

This is the author-created version of the following work:

Galbraith, G.F., Cresswell, B., McCormick, M.I., Bridge, T.C., and Jones, G.P.
(2021) *High diversity, abundance and distinct fish assemblages on submerged coral reef pinnacles compared to shallow emergent reefs*. Coral Reefs, 40 pp. 335-354.

Access to this file is available from:

<https://researchonline.jcu.edu.au/66075/>

© The Author(s), under exclusive licence to Springer-Verlag GmbH, DE part of Springer Nature 2021

Please refer to the original source for the final version of this work:

<https://doi.org/10.1007/s00338%2D020%2D02044%2Dz>

1 **High diversity, abundance and distinct fish assemblages on**
2 **submerged coral reef pinnacles compared to shallow emergent reefs**

3

4 **Galbraith, G.F^{1,2}, Cresswell, B.J^{1,2}, McCormick, M.I², Bridge, T.C^{2,3} and Jones, G.P^{1,2}**

5 **1** Marine Biology and Aquaculture Sciences, College of Science and Engineering, James Cook University, Townsville,
6 4811, Australia

7 **2** ARC Centre of Excellence for Coral Reef Studies; James Cook University, Townsville, 4811, Australia

8 **3** Biodiversity and Geosciences Program, Museum of Tropical Queensland, Queensland Museum Network, Townsville,
9 4810, Australia

10

11

12 Corresponding author gemma.galbraith@jcu.edu.au

13

14

15 **Keywords** Submerged reefs – pinnacles – coral seamounts - offshore fish assemblages –

16 community ecology – biodiversity

17

18

19

20

21

22

23

24

25

26

27

28

29

30 **Abstract**

31 Coral reefs exhibit consistent patterns in biodiversity across multiple spatial scales, from
32 local to global clines in species richness, abundance and community structure. Knowledge of
33 fundamental processes driving these patterns is largely derived from studies of shallow,
34 emergent and nearshore reefs. Although research efforts are expanding to deeper mesophotic
35 coral reef ecology, distinct and isolated reef morphologies like submerged pinnacles or
36 seamounts have received scant attention. Despite being potentially important for connectivity
37 and as refugia, the extent to which established patterns and processes in coral reef ecology
38 apply to these systems is unknown. Here we examine the fish and benthic communities
39 associated with coral reefs found on submerged pinnacles in Kimbe Bay, Papua New Guinea.
40 Community structure and diversity metrics are compared with emergent reefs at the same
41 depth in both near and offshore settings. We then explicitly test whether benthic complexity
42 variables known to influence reef fish communities exhibit similar patterns at each reef type.
43 Pinnacles were characterised by 3.70 times the mean fish abundance and 1.98 times the
44 species richness recorded at the same depths on emergent reefs. Fish community structure
45 showed distinct separation across reef morphologies, with pinnacles most similar to offshore
46 reefs. Benthic habitat complexity did not vary across reef types while fish assemblages were
47 weakly related to benthic habitat variables, with reef morphology the most consistent
48 predictor of fish community metrics. The pinnacles in our study support high coral reef fish
49 biodiversity despite their small habitat area and relative isolation by depth and offshore
50 setting. Our results suggest that habitat-specific environmental conditions are generated by
51 the distinct geomorphology of pinnacles. As coastal reefs become more increasingly
52 disturbed, understanding ecological patterns on deep patch reef habitats like pinnacles will be
53 useful to provide a more holistic understanding of coral reef seascapes and their resilience.

54

55 **Introduction**

56 Coral reefs encompass a range of diverse and complex habitat structures, including fringing
57 reefs, barrier reefs, atolls and isolated patch reefs (Stoddart 1969; Hopley 2011). These
58 recognisable reef types form under different environmental conditions of depth, distance
59 offshore and exposure, and ecological patterns and processes vary in predictable ways along
60 these environmental gradients (Hopley et al. 2007; Malcolm et al. 2010; Williams et al. 2015;
61 Samoily et al. 2019). The stability of different reef structures also varies, and predicting
62 how these patterns and processes may respond to environmental change is now central to
63 much coral reef science (Harvey et al. 2018; Williams et al. 2019). However, most research
64 has been restricted to near-sea-surface, nearshore continuous reef systems, where
65 accessibility has facilitated extensive global studies (Spalding and Grenfell 1997; Bellwood
66 and Hughes 2001; Connolly et al. 2003; Hinderstein et al. 2010). There are significant areas
67 of submerged habitat available for coral reef formation which have historically been
68 overlooked, unexplored and remain understudied (Venn et al. 2009; Harris et al. 2013; Moura
69 et al. 2016; Moore et al. 2017). Interest in these kinds of habitats has accelerated because of
70 the potential for deep reefs to function as a refuge for species being adversely affected by reef
71 degradation in shallow coastal waters (Bridge et al. 2013; Laverick et al. 2016; Macdonald et
72 al. 2018).

73

74 Both the deep-sea and continental shelves possess a variety of distinct bathymetric features
75 that can support rich and diverse coral reef ecosystems where the summits reach the euphotic
76 zone (~0-150m) (Bridge et al. 2011b; Du Preez et al. 2016; Linklater et al. 2019). Global
77 bathymetric mapping reveals large areas (1000's of km²) of deep habitat available for coral
78 reef formation (Vora and Almeida 1990; Bridge et al. 2012; Harris et al. 2013). Submerged
79 reefs can be defined as “isolated elevations of the seafloor, over which the depth of water is

80 relatively shallow but sufficient for navigation (IHO 2008) and have their shallowest points
81 below 10-20m (Thomas et al. 2015). They can support extensive, diverse coral and fish
82 communities, which span both altiphotic (<30m) and mesophotic zones (30-150m) (Bridge et
83 al. 2011a; Roberts et al. 2015; Moore et al. 2017; Cooper et al. 2019). Many deep reefs are
84 likely to be more isolated from physical disturbances (e.g. storms, wave action), fishing
85 pressure and thermally induced bleaching events than emergent near-sea-surface counterparts
86 (Slattery et al. 2011; Lindfield et al. 2016; Baird et al. 2018; Crosbie et al. 2019).

