecological magnets for the abundance, diversity and biomass of**

2   **predatory fishes**

3

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16

17   **Abstract**

18   Predation is a key ecological process regulating the structure and diversity of biological

19   communities, yet predators do not exist homogeneously in nature. Coral reefs possess diverse

20   assemblages of predatory fishes, the distribution and abundance of which is well documented for

21   coastal and emergent reefs. However, for remote, isolated and submerged reefs, such as those found

22   on pinnacles and seamounts, our understanding of predatory fish communities is limited. These

23   features are ubiquitous in the world's oceans and frequently targeted by fishers for their presumed

24   fish aggregation properties. Here we describe communities of predatory fishes on a series of

25   pinnacle reefs and contrast these to regional coastal and offshore emergent reefs. Pinnacles

26   supported 2-4x higher abundance, biomass and diversity of predatory fishes compared to emergent

27   reefs. They also supported unique communities, with 32 out of the 63 predator species in our study

28   found only on pinnacle reefs. For species found on all three reef types, all were most abundant on

29   pinnacles and the 6 taxa driving differences in community structure were most abundant on

30   pinnacles. Together our results show predatory fishes are strongly attracted to pinnacles, although

31   the mechanisms are still unclear. Prioritising the selection of these small ecological magnets in

32   conservation planning would be an effective approach to target the protection of regional reef fish

33   biodiversity.

34

35   **Keywords**

36   Pinnacle reefs, predatory fishes, ecological magnets, biodiversity, community ecology

37

38   **1. INTRODUCTION**

39   Predation is one of the most important processes influencing the diversity and structure of

40   ecological communities (Sih et al. 1985, Kerfoot & Sih 1987, Chase et al. 2002, Barbosa &

41   Castellanos 2005). The presence of predators can limit the possibility of single-species monopolies

42   in prey assemblages, promoting species diversity at lower trophic levels (Paine 1966, Menge &

43   Sutherland 1976). On coral reefs, predation plays a major role in limiting prey population sizes and

44   determining the structure of diverse fish assemblages (Carr, Anderson and Hixon, 2002; Hixon and

45   Webster, 2002; Hixon and Jones, 2005 and reviews in Hixon, 1991 and 2015). Mechanisms by

46   which this occurs may be directly via mortality or injury, or indirectly, where the presence of

47   predators influences the condition (e.g. fecundity, growth) or behaviour of prey species (Beukers &

48   Jones 1998, Bauman et al. 2019). Decreases in predation pressure typically benefit a small number

49   of prey species, with a consequent reduction in overall diversity (Caley 1993) and when removed

50   from coral reefs, the loss of important predator species has been shown to impact ecosystem

51   structure and function (Dulvy et al. 2004, Rosenblatt et al. 2013, Boaden & Kingsford 2015). This

52   is of pressing concern as human exploitation of the world's oceans has resulted in substantial

53   declines in predatory fish abundance of up to 90 % (Myers & Worm 2003).

54

55   Notable examples of overexploitation include the overfishing of large groupers throughout the

56   Indo-Pacific region (Sadovy de Mitcheson et al. 2013) and reef associated sharks globally (Rizzari

57   et al. 2014, MacNeil et al. 2020, Dulvy et al. 2021). Even in isolated offshore reefs (e.g. Pacific

58   Remote Islands Marine National Monument) significant declines in the abundance of predatory fish

59   assemblages have been documented either due to exploitation or large scale disturbances (Knapp et

60   al. 2011, Jacobs et al. 2021). In the absence of exploitation however, predatory fish are an abundant

61   and diverse component of coral reef fish fauna (Sandin et al. 2008, Lester et al. 2009, Friedlander et

62   al. 2010, Rizzari et al. 2014). The abundance and distribution of predatory fish vary across coral

63   reef seascapes and are linked to a number of factors, including habitat type (Espinoza et al. 2014,

64 Hall & Kingsford 2021), depth (Osuka et al. 2022) and topographic complexity (Gratwicke &

65 Speight 2005, Lingo & Szedlmayer 2006, Rogers et al. 2014). Habitat complexity is also important,

66 not only in attracting predators, but in mediating their impact on prey assemblages (Hixon & Beets

67 1993, Beukers & Jones 1998, Almany 2004). However, our present knowledge of predatory reef

68 fishes and the mechanisms that govern their abundance and distribution are largely based on studies

69 from shallow coastal reefs. Understanding predator assemblages across the spectrum of connected

70 habitats and reef types they occupy is a key step in elucidating the ecology of these organisms and

71 predicting future responses to anthropogenic pressures across whole coral reef seascapes.

72

73 One type of understudied coral reef habitat includes submerged features, such as pinnacles and

74 seamounts. These structures are defined as "isolated elevations of the sea floor, over which the

75 depth of water is relatively shallow but sufficient for navigation and have shallowest points below

76 10-20 m" (IHO 2008, Galbraith et al. 2021). Despite being ubiquitous in the world's oceans,

77 seamounts and pinnacles are poorly described within coral reef seascapes and yet may provide

78 substantial quantities of physical habitat for coral associated organisms (Harris et al. 2013, Moore et

79 al. 2017). Coral reef habitat on pinnacles and seamounts differs in form and structure from

80 commonly accepted models of coral reefs, with these reefs lacking traditionally described

81 geomorphological zones such as a reef flat or lagoon (Goreau 1959, Done 1982, Roberts et al. 2015,

82 Galbraith et al. 2021). Instead, coral reef habitat on these structures is exposed to the pelagic

83 environment on all sides, essentially composed entirely of reef crest and slope. Estimates of global

84 numbers of seamount-type features range from 100,000 to 25 million (Wessel et al. 2010) and coral

85 reefs can form networks of habitat patches on the summits of pinnacles and seamounts in tropical

86 oceans. Examples of such networks include the seamounts of the Coral Sea between Australia and

87 New Caledonia (Ceccarelli et al. 2013), the Vittória-Trindade chain off the coast of Brazil

88 (Guabiroba et al. 2022) and seamounts of the Hawaiian Archipelago (Sinniger et al. 2013). Yet

89 despite this habitat potential, relatively few studies have been conducted on seamount and pinnacle

90   reefs globally. A literature search found that of the 36,789 papers on coral reefs published since

91   1965, only 204 of these included the term "seamount", and 81 included the term "pinnacle" (Web

92   of Science core collection search conducted 12 April 2022. Search terms: "Coral reef" only; "Coral

93   reef" AND "Seamount"; "Coral reef" AND "Pinnacle". Date range: 1965 – 2022. Results available

94   at https://github.com/bjcresswell/KimbePreds).

95

96   Like seamounts, pinnacles typically possess small summits with sheer sides descending to

97   substantial depths through the mesophotic and into the aphotic zone (Galbraith et al. 2021). This

98   abrupt topography exposes much of the benthos to open ocean currents, resulting in strong and

99   variable local hydrodynamics, characterised by powerful upwelling and complex eddies (Lavelle &

100 Mohn 2010, Rowden et al. 2010, Galbraith et al. 2022). Such conditions may provide an ideal

101 setting for seasonal aggregations of predators around seamounts and pinnacles (Klimley et al.

102 2005). Recent work has shown that coral reef predator fishes on both pinnacle and atoll reefs may

103 be overwhelmingly sustained by food-webs with pathways originating in offshore pelagic sources,

104 resulting in high abundance and biomass of predators where this occurs (Morato et al. 2010, Fontes

105 et al. 2014, Leitner et al. 2021, Skinner et al. 2021). Pinnacle reefs have also been shown to support

106 highly diverse communities, despite the relatively small surface area available for coral reef

107 organisms on their summits (Galbraith et al. 2021). These assemblages typically contain taxa also

108 found in coastal reefs as well as unique species, not normally encountered on nearshore or emergent

109 reef systems and thus pinnacles may be important in both sustaining unique biodiversity as well as

110 providing refuges for a variety of coral reef taxa. However, to date, there have been no studies that

111 focus on the abundance, diversity, biomass and structure of communities of predatory fishes on

112 coral reef pinnacles.

113

114 The present study describes communities of predatory fishes on a series of submerged pinnacle

115 reefs in a low latitude coral reef system, Kimbe Bay, Papua New Guinea. Recent work from this

region examined whole fish communities on these reefs and found them to support abundant and

diverse fish assemblages (Galbraith et al. 2021). However, these patterns have not been explored

specifically for predatory fishes, which were the conspicuous species driving overall community

differences. The principle aim of the study was therefore to describe predatory fish communities on

the pinnacle reefs and to compare and contrast these with two shallow water reef types, common in

the region: isolated offshore reefs and nearshore fringing reefs. We asked the following questions:

1. Do pinnacle reefs support greater numbers of predators? We hypothesised that predatory
   fish abundance (density or number of individuals per unit area) would be higher on sites
   farther removed from terrestrial disturbance and with access to higher pelagic trophic
   subsidies.