87

88 Although most of the studies investigating the ecology and distribution of submerged coral
89 reef ecosystems have occurred on Australia's Great Barrier Reef, submerged reefs constitute
90 extensive areas of coral reef habitat across most low-latitude continental shelves (Locker et
91 al. 2010; Abbey and Webster 2011; Pinheiro et al. 2015; Heyward et al. 2019). Pinnacle coral
92 reefs are perhaps the most distinct submerged form and we define these as *abrupt, conical*
93 *structures, either isolated or at the summit of a larger bathymetric feature such as ridges or*
94 *banks that reach the euphotic zone, but do not breach the sea surface.* We make a distinction
95 from seamounts, where pinnacles are more closely associated with continental shelves and
96 slopes as opposed to oceanic sea-floor settings. Pinnacles tend to be comparatively smaller
97 structures and unlike seamounts, are not usually formed directly by volcanic activity but
98 instead are often a part of larger bathymetric features. In ecological terms however, pinnacles
99 and seamounts both provide a hard substratum for coral recruitment, forming isolated patch
100 reefs in otherwise open pelagic systems (Veron and Done 1979; Rogers 2004; Koslow et al.
101 2016).

102

103 The geomorphological structure of coral reefs on small seamounts and pinnacles diverges
104 from classical zonation models derived from emergent reefs (Roberts et al. 2015). Summits

105 are usually small in area with steep slopes and walls descending to considerable depths
106 (>500m). They are comprised of only exposed crests surrounded by open waters, with no
107 sheltered reef-flat or lagoon. Currents are often complex and strong as water passes around
108 abrupt topographies (Genin et al. 1986; Boehlert 1988; Lavelle and Mohn 2010). For
109 example, on seamounts interactions between topography and hydrodynamics are suggested to
110 enhance productivity within these habitats (Genin and Dower 2007; Richert et al. 2017).
111 Other studies have shown that upwellings in particular are an important component of bio-
112 physical coupling at seamounts, supporting high diversity and abundance of fishes, often
113 from higher trophic levels (White et al. 2007; Letessier et al. 2019). Given the similarities in
114 structure between seamounts and pinnacles, pinnacles are also likely influenced by
115 upwellings and strong hydrodynamics. The extent of these effects and the potential for
116 enhanced biophysical-coupling on pinnacles depends on numerous factors including pinnacle
117 size, depth, regional circulation patterns, and exposure to large-scale oceanographic processes.
118
119 Despite their widespread occurrence in many coral reef regions, studies specifically focussed
120 on coral reef pinnacles are scarce. In their absence, and given the similarities in physical
121 structure, paradigms from seamount ecology provide useful parallels to inform our ecological
122 understanding of submerged pinnacles. Both shallow seamounts and pinnacles frequently
123 host large aggregations of pelagic fish alongside demersal and reef-associated species (Genin
124 2004; Morato and Clark 2007; Jorgensen et al. 2016) generating hotspots of diversity in open
125 ocean settings (Morato et al. 2010). Schooling mesopredators, highly-mobile apex predators
126 and migrating megafauna also use seamounts as navigational way-points (Garrigue et al.
127 2015; Gargan et al. 2017), and they are significant habitats for feeding (Holland and Grubbs
128 2007), breeding (Litvinov 2007) and refuge (Letessier et al. 2019). For corals, clear,
129 oligotrophic oceanic waters surrounding offshore reefs can enable complex coral habitat to

130 extend to mesophotic depths (Baker et al. 2016; Roberts et al. 2019) concurrently expanding
131 the range of suitable habitat for fishes (Thresher and Colin 1986; Kane and Tissot 2017).

132

133 Explanations of observed spatial variation in patterns of abundance, diversity and richness of
134 reef fish communities often involve habitat variables, including substrate diversity, rugosity,
135 vertical relief and live coral cover (Roberts and Ormond 1987; Hixon and Beets 1993;
136 Munday 2000; Almany 2004; Gratwicke and Speight 2005). Although the nature of these
137 fish-habitat relationships vary spatially, temporally and differ between trophic groups, live
138 coral and habitat complexity remain fundamental drivers of reef fish abundance, richness and
139 diversity (Caley and John 1996; Jones et al. 2004; Pratchett et al. 2008; Coker et al. 2014;
140 Kerry and Bellwood 2015). However, depth associated physical gradients can lead to altered
141 patterns in benthic community composition and habitat complexity (e.g., light, temperature)
142 (Brokovich et al. 2006; Lesser et al. 2009; Roberts et al. 2015). For example, spatial
143 heterogeneity is reduced at depth where coral morphologies tend to be simpler in comparison to
144 shallower depths (Kahng et al. 2012). Other benthic taxa, like sponges, macroalgae and
145 octocorals can be more prominent at greater depths (>30m) (García-Hernández et al. 2018;
146 Lesser and Slattery 2018) and complex morphologies may provide additional or alternative
147 habitat for fishes in these deep habitats (Knudby et al. 2013; Kahng et al. 2017; Spalding et
148 al. 2019). These differences in benthic community composition have been shown to strongly
149 influence patterns of fish abundance and functional composition on submerged reefs
150 (Brokovich et al. 2008; Pereira-Filho et al. 2011; Kane and Tissot 2017; Cooper et al. 2019).

151

152 The high diversity and productivity of pinnacles and shallow seamounts may enhance their
153 potential to act as refuges from disturbance for some reef species (Bak et al. 2005; Bongaerts
154 et al. 2017). In addition, the physical structures of pinnacles may generate further habitat-

155 specific environmental conditions that confer resilience, however this is speculative because
156 the ecological connections between deep and shallow reefs are largely unstudied (Slattery et
157 al. 2011; Bongaerts and Smith 2019). Coral reefs on offshore pinnacles therefore represent
158 physically and potentially ecologically distinct tropical habitats that are relatively accessible
159 for scientific study. Although research is now expanding significantly into submerged and
160 mesophotic coral ecosystems, few studies aim to resolve fine-scale ecological patterns on
161 distinct bathymetric features. Characterising ecological communities on unexplored, deeper
162 forms of coral reef will be critical to understanding their contribution to the maintenance of
163 biodiversity within the wider seascape. Most coral reef systems are composed of mosaics of
164 varied reef morphologies, but baseline knowledge is still required to understand ecological
165 similarities and connectivity between varied forms of emergent and submerged reefs, as well
166 as to inform effective spatial conservation planning.

167

168 Here we provide the first detailed assessment of fish and benthic communities on a series of
169 submerged coral pinnacles in Kimbe Bay, Papua New Guinea, an area renowned in the
170 diving industry for pinnacle diving. To determine whether pinnacles are hotspots for
171 biodiversity we compare fish and benthic communities on pinnacles to emergent reefs in both
172 nearshore and offshore locations. We then examine whether typical drivers of fish diversity,
173 abundance, species richness and community structure apply to pinnacles. Kimbe Bay lies in
174 the Coral Triangle, one of the world's most diverse coral reef regions, but the distribution and
175 abundance of species inhabiting coral reef pinnacles in this area are currently unquantified.
176 Specifically, the aims of this study were to: 1. Describe benthic communities and quantify
177 habitat complexity based on total hard coral cover, benthic cover type richness and benthic
178 diversity across reef morphologies. We predicted that pinnacles and offshore reefs would
179 have highest percentage cover of hard coral at the depths surveyed (20-30m), due to clearer

180 offshore waters and lower terrestrial influence. These factors may also enhance benthic
181 richness and diversity at offshore sites. 2. Characterise fish communities found on offshore
182 submerged pinnacle reefs and compare them to emergent reef morphologies. We expected
183 that abundance would be high given the aggregating properties of physical structures for
184 fishes, but that diversity and species richness may be lower given the relative isolation of
185 pinnacles as small patch habitats. 3. Examine how fish-benthic relationships differ between
186 reef morphologies, specifically the effect of total hard coral cover and benthic diversity on
187 fish diversity, abundance, richness and species evenness. We hypothesised that established
188 relationships between benthic habitats would be evident at all reef habitats, especially where
189 coral cover is highest at offshore locations.

190

191 **Methods**

192 **Study site and survey design**

193 This study took place during October 2018 in Kimbe Bay (5°30'S, 150°05'E, Fig.1), Papua
194 New Guinea, an area with a diverse bathymetry including emergent reefs and submerged
195 pinnacles. The study incorporated 12 reef sites: 4 nearshore emergent reefs, 4 offshore
196 emergent reefs and 4 offshore submerged pinnacle reefs. Nearshore reefs were defined as
197 those <5km from nearest main landmass and offshore reefs were all between 9-25km from
198 nearest main landmass. The distinction between emergent and submerged morphology was
199 made based on crest depth; crests above 10m were considered emergent and those below 10m
200 submerged since reefs deeper than 10 m are unlikely to ever experience breaking waves
201 (Harris et al. 2013; Thomas et al. 2015). The pinnacles in our study rise to within 15-30m of
202 the sea surface from a deep (c.300m, GEBCO 2019) submerged ring central to the bay. The
203 centre of this ring descends to around 600m in the middle of the bay but on the seaward side
204 drops to >1000m on the shelf of the South Bismarck Plate (Fig.1a and b). Offshore emergent

205 reefs in Kimbe Bay are also extensions of this submerged central system but reach the upper
206 0-10m. Many take the form of shallow flat-topped guyots, which also have steep sides and
207 ridges descending to considerable depths. Nearshore emergent sites are gently sloping with
208 hard coral cover down to around 70m (author pers. obs; Longenecker et al. 2019). All
209 surveys were carried out within a 20-30m depth band. For emergent reefs, sites with
210 substantial deep horizontal ridges or low gradient slopes were selected for the study to
211 account for reef slope aspect. Surveys on walls or steep slopes were avoided. Although we
212 control for slope aspect as much as feasibly possible, ecological assemblages vary
213 considerably between reef zones. How these changes manifest between zones on different
214 reef morphologies at different depths is beyond the scope of this current study but is under
215 investigation by this group.

216

217 **Data collection**

218 *Fish and benthic video surveys*

219 Fish and benthic surveys were conducted along 30m x 5m high-definition (HD) video
220 transects within a depth band of 20-30m. Five transects at least 5m apart were conducted at
221 each site which was primarily dictated by the small size of the pinnacles. A diver-operated
222 stereo-video bar (SeaGIS) housing two GoPro Hero-4 cameras was held horizontally to the
223 benthos, facing forwards as the diver swam the transect maintaining a depth of 0.5m above
224 the reef. A second diver followed with a tape reel and indicated to the first diver when 30m
225 was reached. Both divers returned along the tape conducting a video point-intercept transect
226 using another GoPro Hero-4 camera held at 0.5m above the reef pointing directly downward .