2. Do trends in biomass match trends in abundance? If predatory fish assemblages are similar
   across reef types, then patterns in biomass should be similar to patterns in abundance.

3. Which reef types support the greatest diversity of predatory fishes? Patterns in biomass and
   abundance may be driven by large numbers of relatively few taxa and may therefore be
   decoupled from patterns in diversity.

4. Does the composition of predatory fish assemblages vary among reef types? If levels of
   overall diversity are similar across reef types, species composition may also be similar
   across reef types.

2. MATERIALS AND METHODS

2.1. Study site and survey design

This study was conducted in Kimbe Bay, West New Britain Province, Papua New Guinea. This

large tropical embayment is located in the Southern Bismarck Sea in the south-east of the Coral

Triangle (5°30′S, 150°05′E, Fig. 1a) and possesses a range of coral reef habitat types, including the

three selected for this study: tracts of emergent nearshore reefs, emergent offshore reefs, and

141 submerged pinnacle reefs. We surveyed four reefs per habitat type over two survey periods – in

142 October 2018 and again in March 2019 – 12 reefs in total (Fig. 1b).

143

144 Nearshore reef sites were all located within 5 km of the mainland on a network of fringing reef

145 structures, which have shallow (~0-10 m) tops and extend along the length of the bay's shoreline.

146 Offshore sites were also located on reefs with shallow tops, however these were all in remote

147 locations (between 9 and 25 km from the nearest landmass). These reefs rise from a deep geologic

148 structure that encircles the outer portion of the bay (c.300m deep, GEBCO Compilation Group,

149 2019). The centre of this structure drops to ~600m in the middle of the bay (Fig. 1c) and on the

150 northern seaward side drops >1000m to the South Bismarck Plate shelf. The pinnacle reefs in this

151 study also rise from this structure but have summits at depths of 15-30 m. In order to standardise

152 our survey-depth, all transects were therefore conducted on reef slopes between 20-30m and similar

153 gradient slopes were selected on all reef types to account for reef slope aspect, which is known to

154 affect coral reef fish assemblages (Jankowski et al. 2015, Moore et al. 2017, Oakley-Cogan et al.

155 2020). Fishing pressure is also known to reduce numbers of predator fishes on coral reefs (Jackson

156 et al. 2017) and nearshore reefs in Kimbe Bay may experience substantial fishing pressure from

157 nearby human populations. To account for this potential confounding effect, all four nearshore

158 survey sites in this study were situated on reefs included in a locally managed marine area (LMMA)

159 scheme, which prohibits fishing and gleaning (sensu Chapman 1987) on these reefs. Similarly, we

160 used remote offshore reefs in order to incorporate sites which experience similar levels of isolation

161 as the pinnacles (and thus distance from coastal fishing pressure), but with structural characteristics

162 more similar to nearshore, fringing reef systems.

163

164 **2.2. Data collection**

165 High-definition stereo-video surveys were conducted along 30 x 5m (150m^2) belt transects within

166 the 20-30m depth band. Pinnacle reefs are exposed to the pelagic environment on all sides, so on

167 nearshore and offshore reefs, surveys were conducted only on exposed, windward slopes, in order

168 to control for reef exposure. For each reef, 5 transects were conducted during each survey period

169 (i.e., 10 per reef, 120 transects total). A diver-operated stereo-video-system (SVS, SeaGIS,

170 https://www.seagis.com.au/, electronic supplementary material Fig. S1) with two GoPro Hero-4

171 cameras was used to record each survey (Goetze et al. 2019), with the diver maintaining an

172 elevation of 0.5m above the reef. A second diver followed with a transect tape and indicated to the

173 first diver when 30m was reached and also ensured at least 5m separation between transect.

174

175 **2.3. Transect video processing**

176 Fish transect videos were analysed using the software EventMeasure Stereo (SeaGIS), which uses

177 camera geometric calibration to provide a known field-of-view (2.5m either side of the transect, 5m

178 total) and allows accurate length measurements to be made. Every individual fish that entered the

179 lower two-thirds of the screen was identified to species based on Allen et al. (2003), counted and a

180 fork-length measurement made. Only individuals that were readily observable within these

181 parameters were recorded. From all recorded fish observations, occurrences of predators were

182 extracted.

183

184 **2.4. Selection of predator taxa**

185 Individual observations of fishes were considered predators on the following bases: Firstly, we

186 included all species belonging to any of the following nine families of known predatory fishes:

187 Serranidae (groupers, Subfamily Epinephelinae only), Carangidae (jacks and trevallies),

188 Carcharhinidae (Requiem sharks), Scombridae (tunas and mackerels), Lutjanidae (snappers),

189 Lethrinidae (emperors), Cirrhitidae (hawkfishes), Haemulidae (grunts/sweetlips), Sphyraenidae

190 (barracudas). In addition, other species were also selected that met the following three criteria

191 extracted from FishBase (Froese and Pauly, 2022): feeding guild = piscivore, trophic level ≥3.7,

192 and max length (for species) ≥30cm. This resulted in the inclusion of a further six species in the

193   analysis: *Epibulus insidiator* (sling-jaw wrasse, piscivore, trophic level 4.01, max length 54cm),

194   *Myripristis botche* (blacktip soldierfish, piscivore, trophic level 4, max length 30cm), *Oxychelinus*

195   *digramma* (cheeklined wrasse, piscivore, trophic level 3.7, max length 40cm), *Platax teira* (teira

196   batfish, piscivore, trophic level 3.95, max length 70cm), *Priacanthus hamrur* (lunar tailed bigeye,

197   piscivore, trophic level 3.82, 45cm), *Sargocentron spiniferum* (sabre squirrelfish, piscivore, trophic

198   level 3.80, 51cm). Finally, one generalist carnivore with a high-trophic level and very large

199   maximum length was also included in the study: *Cheilinus undulatus* (humphead wrasse, trophic

200   level 3.99, 229cm max length). In total 63 taxa from 13 families, from the wider Kimbe Bay fish

201   community were included as predators in all subsequent analyses (see SI Table). A number of

202   predator taxa that are known to exist in the region were not included (e.g. *Gymnothorax spp.*) as

203   these were not recorded on any transect in our study.

204

205   **2.5. Quantifying the effect of reef type**

206   All analyses were performed in *R version 4.0.3* (R Core Team, 2020). All data exploration and

207   graphic production was conducted using base R, the *tidyverse* family of R packages (Wickham et al.

208   2019) and *arsenal* (Heinzen et al., 2021). Generalised linear mixed effects models (GLMMs) were

209   constructed using the package *glmmTMB* (Brooks et al. 2017a) to measure the effect of reef type on

210   the abundance, biomass and diversity of predatory reef fishes. GLMM diagnostics were performed

211   using the *DHARMa* package (Hartig 2022) to assess the assumptions of the model including

212   homogeneity of variance, dispersion and outliers, and additional checks for zero inflation. Model

213   selection was informed from the Akaike Information Criterion using the AIC function in base R.

214   Tukey post-hoc pairwise contrasts and 95% confidence intervals in estimated marginal means were

215   calculated using the package *emmeans* (Lenth 2021) and are reported as either a contrast size (in the

216   measurement units) or ratio between reef types. Fully reproducible code and data are available at:

217   https://github.com/bjcresswell/KimbePreds.

218

219 **2.6. Abundance and biomass**

220 Animal abundance (or, strictly speaking, density when measured as numbers per unit of area) was

221 extracted from the video as numbers of individual predator fishes observed per transect ($N.150m^{-2}$).

222 From the recorded fork-lengths, biomass for each individual fish observation was calculated using

223 the length-weight equation:

224

225 $$W = aL^{b}$$

226

227 where L represents fish fork length (cm), W is weight in grams and a and b are species-specific

228 constants obtained from FishBase (Froese & Pauly 2022) using the R package *rfishbase* (Boettiger

229 et al. 2012). Transect biomass totals were then calculated as $kg.150m^{-2}$.

230

231 Variation in predator fish abundance and biomass across reef types was assessed using GLMMs,

232 with reef type as the fixed effect and individual reef in each survey period as the random effect to

233 account for temporal and site-specific variation in the presence of predators. Prior work in our study

234 system has reported large variation in whole fish assemblages across the seascape, with some reefs

235 supporting very small numbers of fishes (Galbraith et al. 2021). In order to model predator

236 abundance and biomass as a proportion of this, abundance and biomass of whole fish assemblages

237 were included in both models as a log offset term (Zuur et al. 2008, Brooks et al. 2017b). For

238 abundance a negative binomial residual distribution was selected for the final model and for

239 biomass a Tweedie distribution was selected, both with log-link functions.