227

228 *Benthic video PIT analysis*

229 Transect tapes were marked with two random points per meter. The HD-video footage was
230 replayed at a low frame rate and the benthos immediately underneath each point (60
231 points/30m) identified and placed into one of 47 categories groups (Table S11). These 47
232 groups were used to calculate three metrics of benthic complexity; benthic diversity (H'),
233 benthic richness and total hard coral cover, all of which have been previously shown to be
234 useful characterisations of community composition and correlate with the community
235 structure of coral reef fishes (Bell and Galzin 1984; Messmer et al. 2011; Komyakova et al.
236 2013).

237

238 Fourteen broader categories of benthic cover type were derived from the 47 original fine
239 scale categories. These measures have been previously shown to correlate with aspects of fish
240 diversity and abundance (Table S11). These 14 groups were: massive and sub-massive coral,
241 encrusting coral, laminar coral, complex coral, algae, coralline crustose algae (CCA), soft
242 corals and octocorals, encrusting porifera, complex porifera, other hexacorals, coral rubble,
243 sand and silt, rock and reef matrix. We chose these groups based on similar submerged reef
244 studies on the GBR (Macdonald et al. 2016; Cooper et al. 2019), but as reefs in Kimbe Bay
245 possess a conspicuous abundance of morphologically distinct sponges and other forms of
246 hexacorallia and octocorallia (Horowitz et al. 2020) we also included these groups.

247

248 *Fish video transect analysis*

249 Fish transect videos were analysed in the stereo-video software Eventmeasure (SeaGIS)
250 which uses camera calibration to provide a known field-of-view (2.5m either side of the
251 transect). Every individual fish that entered the lower two thirds of the screen was counted
252 and identified to species based on Allen et al. (2003). Only individuals that were readily
253 observable within these parameters were recorded i.e. not obscured by the benthos or within

254 crevices. This means the surveys represent the relative abundance of non-cryptic species
255 (Brock 1982 ; Caldwell et al. 2016).

256

257 **Statistical analysis**

258 All analysis was performed in R (R Core Development Team 2020) and plots produced using
259 the packages ggplot2 (Wickham 2016) and ggvegan (Simpson 2019).

260

261 *Fish and benthic assemblages*

262 To test for differences in fish and benthic assemblages between reef morphologies, a one-way
263 permutation-based multivariate ANOVA (PERMANOVA) was performed with Hellinger
264 transformed species abundance data (Anderson 2001:Lengendre and Galagher 2001) using
265 the function “adonis” in vegan. Post-hoc tests were then conducted to identify significant
266 between-group differences identified by the PERMANOVA using “emmeans” (Lenth 2019).
267 For each analysis 999 permutations were performed to calculate p-values. Although generally
268 considered robust to heterogeneity in data sets, PERMANOVA tests between-group variation
269 where a significant result can either suggest differences in location of centroids between
270 groups or, that average within-group dispersion is not equal (Anderson and Walsh 2013).
271 PERMDISP is a resemblance-based permutation test focused strictly on the null hypothesis
272 of homogeneity of multivariate dispersions (Anderson 2006) and was used to test the
273 hypothesis of equal within group dispersion. This test can additionally provide insights into
274 within group variation. The function “betadisp” in vegan was used to perform the
275 PERMDISP test. The SIMPER routine (Clarke and Warwick 2001) was then used to identify
276 species and benthic variables contributing the most dissimilarity among reef types using the
277 “simper” function in vegan.

278

279 *Fish biodiversity and benthic complexity*

280 Differences in mean fish species richness, total fish abundance (individuals/150m²), fish
281 diversity (Simpson's Index), evenness (Pielou's J'), benthic richness and benthic diversity
282 (H') were identified using Generalised Linear Mixed Effects Models (GLMMs) with "reef
283 type" as the categorical main effect and "site" nested within reef type as a random factor
284 using the package "lme4". Standard exploratory techniques were used to assess appropriate
285 error structures to apply to each GLMM (See Tables S1,S2 and S6). Differences between reef
286 types of mean percentage cover of the 14 benthic cover categories were also tested using
287 GLMMs fitted in the same way. For all GLMMs, model fits were evaluated using residual
288 plots and performed using the packages "lme4" and "MASS" (Venables and Ripley 2002;
289 Bates et al. 2015). Differences between means at each reef habitat type were tested using
290 likelihood ratio tests (negative binomial models), conditional F-tests (gaussian models) and
291 adjusted Tukey's HSD post-hoc pair-wise tests using the packages "car" (Fox and Weisberg
292 2019), "pbkrtest" (Halekoh, 2014) and "emmeans" (Lenth 2019). Contrast estimates and 95%
293 confidence intervals are presented in Tables S1,S2 and S6.

294

295 *Fish-benthic relationships*

296 To explicitly examine the nature and strength of relationships between fish and two metrics
297 of benthic habitat complexity (benthic diversity and total hard coral) we used GLMMs . Only
298 these two habitat complexity metrics were examined as benthic richness was found to be
299 highly correlated with benthic diversity and several other benthic cover categories. The effect
300 of total percentage hard coral and benthic diversity on fish richness, diversity, evenness and
301 abundance were tested in 8 separate models with either Negative Binomial (abundance and
302 richness) or Gaussian (diversity and evenness) error distribution. For all models the main
303 effect was either total hard coral percentage or benthic diversity, with "reef type" as a fixed

304 effect. An interaction term between the main effect and “reef type” was included in each
305 model to test whether the nature of any relationship varied between reef morphologies. “Site”
306 was included as a random factor nested within “reef type”. Likelihood-ratio tests with a null
307 model were used to determine model fit and overall goodness-of-fit of all models was
308 assessed via standard techniques of Q-Q plots (normality), residuals plotted against predicted
309 values against all explanatory variables (homogeneity of variance) and calculations of
310 dispersion. Pseudo-R-Square estimates (Nakagawa and Schielzeth 2013; Nakagawa et al.
311 2017) were obtained for all mixed-effects models using `r.squaredGLMM` from the “MuMIn”
312 package (Bartoń 2019). This produces a marginal $R^2_{GLMM(m)}$ (an approximation variance
313 explained by fixed effects) and a conditional $R^2_{GLMM(c)}$ (an approximation of variance
314 explained by the entire model including fixed and random effects). Estimates and 95%
315 confidence intervals for each models’ effects were calculated where the evidence does not
316 support a significant effect at the 0.05 level if the confidence interval contains zero. Tests of
317 fixed factor main effects were conducted using likelihood-ratio tests for GLMMs and
318 conditional F-tests with Kenward-Roger correction for GLMMs with gaussian error family.
319 Correlation analysis and simple slopes tests using “emmeans” were performed to further
320 explore these relationships.

321

322 Finally, distance based multiple linear modeling was used to examine the multivariate
323 relationship between differences in fish communities and benthic habitat to find the
324 combination of benthic variables that best explained the greatest variation in fish community
325 structure. Benthic variables included all 14 benthic categories, benthic diversity and benthic
326 richness. Multicollinearity was explored between all benthic variables using Spearman’s rank
327 correlation. Benthic richness was highly correlated with benthic diversity (Spearman’s rho, ρ

328 = 0.78, $p < 0.001$) and complex hexacorals ($\rho = 0.48$, $p = 0.001$) so was removed prior to
329 model fitting.

330

331 The function “ordiR2step” in vegan was then used to conduct stepwise forward selection
332 based on the Akaike Information Criterion (Akaike et al. 1973) of variables from all 14
333 benthic categories as well as benthic diversity. The stepwise routine was run using 9999
334 permutations and adjusted R^2 as the selection criterion (Blanchet, Legendre and Borcard
335 2008). Each model proposed by “ordiR2step” was tested for significance using vegan’s
336 permutational ANOVA function (Monte Carlo permutation test) and only constraints with p
337 < 0.05 after adjustment for multiple testing selected for the final model. The most suitable
338 model to explain the relationship between benthic cover types and variation in fish
339 assemblages between reef habitat types was visualized by constrained ordination using
340 distance-based redundancy analysis (db-RDA) (Anderson et al. 2008). db-RDA can be used
341 when the response data are available as a dissimilarity matrix and provides an opportunity to
342 use ecological distances in constrained ordination analysis (Paliy and Shankar 2016). Benthic
343 variables from the final model were overlaid as a vector, together with fish species that were
344 most correlated with assemblage variation.

345

346 **Results**

347 **Benthic communities show similar complexity between reef types**

348 We found no significant difference in any of the benthic complexity metrics between reef
349 morphologies; benthic diversity (F-test, $F = 2.25$, $p = 0.33$), benthic richness (F-test, $F =$
350 4.01 , $p = 0.11$) or total hard coral (F-test, $F = 2.01$, $p = 0.37$) (Figure 2, Table S2). Pinnacle
351 reefs however, showed the greatest range in both benthic diversity (1.94 – 2.52) and benthic
352 richness (12.20 - 17.41) compared to offshore (benthic diversity = 2.12 - 2.23, benthic

353 richness = 12.40 - 13.80) and nearshore emergent reefs (benthic diversity = 2.03-2.31,
354 benthic richness = 12.60 - 14.00) suggesting high variability between individual pinnacle
355 sites (Table S5).

356
357 Of the 14 benthic cover types, 8 showed significant differences in mean percentage cover
358 between reef morphologies (Fig.3, Table S6). Pinnacle reefs were characterised by highest
359 mean percent cover of complex hard corals, massive and sub-massive hard corals, encrusting
360 hexacorals and octacorals. Offshore reefs had the lowest mean percent cover of complex hard
361 corals, but high proportions of laminar hard corals and encrusting porifera. Nearshore reefs
362 were notably high in algae. Benthic communities were similar to each other ranging between
363 34-40% dissimilarity (Table 1). Highest overall dissimilarity was between pinnacle and
364 nearshore reefs (40%). Benthic cover types contributing the most to overall dissimilarity were
365 algae, complex hard coral, encrusting hexacoral, rubble and massive hard coral (Table 1).
366 Although PERMANOVA indicated significant differences in benthic community
367 assemblages among reef types (Pseudo-F = 4.74, 999 permutations, $p(\text{perm}) = 0.001$) the
368 PERMDISP test also yielded a significant result ($F = 4.16$, $p = 0.02$). This further suggests
369 unequal within-group dispersion which was also apparent in exploratory multivariate plots
370 (Fig.S1).

371

372 **Reef fish biodiversity and assemblages differ between reef types**

373 A total of 11,460 individual fishes representing 230 species and 87 genera were recorded
374 across all transects from the 12 reefs. Pinnacles had the highest total number of species (172)
375 and also the highest number of unique species (75) (Fig.4). The numerous unique species
376 included many larger predatory species including *Pinjalo lewisi*, *Caranx melampygus*,
377 *Caranx sexfasciatus*, *Carcharhinus amblyrhynchos* and *Caracharinus melanopterus* that
378 were not observed on emergent reefs (Table S3). Offshore emergent reefs had the lowest total