240

241 **2.7. Diversity**

242 Shannon-Wiener index was used to quantify diversity ($H.150m^{-2}$) since it accounts for both the

243 number and evenness of species present while being sensitive to the presence of rare taxa (33

244 species in our study had total bay-wide observations of 4 or less). Species richness was considered

245   as a diversity metric but not included as it does not account for evenness of distribution. Simpson's

246   index was also considered but not included for the related reason that it penalises rarity and

247   attributes any survey with 0 observations a score of 1 (21 of the 120 transects across our study had 0

248   observations of predatory fishes). Differences in diversity were assessed using GLMMs with the

249   same fixed and random effect as above. A Tweedie distribution was selected for the final model.

250

251   **2.8. Assemblage composition**

252   In total, 21 transects from offshore and nearshore reefs contained no observations of predators so an

253   analytical approach that is robust to large numbers of zero observations was required. The package

254   *mvabund* (Wang et al., 2020) was therefore used to assess multivariate differences in predator

255   assemblage composition between reef types. The manyglm function of this package was used to fit

256   a multivariate generalised linear model (GLM). As the underlying data were count data, both

257   Poisson and negative binomial distributions were tested for fit. Model diagnostics were conducted

258   using the functions plot.manyglm (to produce residual vs fit- and QQ- plots) and meanvar.plot (to

259   check mean-variance relationships). Model fits were also compared using Akaike Information

260   Criterion using the AIC function in base R. The negative binomial model was selected for pairwise

261   multivariate comparisons, which was conducted using the anova.manyglm function.

262

263   It is not possible to include random effects in manyglm, however reef site was accounted for as a

264   random factor in the model by using probability integral transform (PIT) residual bootstrapping

265   (aka PIT-trap resampling, (Warton et al. 2017)) in the package *permute* (Simpson, 2019).

266   Multivariate models from *mvabund* produce likelihood ratio test (LRT) statistics and corresponding

267   permutation P values, both for multivariate pairwise comparisons (*i.e.*, between reef types) and for

268   univariate scoring of species' contributions to overall differences. The latter were drawn from the

269   model by including the term p.uni = 'adjusted', which corrects P values to control the family wise

270   error rate across species, using a resampling-based multiple testing procedure (Westfall et al. 1993).

271

272   Differences in assemblage composition across reef types were visualised using a non-metric

273   multidimensional scaling in the package *vegan* (Oksanen et al. 2022). A constant fraction (0.001)

274   was added to all species observations, to allow the inclusion of transects with zero predator

275   observations. Species scores were overlaid for taxa identified as significantly driving differences in

276   the multivariate model and alpha and beta diversity were visualised using the package *ggvenn* (Yan,

277   2021). Differences in abundance for taxa significantly driving assemblage composition were

278   visualised in point and line plots using *ggplot2* (Wickham et al. 2019).

279

280 **3. RESULTS**

281 In total, 2,560 predatory fishes representing 63 different taxa from 13 families were observed over

282 120 transects on 12 reefs in Kimbe Bay. From these data, we explored the effect of reef type

283 (submerged pinnacle reefs, offshore emergent reefs, and nearshore emergent reefs) on the

284 abundance, biomass and diversity of predatory reef fishes, and investigate patterns of community

285 composition across these habitats.

286

287 **3.1 Abundance, biomass and diversity**

288 The GLMMs provided evidence that pinnacle reefs supported a greater abundance, biomass and

289 diversity of predatory fishes, though the strength of the effect of reef type depended on the

290 indicator.

291

292 Mean predator numbers were significantly higher on pinnacles than on both nearshore and offshore

293 reefs, while there was no observable difference in predator abundance between offshore and

294 nearshore reefs (Fig. 2a and d, electronic supplementary material Table S1). On average, pinnacles

295 supported 16.6 predators.150m^{-2} (95% CI [7.9-25.3]), compared to 5.4 predators.150m^{-2} (95% CI

296 [2.4-8.4]) for offshore reefs, and 5 predators.150m^{-2} (95% CI [1.9-8.1]) for nearshore reefs.

297

298 Mean predator biomass also differed between reef types, with pinnacle reefs supporting 27

299 kg.150m^{-2} (95% CI [17.2-36.8]) compared to 7.1 kg.150^{-2} on nearshore reef types (95% CI [3.2-

300 11]) and 19.9 kg.150^{-2} on offshore reef types (95% CI [7.3-32.5]). The greater biomass on pinnacle

301 reefs compared to nearshore reefs was significant (biomass contrast ratio 3.8:1 (95% CI [1.73-

302 8.37]), though the differences in biomass between pinnacles and offshore, or offshore and nearshore

303 were not statistically significant (Fig. 2b and e, electronic supplementary material Table S2).

304

305 Similar patterns were found in the diversity of predatory reef fishes (Fig. 2c and f, electronic

306 supplementary material Table S3), where mean Shannon diversity (H) ranged from 0.27 to 1.24

307 150m^{-2} among reef types. Pinnacles supported a greater diversity of predatory fishes than offshore

308 reefs (H contrast ratio: 2.48:1, 95% CI [1.42-4.34]) and nearshore reefs (H contrast ratio: 4.54:1,

309 95% CI [2.30-8.98], Fig. 2c and f). Offshore reefs, also had higher average diversity levels than

310 nearshore reefs, although the magnitude of this effect was less than for pinnacle to other reefs (H

311 contrast ratio: 1.83:1, 95% CI [0.85-3.93]).

312

313 **3.2. Assemblage composition**

314 Of the 63 predator fish taxa observed during this study, 53 (84%) were observed on pinnacle reefs

315 and just six species were shared by all three reef-types (Fig. 3b). These were *Carangoides bajad,*

316 *Cephalopholis microprion, Lutjanus biguttatus, Lutjanus gibbus, Macolor macularis, Plectropomus*

317 *oligacanthus* and all were most abundant on pinnacle reefs (Table 1). Pinnacles also had the largest

318 number of unique species (32), while nearshore and offshore reefs had 4 and 2 unique species,

319 respectively (Fig. 3b, electronic supplementary material Table S4). Ten taxa were not observed on

320 pinnacles and the multivariate GLM identified significant differences in community composition

321 between reef types (total multivariate LRT = 507, df = 119, p = 0.02), with the biggest pairwise

322 difference being between pinnacle and nearshore reefs (LRT = 339, p = 0.001, Table 2).

323

324 The multivariate GLM also identified six species significantly driving these differences in

325 community composition: *Sphyraena qenie* (LRT 31.07, p = 0.02), *Caranx sexfasciatus* (LRT 32.01,

326 p = 0.02), *Macolor macularis* (LRT 58.08, p = 0.02), *Caranx melampygus* (LRT 35.33, p = 0.02),

327 *Lutjanus gibbus* (LRT 23.61, p = 0.045) and *Cephalopholis cyanostigma* (LRT 22.14, p = 0.045).

328 These taxa were all most abundant on pinnacle reefs, with the two *Caranx* species and *Sphyraena*

329 *qenie* entirely absent from any survey on nearshore or offshore emergent reefs. The two lutjanid

330 taxa were present across all reef types although *Macolor macularis* was c.4-100 times more

331 abundant on pinnacle reefs than the other two reef types while *Lutjanus gibbus* was 5-10 times

332 more abundant. The serranid, *Cephalopholis cyanostigma* was not observed at all on nearshore reefs

333 and while relatively rare on both other reef types, was nearly 50% more abundant on pinnacles than

334 offshore reefs (Table 2, Fig. 4). This broad pattern was also followed at family-level, with the

335 pinnacle reefs supporting 6 predator families with representatives not found on the other two reef

336 types. This included the only observations of reef sharks, *Carcharhinus amblyrhynchos*, of which

337 there were just six observed on two of the pinnacles (electronic supplementary material Table S4).

338 Members of the nocturnal families Holocentridae and Priacanthidae were also only observed on one

339 pinnacle, Bradford Shoals. Neither nearshore nor offshore reefs had families not observed on

340 pinnacle reefs. The multivariate visualisation identified the same pattern, with substantial separation

341 of communities across reef types and species scores for the 6 significant taxa strongly aligning with

342 the first NMDS axis (Fig. 3a).

343

344 **4. DISCUSSION**

345 Our results highlight a strong effect of reef type on the abundance, biomass and diversity of

346 predatory fishes in Kimbe Bay, Papua New Guinea and suggest that pinnacle reefs are particularly

347 important in driving these patterns. Pinnacle reefs support significantly (2-4x) more abundant and

348 diverse assemblages with higher biomass densities than nearby coastal and offshore emergent reef

349 types. Predator assemblages were also distinct on pinnacles compared to those of emergent reef

350 habitats, with over 50% of the taxa recorded across our study being observed only on pinnacle

351 reefs. Similar accumulations of diversity and biomass have been reported for broader fish

352 assemblages on the pinnacles used in this study (Galbraith et al. 2021) and for predator taxa on

353 pinnacles and seamounts across the wider Indo-Pacific (Letessier et al. 2019). Overall, this suggests

354 offshore pinnacle reefs are biodiversity "hotspots" for a range of species, including predatory fishes

355 that are either resident on, or are attracted to and aggregate around these unique structures. Given

356 the multiple lines of evidence emerging for these effects, we propose pinnacle reefs may function as

357 "ecological magnets", concentrating both biota and associated ecological interactions across

358 multiple trophic levels into small focal points, with the capacity to sustain large numbers of

359 predators. The obvious conservation value of these habitats, in combination with small individual

360 area and high potential for exploitation, highlights the need to incorporate pinnacle reefs into future

361 management plans, with reducing fishing pressure and other human impacts a high priority.