379 number of species recorded (87) and also only 3 unique species. Of the total 230 species
380 observed across all reef types, only 47 (20.5%) were shared by all three (Fig.4).
381
382 The pinnacles in our study supported almost twice the mean number of fish species per unit
383 area (32.45) as near (16.35) and offshore reefs (16.50) (Fig.5; LRT, $\chi^2 = 62.10$, $p < 0.001$).
384 We also found a clear increasing trend in fish abundance from nearshore to offshore reefs,
385 culminating in 6.57 times observed total abundance on the pinnacles compared to nearshore
386 reefs (LRT, $\chi^2 = 68.74$, $p < 0.001$). High variation in abundance on pinnacles was due to
387 large schools of *Sphraena qeini* and *Acanthurus thompsoni* recorded in several transects at
388 multiple sites, similarly, large schools of *Caesio sp.* drove higher abundance on offshore sites
389 compared to nearshore reefs. Consequently, species evenness showed significant differences
390 across reef morphologies (F-test, $F = 31.52$, $p < 0.001$). Simpson's diversity was highest on
391 nearshore reefs (0.80) and lowest on offshore reefs (0.72) but differences were not significant
392 between the reef morphologies (F-test, $F = 5.10$, $p = 0.07$). (Fig.5, Table S1).
393
394 The local structure of fish assemblages was clearly distinct between reef types
395 (PERMANOVA; pseudo-F = 8.67, 999 permutations, p (perm) = 0.001). Unlike benthic
396 communities, fish communities showed high dissimilarity between all reef types ranging
397 between 74.5-87.8% (Table 1). The combination of species contributing most to these
398 differences consistently included *Pseudanthias tuka*, *Caesio cuning*, *A. thompsoni*, *P.*
399 *nigromanus* and *Ctenochaetus tominiensis*. The only different species to appear in the top
400 five overall contributors to community dissimilarity between nearshore and offshore reefs
401 was *C. anarzae* (Table 1). Species composition of pinnacles was most similar to offshore
402 emergent reefs and most distinct from Inshore emergent reefs (Table 1, Fig.S2). Again,
403 although the result of the PERMANOVA indicated distinct fish assemblages among reef

404 types, the result of the PERMDISP test ($F = 3.97$, $p = 0.02$, Table S2a) suggests that there is
405 also unequal within-group dispersion. Notably, nearshore reefs showed more variable
406 assemblage structure than offshore or pinnacle reefs (Fig.S2a).

407
408

409 **Fish-habitat relationships – weak associations at all reef types**

410 “Reef type” had a significant effect on fish abundance and richness in models for total hard
411 coral cover (LRT abundance; $p = 0.002$, richness; $p = 0.002$) and benthic diversity
412 (abundance $p = 0.003$, richness; $p = <0.001$), but had no effect on fish diversity or evenness
413 in any model (Table 2). Neither benthic diversity nor total hard coral cover had a significant
414 effect on any fish metric across all 8 models, and there was also no significant interactions
415 between independent variables (Fig. 6, Table 2). Table S9 for estimate coefficients and
416 confidence intervals. Offshore reef showed moderate positive correlation between benthic
417 diversity and fish diversity ($\rho = 0.30$, $p = 0.20$), whereas pinnacle and nearshore reefs showed
418 weak negative relationships (pinnacles; $\rho = -0.07$, $p = 0.76$; nearshore ($\rho = -0.13$, $p = 0.57$)).
419 None of the relationships however, were significant ($p < 0.05$). Other contrasting patterns
420 included a negative relationship between abundance and hard coral cover on pinnacle reefs (ρ
421 $= -0.42$, $p = 0.07$), whereas nearshore reefs showed a weak positive trend ($\rho = 0.32$, $p = 0.16$)
422 and there was no correlation between fish abundance and hard coral cover on offshore reefs
423 ($\rho = -0.03$, $p = 0.89$). Benthic diversity and fish diversity showed a moderate negative
424 association on offshore reefs ($\rho = -0.29$, $p = 0.22$), but was moderately positive on pinnacles
425 ($\rho = 0.07$, $p = 0.78$ and nearshore reefs ($\rho = 0.29$, $p = 0.22$). Again, none of these contrasting
426 relationships were found to be significant. Benthic diversity and hard coral cover had
427 reasonable explanatory power in respective models for fish richness and abundance with
428 $R^2_{(m)}$ ranging between 52-54%. Fish diversity and evenness however were poorly explained

429 by benthic diversity or hard coral cover in combination with reef type with $R^2_{(m)}$ ranging
430 between 7-13% (SI Table S8 and S9).

431

432 The full distance based linear model containing all 14 benthic habitat variables (Table S11)
433 together with benthic diversity explained 21.98% of variation in fish communities. After
434 adjusting for multiple testing, the final model indicated 3 variables were significant in
435 explaining variability in fish communities (cumulative $Adj.R^2 = 0.2198$; Algae (5.84%),
436 encrusting octocorals (3.90%) and encrusting porifera (3.25%) (Table S7). When visualized
437 in the db-RDA plot, the first two axes represented together 74.06% of fitted variation and
438 15.32% of total variation (Fig.7a). Species most correlated with increasing algal cover
439 included *C. tominiensis*, *P. nigromanus* and *C. rollandi*. *P. tuka* showed strongest correlation
440 with octocorals, whereas *Naso vlamingii* and *A. thompsoni* were more associated with higher
441 cover of encrusting Porifera more prevalent on offshore and pinnacle reefs (Fig.7b).

442

443 **Discussion**

444 **Benthic assemblages – similar complexity but varied composition**

445 Our study presents the first baseline assessment of fish and benthic communities on
446 submerged pinnacles in the Coral Triangle. The benthic habitat structure on pinnacles did not
447 differ markedly from emergent reefs, although there were differences in coral growth forms
448 and proportional cover. Although we accounted for the effect of reef slope aspect through site
449 selection across morphologies, the flat tops of pinnacle summits in clear, offshore locations
450 experience greater irradiance at the same depth than emergent reefs (Lesser et al. 2009). This
451 perhaps explains higher complex and massive coral morphologies on pinnacles at these
452 depths, which strongly influence the abundance and distribution of many coral-associated
453 fishes (Jones et al. 2004; Coker et al. 2014; Pratchett 2014). Cooper et al. (2019) suggest that

454 submerged reefs on the Great Barrier Reef support higher numbers of individual fishes than
455 inshore sites as a result of clearer waters allowing greater light penetration for photosynthetic
456 processes, resulting in increased feeding opportunities across a range of functional groups. In
457 our study the four species of obligate-coral feeding butterflyfish observed were all were
458 recorded on pinnacles, where complex coral cover was highest, but not on nearshore or
459 offshore reefs. This follows established patterns for coral obligates and suggests that fine-
460 scale differences in benthic communities are more important for some fish species than
461 broader, simple measures of overall complexity.

462

463 Although situated in similarly remote positions in the bay, benthic communities on offshore
464 emergent reefs had the lowest proportion of complex hard coral and were dominated by
465 laminar coral and encrusting porifera. Corals adapting to lower light at greater depths also
466 often display flatter, low relief morphologies. Shading by steep walls and emergent shallow
467 crests reduces light irradiance on the lower reef slopes of emergent reefs (Lesser et al. 2009).
468 Flatter coral morphologies have been shown to influence fish-habitat associations,
469 constraining the depth distribution of some species (Brokovich et al. 2008; Lesser et al. 2009;
470 Smallhorn-West et al. 2017), which may partly explain low fish diversity on offshore reefs
471 despite their offshore position.

472

473 The high algal cover on nearshore reefs is likely due to close proximity to large-scale
474 terrestrial agricultural activity, including high levels of deforestation and associated high
475 inputs of allochthonous run-off (Munday 2004; Green et al. 2009). High algal cover tends to
476 be a characteristic of degraded coastal reefs (Hughes 1994; Graham et al. 2006; Roth et al.
477 2018) and altered fish communities (Jones et al. 2004; Chong-Seng et al. 2012; Ainsworth

478 and Mumby 2015). This may be driving lower fish diversity and abundance at nearshore sites
479 than would naturally be found without chronic land-based disturbances.

480

481 **Fish assemblages - unique fish communities found on pinnacles**

482 We found that submerged pinnacles support highly diverse, abundant and distinct fish
483 assemblages, with many unique species not found at the equivalent depth on emergent reefs
484 in either nearshore or offshore locations. Our findings confirm our expectation that distinct
485 submerged physical structures possess high abundance of fishes, in this case driven by large
486 schools of *S. qeni*, *Caranx sp.* and *A. thompsoni*. Associative behaviour between fish and
487 physical structures is well known (Fréon and Dagorn 2000) and explanations for this
488 behaviour are thought to include resting, spawning, seeking shelter from predators and access
489 to cleaning stations and feeding opportunities (Paterson 1998; Barreiros et al. 2002) however
490 these paradigms are untested for the pinnacles in our study.

491

492 Contrary to our expectations there was no difference in diversity across the three reef
493 morphologies. Pinnacles however, did have the highest species richness and number of
494 unique species. Although we did not directly measure habitat area or isolation by distance,
495 Kimbe Bay's nearshore reefs are larger reefs, closely situated to each other and also to
496 coastal nursery habitats (Green et al. 2009). Nearshore reefs may therefore be expected to
497 receive higher numbers of juveniles and recruits (sources of immigration) and support higher
498 absolute numbers of individuals and species, over a larger overall area of available habitat
499 (MacArthur and Wilson 1967). Although these patterns are less established than in terrestrial
500 ecology, biogeographic factors are known to influence marine habitats and reef fish
501 communities (Mora et al. 2003; Kulbicki et al. 2013; Bennett et al. 2018; Quimbayo et al.
502 2018), albeit with contrasting results. Sandin et al. (2008) found classical relationships

503 between reef fish abundance and isolation (negative) and habitat area (positive), but others
504 have shown that increasing isolation from land-based disturbance and associated
505 geographical environmental gradients leads to increased biomass and abundance, (DeMartini
506 et al. 2008; Stallings 2009; Williams et al. 2011; Brewer et al. 2012; Kattan et al. 2017).

507

508 Given the relatively small area of Kimbe Bay (15x25km) and the strong dispersal capabilities
509 of many fishes (Mora et al. 2003; Almany et al. 2017; Bode et al. 2019) it is unlikely that
510 horizontal dispersal ability limits offshore recruitment and may explain the weak
511 biogeographic patterns in diversity observed (Hobbs et al. 2012). Nevertheless, the offshore
512 emergent reefs and pinnacles are similarly isolated from nearshore habitats, yet there is still
513 an anomaly between abundance and richness on these two morphologies. This may be
514 attributable to high temporal variability in species abundances as some evidence suggests that
515 small isolated reefs are subject to greater demographic and environmental stochasticity
516 (Mellin et al. 2010). The persistence of the patterns observed in this study should therefore be
517 assessed by replicated surveys to identify longer-term trends in biodiversity metrics.

518

519 The pinnacles in Kimbe Bay appear to provide sufficient habitat to support high fish
520 diversity, abundance and richness, despite their small size and relative isolation from other
521 reefs by both depth and distance. As small, island-like habitats in offshore, reefs on
522 submerged pinnacles represent patchy habitats with high perimeter-to-area ratios. The
523 interface of the coral reef and pelagic environment represents the edges of both these distinct
524 marine habitats. The term “edge effect” is used to describe the influence of the mixed
525 environment created at the boundaries of conjoining habitats on ecological community
526 structure and processes (Fahrig 2003; Fonseca, 2008). Here, species associated with adjacent
527 habitats are brought into contact which may lead to novel interactions, the formation of

528 dispersal barriers or the creation of spatial subsidies (Fagan et al. 1999). Edge effects,
529 however, are generally not well known in marine environments as the theoretical base is
530 rooted in terrestrial ecology (but see Smith et al. 2007; Sambrook et al. 2016). Yet, given
531 their small size and typical isolated position within seascapes, it seems plausible that coral
532 reefs on submerged pinnacles experience some of form of edge effect. The combination of
533 coral reef and pelagic habitat theoretically increases habitat heterogeneity; not necessarily in
534 terms of structural complexity but by increasing the breadth of resources available to a wider
535 range of species and individuals. This could explain the presence of both highly reef-
536 associated and mobile pelagic species observed at pinnacle sites, leading to high species
537 richness, distinct community structures and the highest number of unique species.