362

363 While patterns in abundance, biomass and diversity among reef types were similar, the drivers of

364 these may be different. The significant contrast in overall abundance (on average over three times

365 greater on pinnacle reefs) was in part due to substantial schools of barracuda (*Sphyraena sp.*) and

366 trevally (*Caranx spp.*), neither of which were observed at nearshore or offshore emergent reefs.

367 This was particularly noticeable at one pinnacle site (Bradford Shoals, electronic supplementary

368 material Fig. S2) where schools of several hundred *S. qenie* markedly influenced overall abundance

369 and biomass patterns. For these and other similar species, pinnacles may be acting as sites of daily

370 aggregations, with pelagic foraging potentially occurring elsewhere at night, although anecdotal

371 evidence suggests that these two taxa may also be nocturnally active in the immediate vicinity of

372 the pinnacles (Pers. obs., 2019). Other species of predatory fishes on pinnacles may be less likely to

373 make substantial movements away from these structures, which are isolated from other coral reef

374 habitat by many kilometres of distance and hundreds of meters depth of water. Despite this

375 isolation, patterns of distribution and abundance were consistent across the whole predator

376 assemblage: 19 out of the 20 most commonly observed species in our study were more abundant on

377 pinnacles than the other two reef types. Most of these were lutjanids and serranids, likely to have

378 stronger habitat associations and smaller home ranges compared to the carangids and sphyraenids in

379 this study, particularly when found on pinnacle reef summits (Afonso et al. 2016). Inclusion or

380 exclusion of nocturnal species may also influence overall patterns in a study like this, however

381 overall numbers of such taxa were in single digits and unlikely to alter the patterns we observed.

382

383 Differences in predator biomass were similar to abundance. However, while pinnacles had the most

384 overall biomass, there was also a two-fold difference between offshore and nearshore reef types.

385 The fact that the differences in biomass between pinnacles and offshore reefs were less striking than

386 differences in abundance might be attributed to the high levels of diversity on the pinnacles, where

387 there were numerous smaller-bodied lutjanid and serranid species, either absent or less abundant on

388 offshore reefs (e.g., *Pinjalo* spp. and *Cephalopholis* spp.). Such species may have been truly absent

389 on offshore reefs or may have been more cryptic in these habitats compared to pinnacles and thus

390 less likely to be detected during our surveys. As species are accumulated in survey counts, there is

391 an increasing chance that these will be because of smaller, rarer and more cryptic taxa, rather than

392 common or large-bodied species. As a consequence for the predator assemblages in our study, high

393 abundance, combined with high diversity may actually translate to relatively lower observed

394 biomass. A complementary explanation is that large-bodied predators, more commonly found on

395 the pinnacles may skew biomass estimates on these structures, although numbers of sharks

396 observed across the entire study were low.

397

398 Diversity patterns across reef types were again similar, with the pinnacles supporting c. 2-5 times

399 more predator fish diversity than offshore or nearshore reefs respectively. Strong species-habitat

400 linkages behind this trend are likely due to the presence of a range of unique or enhanced beneficial

401 resources available on pinnacles. These may take the form of food, shelter, navigation or mating

402 opportunities, each operating at different strengths across taxa and for specific life-history events or

403 phases. The actual structure of pinnacles may also promote two other ecological phenomena that

404 could enhance biodiversity: Firstly, pinnacle summits are small, which means their occupants must

405 live in close proximity. Such proximity may increase competition, in turn promoting strong

406 resource partitioning and high levels of assemblage diversity, or alternatively may promote positive

407 species interactions between predator species that enhance prey detection and capture (Auster et al.

408 2013, 2019, Campanella et al. 2019). Secondly, the "conical" shape of pinnacle summits means that

409   a large amount of reef surface area is in contact with, and influenced by surrounding ocean water,

410   increasing the potential for edge effects on these habitats. Edge effects can promote diversity

411   (Bellaver et al. 2023), particularly for small, isolated habitat patches (Ting & Shaolin 2008).

412   Potential implications of high predator diversity on wider communities on pinnacles seem obvious:

413   prey species must avoid a larger variety of predator taxa ("diffuse predation" *sensu* Hixon 1991).

414   That whole fish assemblages on pinnacles are also the most diverse within Kimbe Bay (Galbraith *et*

415   *al.,* 2021) supports the concept of predation together with competition as interacting regulators of

416   diversity at lower trophic levels, at least in our study system.

417

418   Differences in diversity were also reflected in the important differences in community composition

419   between reef types. While this can be mainly attributed to variability in abundance of just six

420   species identified by the multivariate GLM, only six other taxa were shared by all three reef types

421   and, despite being relatively small, pinnacles possessed 32 unique species. However, the pinnacles

422   also supported all but 10 out of the 63 taxa observed in this study. This number is reduced to 4

423   when offshore reefs are included, suggesting that the isolation and depth of both offshore and

424   pinnacle reefs collectively provide a valuable potential source of biodiversity refugia and, if used as

425   spawning locations, an important larval resupply source for other reefs in the area. This may be

426   particularly important for predatory fish populations and communities on shallow, nearshore reefs,

427   which may be particularly impacted by localised anthropogenic disturbances such as overfishing,

428   pollution and coastal development. Spatial differences in assemblage structure also have

429   implications for overall seascape connectivity and diversity: organisms with restricted distributions

430   (less than 10% of taxa were recorded on all three reef types) are less able to utilise the spectrum of

431   otherwise available habitats in the course of their existence. Any local threat to such a taxon would

432   directly translate to a seascape effect. Further, while gamma diversity may be high across our study

433   system, correspondingly high levels of beta diversity may actually decrease functional redundancy

434 among predators at a local scale and therefore in predation as an ecosystem process, a pattern

435 observed in other trophic guilds of coral reef fishes (Bellwood et al. 2003).

436

437 Differences in benthic habitat, quality and complexity, as well as frequency and intensity of

438 disturbances, are known drivers of diversity and abundance on coral reefs. However, recent work on

439 the same reefs used in this study found no effect of variation in benthic composition on broad fish

440 community structure (Galbraith et al. 2021). Rugosity, the number and size of holes, crevices and

441 overhangs and reef aspect are additional benthic structural complexity measures which have been

442 linked to reef-scale variability of fish communities, including predators (Hixon 2015, Agudo-

443 Adriani et al. 2019). Alternatively, more detailed measures of habitat complexity and quality may

444 therefore be needed to elucidate the relationships between fish communities and the types of reef

445 habitat in our study system. Furthermore, site quality, prey availability and the presence of

446 conspecifics are potential covariates and may confound the perceived effect of relatively simple

447 habitat metrics such as total coral cover. Direct links between predatory fishes and benthic systems

448 are likely more ambiguous over time and space (e.g. diurnal foraging behaviour (Papastamatiou *et*

449 *al.*, 2015; Williams *et al.*, 2018)). Clearly, further study is warranted on dietary pathways and

450 predation pressure to better understand links between predator fishes and benthic trophodynamics in

451 these systems.

452

453 Movement of water at all scales is also a known driver of community ecology in coastal systems

454 (Young et al. 2021) and seamounts or pinnacles (Klimley et al. 2005, Campanella et al. 2021,

455 Bridges et al. 2022). Recent work in our study system has demonstrated the importance of

456 hydrodynamic forces in shaping wider biological communities (Galbraith et al. 2022) where

457 pinnacles are characterised by strong ocean currents leading to localised upwelling and complex

458 eddies. These same hydrodynamics may be particularly important for predator species: fishers and

459 divers have long utilised local knowledge of currents, eddies and other water movement to inform

460   where and when to seek out aggregations of charismatic predator species (Richert et al. 2017).

461   Precisely what benefit such currents may provide to predatory fishes is yet to be described (but see

462   Fisher *et al.*, 2018), however a growing body of work suggests that reef food webs that are exposed

463   to allochthonous pelagic nutrient inputs may receive a substantial benefit from these. A recent study

464   in the Maldives demonstrated that, for a number of coral reef predator taxa, trophic pathways with

465   offshore pelagic origins are far more important in diets than local, reef-based sources (Skinner et al.

466   2021). These pathways may sustain wider fish productivity, even on degraded reefs (Morais &

467   Bellwood 2019). Given that mobile predators themselves may act as vectors of nutrients from the

468   wider pelagic environment onto coral reefs (Williams et al. 2018), where reefs host large numbers

469   of these predator taxa, such nutrient inputs may be particularly important. Despite this, these inputs

470   to coral reefs are often referred to as "pelagic subsidies" or "contributions" to "nutrient cycling"

471   (Papastamatiou et al. 2015, Morais & Bellwood 2019), but if these paradigms hold across a wide

472   biogeographic area, the term "pelagic dominated sources" may be more appropriate.

473

474   Predator assemblages on coastal reefs of the region may be affected by extensive local agricultural

475   activity and associated terrestrial runoff, which is known to promote high algal cover and

476   smothering of the benthos with sediment (Beger & Possingham 2008). Both of these processes are

477   characteristic of reef degradation and are potential drivers of altered fish communities (Fabricius

478   2005). Habitat degradation by coral bleaching events has also affected the reefs of Kimbe Bay over

479   the past two decades (Jones et al. 2004) and recovery of reef communities from these bleaching

480   events has varied, with reefs farther offshore showing greater ability to recover compared to those

481   closer to terrestrial stressors (e.g., sedimentation from runoff) (Munday 2004). Relationships

482   between benthic habitat dynamics and fish community structure can vary as a product of seascape

483   position and temporal stochastic environmental change (Tsai et al. 2022).

484

485   Another explanation for low levels of abundance, diversity and biomass observed on nearshore

486   reefs is the possibility of direct anthropogenic disturbance. The most obvious example of such

487   disturbance is that of increased fishing pressure closer to shore. If present, the expected effect of

488   this would be decreased numbers of certain fishery target species, but is less likely to account for

489   the absence of over two-thirds of the taxa across our study (41 of 63 species) on coastal reefs.

490   Additionally, we took steps to control for fishing pressure by using only nearshore reefs that are

491   protected under the locally managed marine area scheme, established in 2007. This program is

492   widely regarded to be effective and the local community are effectively engaged in enforcing

493   protection on these reefs (Green et al. 2009). Conversely, both the pinnacles and offshore reefs may

494   experience some degree of residual protection thanks to their remote and isolated settings. Offshore

495   reefs with emergent crests may be easier to locate for the limited numbers of local fishers with the

496   means of accessing these reefs such as power-boats, while the pinnacles can only be located with

497   GPS equipment. Given that both powered vessels and GPS technology are typically unavailable to

498   subsistence and artisanal fishers of the region, fishing pressure alone is unlikely to explain

499   differences in predator fish communities between these two reef types. The second form of direct

500   anthropogenic disturbance that may be operating is altered fish behaviour (and thus presence or

501   absence in our surveys) as a result of the presence of divers in the water (Dearden et al. 2010). Such

502   an effect may have occurred during our surveys, however it seems likely that this effect would have

503   been similar across reef types, rather than differing between them, and likely affected cryptic taxa

504   (Goetze et al. 2019), rather than the large bodied predators that were the focus of this study. In

505   addition, we aimed to use best practice methods for in-water surveys, including the use of a second

506   diver to deploy transect tapes (Dickens et al. 2011).

507

508   In conclusion, our study reveals distinct patterns in predator fish abundance, diversity and

509   community structure on pinnacle reefs and raises questions about why and how these habitats

510   support unique communities of these organisms. Broadly, our results lend weight to international

511 calls for protecting pinnacle and seamount structures as unique hotspots of biodiversity and

512 commercially valuable predatory species (Pitcher et al. 2010, Richert et al. 2017, Watling & Auster

513 2017). Further work is required to better understand these unique systems, their biological

514 communities and broader ecological role in wider coral reef seascapes. From a conservation

515 perspective, large predatory fishes are clearly under considerable threat from extreme overfishing

516 throughout the world's oceans (Myers & Worm 2003). Pinnacles represent quintessential

517 "biodiversity hotspots" (*sensu* Myers, 1988), where a large proportion of the abundance, biomass

518 and diversity of predators is confined to small geographic areas. At an oceanic scale, pinnacles may

519 be mere dots in the wider seascape, but they appear to function as ecological magnets, attracting

520 individuals, species and big fish. While in one sense this makes them vulnerable, it also makes it

521 possible to conserve a large proportion of species assemblages in relatively few and small marine

522 protected areas. Such areas however must allow pinnacle reefs to remain unmarked and maximise

523 their inherent safeguard against exploitation, namely isolation.

524

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534

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798 **Tables**

799 Table 1. Average predator fish abundance (numbers per 150m^{-2} ±SE) of the 20 most abundant species in this study. Taxa are sorted based on LRT scores and P values from the

800 multivariate GLM. * denotes taxa significantly contributing to differences in assemblage composition. † denotes taxa encountered across all reef types. †† denotes taxa designated as

801 planktivores, however literatures suggests this is likely combined with piscivory for these species (Allen, 1985)

802

Taxa	Common name	Family	Trophic group	Mean fish abundance by reef type (n transect^{-1})									Total n	LRT	P-val
				Pinnacle			Offshore			Nearshore					
Macolor macularis †*	Midnight snapper	Lutjanidae	Planktivore††	4.83	±	1.69	1.23	±	0.32	0.05	±	0.03	244	58.08	0.002
Caranx melampygus*	Blue-fin trevally	Carangidae	Piscivore	0.98	±	0.28	0	±	0	0	±	0	39	35.33	0.002
Sphyraena qenie*	Chevron barracuda	Sphyraenidae	Piscivore	31.88	±	23.05	0	±	0	0	±	0	1275	31.07	0.006
Caranx sexfasciatus*	Big-eye trevally	Carangidae	Piscivore	7.55	±	3.5	0	±	0	0	±	0	302	32.01	0.006
Lutjanus gibbus †*	Paddletail snapper	Lutjanidae	Invertivore	1.63	±	0.6	0.28	±	0.13	0.15	±	0.07	82	23.61	0.045
Cephalopholis cyanostigma*	Bluespotted hind	Serranidae	Piscivore	0.48	±	0.17	0.33	±	0.08	0	±	0	32	22.14	0.045
Macolor niger	Black-and-white snapper	Lutjanidae	Planktivore††	1.58	±	1.17	0.05	±	0.05	0	±	0	65	18.26	0.162
Plectropomus oligacanthus †	Highfin coral trout	Serranidae	Piscivore	1.03	±	0.29	0.25	±	0.08	0.1	±	0.06	55	16.46	0.172
Lutjanus bohar	Red bass	Lutjanidae	Piscivore	0.38	±	0.14	0	±	0	0.03	±	0.03	16	17.6	0.172
Cephalopholis miniata	Coral grouper	Serranidae	Piscivore	0.25	±	0.11	0	±	0	0	±	0	10	13.98	0.218
Lutjanus biguttatus †	Two-spot snapper	Lutjanidae	Invertivore	2.95	±	1.3	0.38	±	0.13	0.15	±	0.07	139	12.72	0.245
Cephalopholis urodeta	Darkfin hind	Serranidae	Invertivore	0.45	±	0.43	0	±	0	0	±	0	18	11.17	0.253
Lutjanus monostigma	Onespot snapper	Lutjanidae	Piscivore	0	±	0	0.25	±	0.11	0.08	±	0.04	13	10.14	0.431
Platax teira	Teira spadefish	Ephippidae	Piscivore	0.78	±	0.7	0.05	±	0.03	0	±	0	33	8.28	0.621
Carangoides bajad †	Orange-spotted trevally	Carangidae	Piscivore	0.3	±	0.12	0.03	±	0.03	0.05	±	0.03	15	7.32	0.621
Variola albimarginata	Coronation trout	Serranidae	Piscivore	0.2	±	0.1	0.03	±	0.03	0	±	0	9	8.82	0.621
Pinjalo lewisi	Slender pinjalo	Lutjanidae	Planktivore††	1.3	±	1.16	0	±	0	0	±	0	52	4.49	0.841
Monotaxis heterodon	Redfin emperor	Lethrinidae	Piscivore	0.43	±	0.3	0.03	±	0.03	0	±	0	18	4.46	1
Cephalopholis microprion †	Freckled hind	Serranidae	Piscivore	0.25	±	0.16	0.03	±	0.03	0.08	±	0.04	14	4.22	1
Pinjalo pinjalo	Pinjalo snapper	Lutjanidae	Invertivore	0.33	±	0.33	0	±	0	0	±	0	13	2.22	1

803

804   Table 2. Pairwise contrasts in assemblage composition across all reef types.

Pairwise contrast	LRT	Adjusted P-val
Pinnacle vs Nearshore	338.6074	0.001
Pinnacle vs Offshore	268.4959	0.001
Offshore vs Nearshore	87.0182	0.001

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Coral reef pinnacles as predator magnets

807 **Figures**
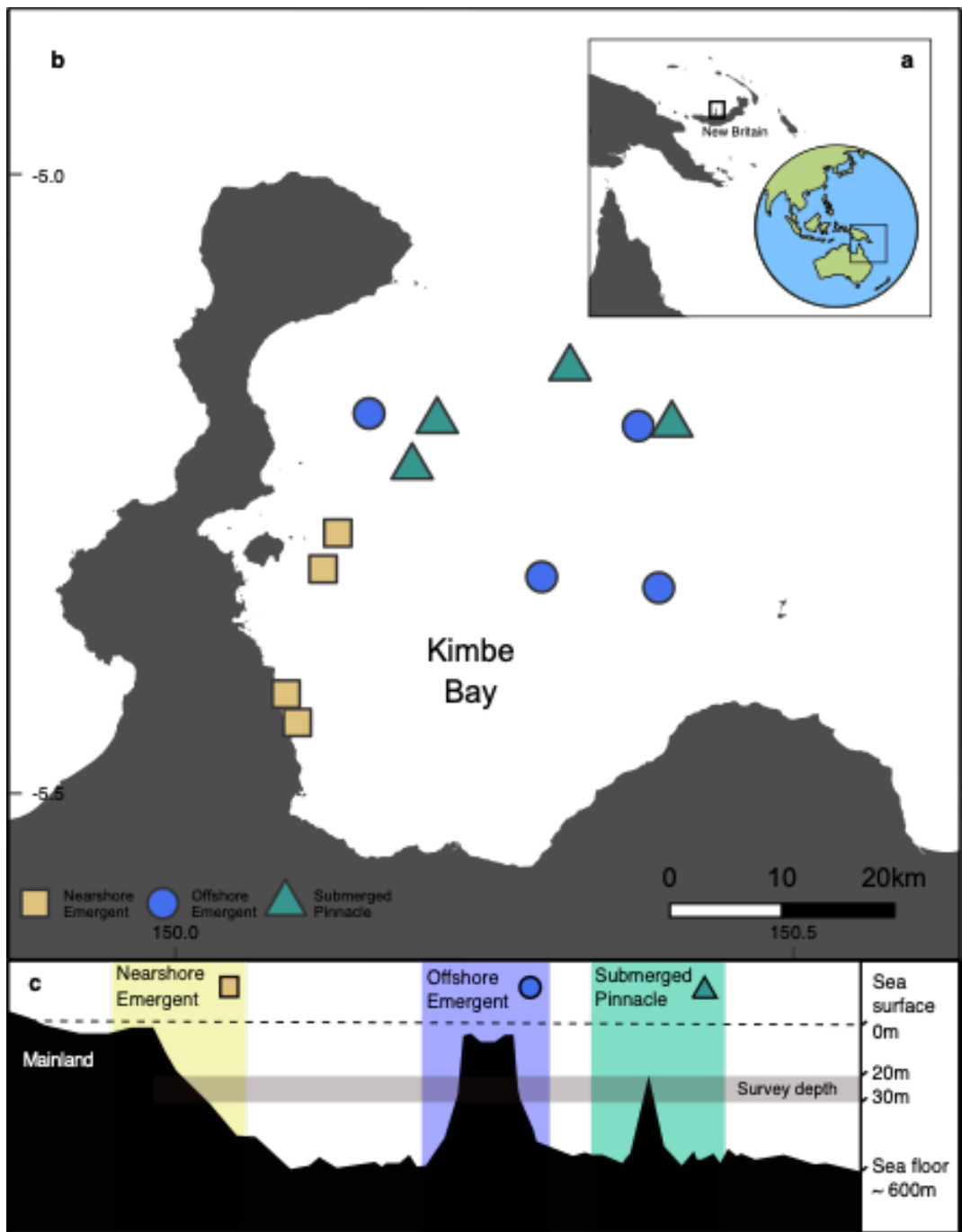
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810 **Fig. 1.** Study area locations and visual representation of the seascape. (**a**) Kimbe Bay, situated in

811 the Bismarck Sea on the north coast of the province of West New Britain, Papua New Guinea, (**b**)

812 Focal sites include four nearshore emergent reefs, four offshore emergent reef and four submerged

813 pinnacles situated throughout Kimbe Bay, (**c**) Visual representation of the sea floor showing the

814 three reef types and depth zone (20-30m) surveyed.

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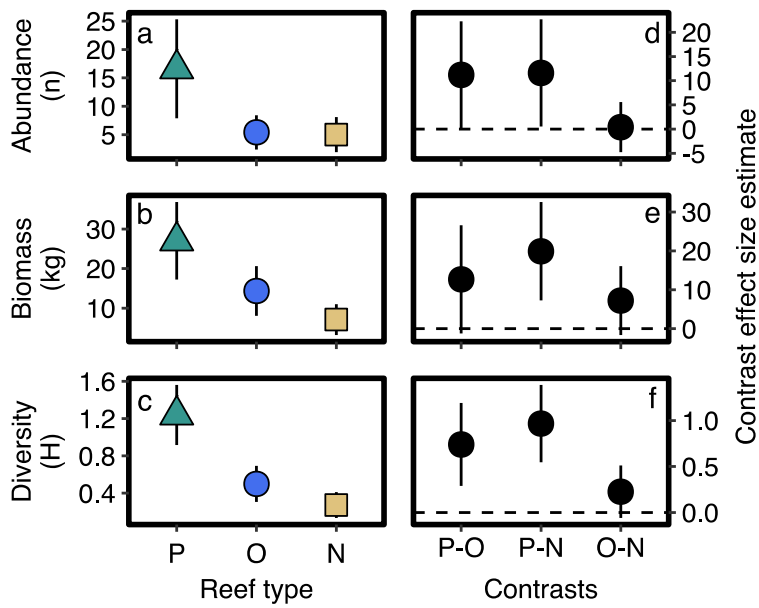
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818   **Fig. 2.** Estimated marginal means (± CI 95%) for **(a)** Abundance (numbers. $150m^{-2}$), **(b)** Biomass

819   (kg. $150m^{-2}$) and **(c)** diversity (Shannon-Wiener H. $150m^{-2}$) and pairwise contrasts (± CI 95%) (**(d),**

820   **(e), (f)**). Contrasts with 95% CI. CIs that cross the zero level are considered non-significant. P=

821   Pinnacle reef, N= nearshore reef, O= offshore reef. Post-hoc pairwise contrasts: P-O = Pinnacle-

822   Offshore, P-N= Pinnacle-Nearshore, O-N=Offshore-Nearshore.

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Coral reef pinnacles as predator magnets
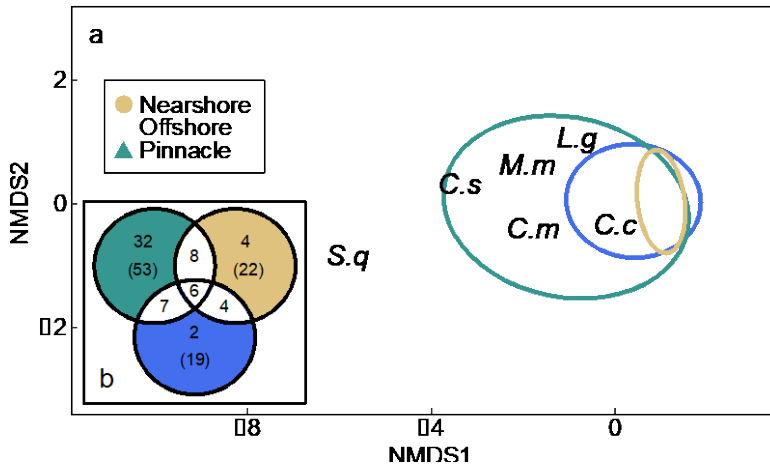
Fig. 3. Differences in assemblage composition across reef types. (**a**) NMDS with 95% CI ellipses presented. Species loadings plotted for the six significant taxa identified in the multivariate GLM: *Macolor macularis* (M.m), *Caranx melampygus* (C.m), *Sphyraena qenie* (S.q), *Caranx sexfasciatus* (C.s), *Lutjanus gibbus* (L.g), *Cephalopholis cyanostigma* (C.c). Stress = 0.15. (**b**) Alpha and beta diversity (shared and unique taxa) across reef types. Numbers in parentheses are total numbers of species observed at each reef type.

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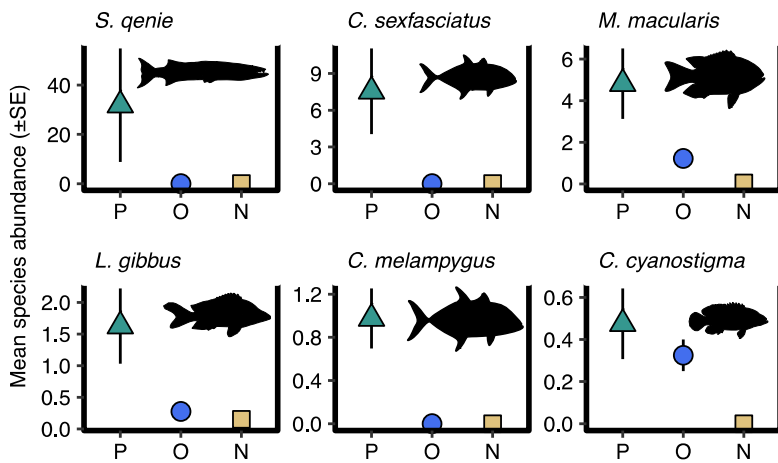
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834 **Fig. 4.** Abundance (numbers. $150m^{-2}$ ($\pm$ CI 95%)) of the six major taxa driving significant

835 differences in predator assemblage composition between reef types.

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Coral reef pinnacles as predator magnets

852   Electronic supplementary information

853

854   Table S1. Estimated marginal means of abundance ($n.150m^{-2}$) of predatory fishes across reef types and pairwise contrast

855   effect sizes and ratios.

Reef type	Abundance ($N\ 150m^{-2}$)	95% CI	DF	Pairwise contrast	Effect size ($N\ 150m^{-2}$)	95% CI	Effect ratio (x:1)	95% CI
Pinnacle	16.6	7.9-25.3	115	Pinnacle - Offshore	11.2	0.2-22.2	3.07	1.23-7.68
Offshore	5.4	2.4-8.4	115	Pinnacle - Nearshore	11.6	0.5-22.7	3.32	1.26-8.77
Nearshore	5	1.9-8.1	115	Offshore - Nearshore	0.4	-4.8-5.6	1.08	0.4-2.93

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857

858   Table S2. Estimated marginal means of predatory fish biomass ($kg.150m^{-2}$) across reef types and pairwise contrast effect

859   sizes and ratios.

Reef type	Biomass ($kg\ 150m^{-2}$)	95% CI	DF	Pairwise contrast	Effect size ($kg\ 150m^{-2}$)	95% CI	Effect ratio (x:1)	95% CI
Pinnacle	27	17.2-36.8	114	Pinnacle - Offshore	12.7	-1.2-26.6	1.88	0.95-3.72
Offshore	14.3	8-20.6	114	Pinnacle - Nearshore	19.9	7.3-32.5	3.8	1.73-8.37
Nearshore	7.1	3.2-11	114	Offshore - Nearshore	7.2	-1.6-16.1	2.02	0.87-4.69

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861

862   Table S3. Estimated marginal means of predatory fish diversity ($H.\ 150m^{-2}$) across reef types and pairwise contrast effect

863   sizes and ratios.

Reef type	Shannon diversity ($H\ 150m^{-2}$)	95% CI	DF	Pairwise contrast	Effect size ($H\ 150m^{-2}$)	95% CI	Effect ratio (x:1)	95% CI
Pinnacle	1.24	0.92-1.56	114	Pinnacle - Offshore	0.74	0.29-1.19	2.48	1.42-4.34
Offshore	0.5	0.31-0.69	114	Pinnacle - Nearshore	0.97	0.55-1.39	4.54	2.3-8.98
Nearshore	0.27	0.13-0.41	114	Offshore - Nearshore	0.23	-0.57	1.83	0.85-3.93

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866   Table S4. Average predator fish abundance (N 150m^{-2} ± SE) of all species observed in this study.

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Family	Taxa	Mean fish abundance by reef type (N 150m^{-2} ± SE)									Study total N
		Pinnacle			Offshore			Nearshore			
Carangidae	*Carangoides bajad*	0.3	±	0.12	0.03	±	0.02	0.05	±	0.03	15
Carangidae	*Caranx ignobilis*	0.07	±	0.04	0	±	0	0	±	0	3
Carangidae	*Caranx melampygus*	0.98	±	0.28	0	±	0	0	±	0	39
Carangidae	*Caranx sexfasciatus*	7.55	±	3.5	0	±	0	0	±	0	302
Carangidae	*Elagatis bipinnulata*	0.07	±	0.06	0.05	±	0.03	0	±	0	5
Carcharhinidae	*Carcharhinus amblyrhynchos*	0.12	±	0.08	0	±	0	0	±	0	5
Carcharhinidae	*Carcharhinus melanopterus*	0.03	±	0.02	0	±	0	0	±	0	1
Cirrhitidae	*Paracirrhites forsteri*	0.12	±	0.06	0	±	0	0	±	0	5
Ephippidae	*Platax teira*	0.78	±	0.7	0.05	±	0.03	0	±	0	33
Haemulidae	*Plectorhinchus chaetodonoides*	0	±	0	0	±	0	0.03	±	0.02	1
Haemulidae	*Plectorhinchus picus*	0.03	±	0.02	0	±	0	0	±	0	1
Holocentridae	*Myripristis botche*	0.03	±	0.02	0	±	0	0	±	0	1
Holocentridae	*Sargocentron spiniferum*	0.1	±	0.08	0	±	0	0	±	0	4
Labridae	*Cheilinus undulatus*	0.1	±	0.05	0	±	0	0	±	0	4
Labridae	*Epibulus insidiator*	0	±	0	0.03	±	0.02	0	±	0	1
Labridae	*Oxycheilinus digramma*	0	±	0	0.07	±	0.06	0.05	±	0.03	5
Lethrinidae	*Gymnocranius grandoculis*	0	±	0	0.05	±	0.03	0	±	0	2
Lethrinidae	*Lethrinus erythracanthus*	0.07	±	0.06	0	±	0	0	±	0	3
Lethrinidae	*Lethrinus ornatus*	0.03	±	0.02	0	±	0	0	±	0	1
Lethrinidae	*Monotaxis grandoculis*	0.1	±	0.06	0	±	0	0.05	±	0.03	6
Lethrinidae	*Monotaxis heterodon*	0.42	±	0.3	0.03	±	0.02	0	±	0	18
Lutjanidae	*Lutjanus biguttatus*	2.95	±	1.3	0.38	±	0.13	0.15	±	0.07	139
Lutjanidae	*Lutjanus bohar*	0.38	±	0.14	0	±	0	0.03	±	0.02	16
Lutjanidae	*Lutjanus boutton*	0	±	0	0.03	±	0.02	0.03	±	0.02	2
Lutjanidae	*Lutjanus carponotatus*	0.05	±	0.05	0	±	0	0.03	±	0.02	3
Lutjanidae	*Lutjanus ehrenbergii*	0.07	±	0.04	0	±	0	0.03	±	0.02	4
Lutjanidae	*Lutjanus fulvus*	0.03	±	0.02	0	±	0	0	±	0	1
Lutjanidae	*Lutjanus gibbus*	1.62	±	0.6	0.28	±	0.13	0.15	±	0.07	82
Lutjanidae	*Lutjanus kasmira*	0.17	±	0.09	0	±	0	0	±	0	7
Lutjanidae	*Lutjanus monostigma*	0	±	0	0.25	±	0.11	0.07	±	0.04	13
Lutjanidae	*Lutjanus papuensis*	0.03	±	0.02	0	±	0	0	±	0	1
Lutjanidae	*Lutjanus rivulatus*	0.03	±	0.02	0	±	0	0	±	0	1
Lutjanidae	*Lutjanus russellii*	0	±	0	0.03	±	0.02	0.03	±	0.02	2
Lutjanidae	*Lutjanus semicinctus*	0	±	0	0	±	0	0.12	±	0.06	5
Lutjanidae	*Macolor macularis*	4.82	±	1.69	1.23	±	0.32	0.05	±	0.03	244
Lutjanidae	*Macolor niger*	1.57	±	1.17	0.05	±	0.05	0	±	0	65
Lutjanidae	*Pinjalo lewisi*	1.3	±	1.16	0	±	0	0	±	0	52
Lutjanidae	*Pinjalo pinjalo*	0.32	±	0.32	0	±	0	0	±	0	13
Priacanthidae	*Priacanthus hamrur*	0.03	±	0.02	0	±	0	0	±	0	1

| Family	Species										
Scombridae	*Grammatorcynus bilineatus*	0.05	±	0.05	0	±	0	0	±	0	2
Scombridae	*Gymnosarda unicolor*	0.07	±	0.04	0.05	±	0.03	0	±	0	5
Serranidae	*Anyperodon leucogrammicus*	0	±	0	0	±	0	0.03	±	0.02	1
Serranidae	*Cephalopholis argus*	0.15	±	0.07	0	±	0	0.03	±	0.02	7
Serranidae	*Cephalopholis cyanostigma*	0.48	±	0.17	0.32	±	0.07	0	±	0	32
Serranidae	*Cephalopholis leopardus*	0.05	±	0.05	0	±	0	0.05	±	0.05	4
Serranidae	*Cephalopholis microprion*	0.25	±	0.16	0.03	±	0.02	0.07	±	0.04	14
Serranidae	*Cephalopholis miniata*	0.25	±	0.11	0	±	0	0	±	0	10
Serranidae	*Cephalopholis sexmaculata*	0.03	±	0.02	0	±	0	0	±	0	1
Serranidae	*Cephalopholis sonnerati*	0.03	±	0.02	0	±	0	0	±	0	1
Serranidae	*Cephalopholis urodeta*	0.45	±	0.43	0	±	0	0	±	0	18
Serranidae	*Diploprion bifasciatum*	0	±	0	0	±	0	0.05	±	0.03	2
Serranidae	*Epinephelus areolatus*	0.03	±	0.02	0	±	0	0	±	0	1
Serranidae	*Epinephelus coeruleopunctatus*	0.03	±	0.02	0	±	0	0.03	±	0.02	2
Serranidae	*Epinephelus fasciatus*	0.05	±	0.05	0	±	0	0	±	0	2
Serranidae	*Epinephelus polyphekadion*	0.03	±	0.02	0	±	0	0	±	0	1
Serranidae	*Epinephelus tauvina*	0.03	±	0.02	0	±	0	0	±	0	1
Serranidae	*Gracila albomarginata*	0.05	±	0.03	0	±	0	0	±	0	2
Serranidae	*Plectropomus laevis*	0.03	±	0.02	0	±	0	0	±	0	1
Serranidae	*Plectropomus leopardus*	0.12	±	0.05	0	±	0	0	±	0	5
Serranidae	*Plectropomus maculatus*	0.05	±	0.03	0	±	0	0.03	±	0.02	3
Serranidae	*Plectropomus oligacanthus*	1.02	±	0.29	0.25	±	0.08	0.1	±	0.06	55
Serranidae	*Variola albimarginata*	0.2	±	0.1	0.03	±	0.02	0	±	0	9
Sphyraenidae	*Sphyraena qenie*	31.88	±	23.05	0	±	0	0	±	0	1275

868
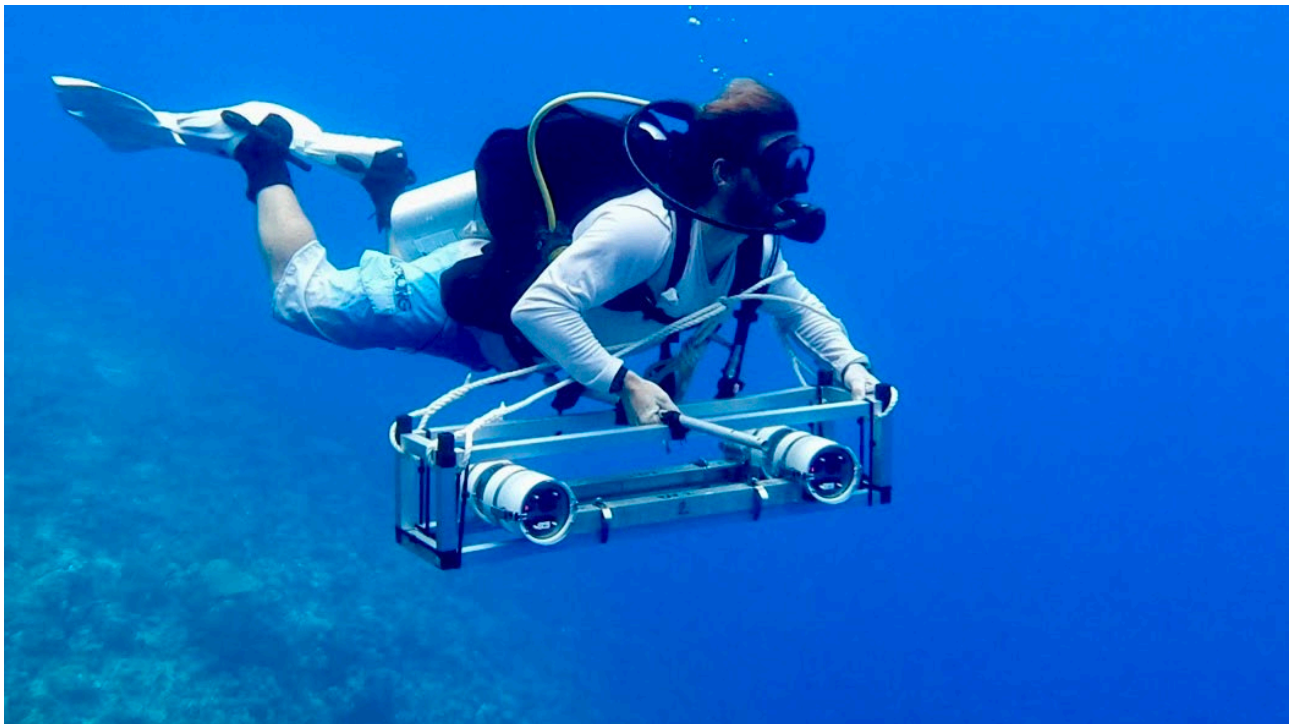
869

870 Fig. S1. Diver with stereo video system.

871
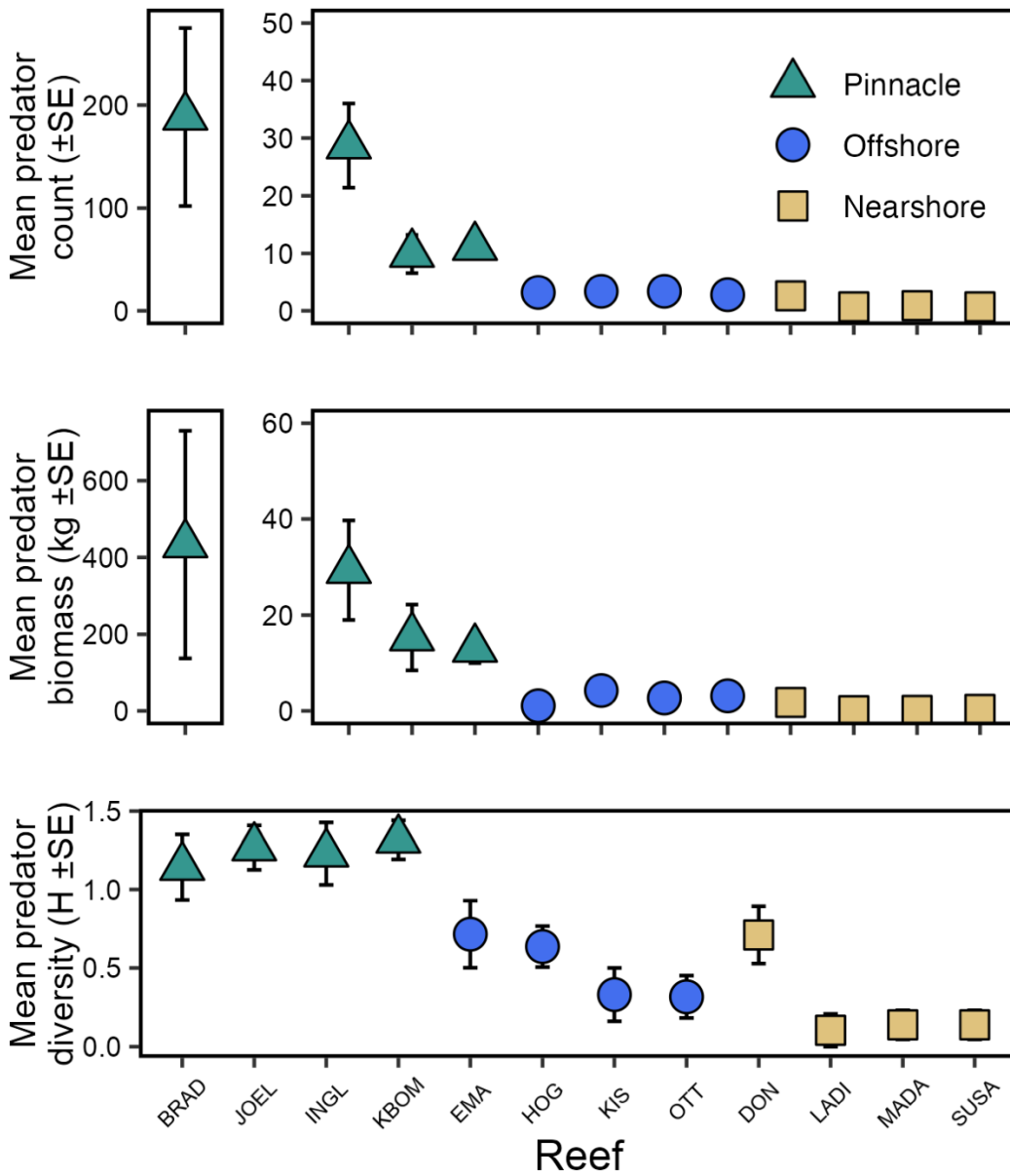
872

873

874   Fig. S2. Mean abundance, biomass and diversity values ($150m^{-2}$) for individual study sites. Point shape and colour

875   signifies reef types, error bars ±SE.

876