538

539 **Weak fish-habitat relationships**

540 Species richness, abundance and composition on pinnacles was only weakly related to habitat
541 structure and is most likely driven by other aspects of the unique morphology of pinnacle
542 habitats. Empirical studies examining linear correlations between reef fish and simple habitat
543 variables have similarly shown contrasting and or surprisingly weak relationships (reviewed
544 in Jones and Syms 1998), but most have been conducted at shallow depths (<20m). Our
545 surveys were conducted at 20-30m and it is known that some fish-habitat links can decline
546 with increasing depth on emergent reefs, usually attributable to declining complex and
547 branching coral cover and the changing influence of other abiotic factors (Brokovich et al.
548 2008). This may explain the lack of strong fish-benthic relationships at all reef morphologies.

549

550 Although live coral cover is consistently the most important habitat variable affecting the
551 distribution of many coral-associated fishes (Coker et al. 2014), the generalisation of simple
552 linear patterns in fish-habitat relationships is further complicated by the huge variety of ways

553 different species utilise coral reefs (Jones and Syms 1998). For example, some species will
554 alter habitat associations during ontogeny (Bonin et al. 2011; Komyakova et al. 2018) and
555 positive effects of habitat complexity on fish abundance can depend on numerous predator-
556 prey and conspecific interactions (Beukers and Jones 1998; Almany 2004). The different
557 proportions of certain benthic cover types and morphologies may also reflect the distinct fish
558 communities, where certain morphologies or benthic organisms provide more or less
559 favourable habitat for certain fishes. A detailed investigation of trophic assemblage
560 composition and potential differences in condition (e.g. body size, growth rates) would help
561 to further understand how different types of reef habitat could confer benefits to particular
562 functional groups and individuals.

563

564 Many fish species have less direct relationships with biogenic micro-habitats in general,
565 instead, being attracted to physical structure and associated abiotic conditions (Auster 2007).
566 In our study, the negative relationship between fish abundance and hard coral cover on the
567 pinnacles (Fig.8g) was largely a result of the high percentage cover of encrusting
568 corallimorph colonies (Hexacorallia) combined with the presence of large schools of *S. geni*
569 and *A. thompsoni*. Mobile mesopredators tend to use coral reefs less directly than highly site-
570 attached fishes, hunting and foraging in other adjacent connected habitats during different
571 diurnal periods (Papastamatiou et al. 2015) while high abundances of planktivores like *A.*
572 *thompsoni* at reef edges and greater depths is likely driven by proximity to higher plankton
573 availability brought by strong currents (Thresher and Colin 1986; Hobson 1991; Quimpo et
574 al. 2018). Stronger currents on reefs can be a product of both offshore positions receiving
575 higher exposure to wind-generated water motion and waves but also interactions between
576 reef topography and oceanographic processes (Hearn 2011). Fish species on abrupt physical
577 structures may therefore have less direct relationships with biogenic habitat, but instead rely

578 on favourable feeding and abiotic conditions generated at dynamic all-surrounding
579 boundaries between reef and pelagic habitats.

580

581 **Hydrodynamics and pelagic influence as drivers of fish communities on pinnacles**

582 We propose that both habitat-specific physical processes and high pelagic influences are
583 plausible mechanisms which explain distinct and highly abundant fish communities on small
584 offshore submerged pinnacle reefs. On shallow emergent reefs, the crest is the most diverse
585 and productive zone (Done 1983; Russ 1984, 2003) where reef fish communities benefit
586 significantly from oceanic production (Wyatt et al. 2012; Fisher et al. 2018; Le Bourg et al.
587 2018). Pinnacle reefs diverge from classical models of spatial reef zonation where, as the
588 summits are small in area, lacking any significant area of back-reef or flat; they are composed
589 almost entirely of reef crest. Furthermore, the pelagic environment surrounds not only the
590 circumference of reef but also constitutes a significant water column of pelagic habitat above
591 the benthos. Thus, on a pinnacle the majority of the reef may experience high pelagic
592 energetic inputs via multidirectional currents, not just at the seaward edge as on emergent
593 reefs. For example, high abundances of planktivores found at reef edges fix important
594 allochthonous inputs (Wyatt et al. 2012) and exposed zones on emergent reefs have been
595 shown to receive significant pelagic energetic subsidies through this mechanism, explaining
596 exceptional levels of productivity even on low coral-cover reefs (Morais and Bellwood
597 2019).

598

599 Hydrology on coral reefs can therefore shape reef-fish assemblages (Fulton and Bellwood
600 2005; Eggertsen et al. 2016) and submerged topographies can generate distinct hydrodynamic
601 environments, upwellings and currents, which are important mechanisms for nutrient and
602 plankton retention (Genin et al. 1986; Lueck and Mudge 1997; Fulton et al. 2005; Morato et

603 al. 2009; Lavelle and Mohn 2010; Mosquera Giménez et al. 2019). This extension of the
604 species-energy hypothesis (Wright 1983) has been proposed as a mechanism that allows
605 these habitats to support abundant communities, often composed of species from high trophic
606 levels (Pitcher and Bulman 2007; Jorgensen et al. 2016; Richert et al. 2017). The presence of
607 diverse and abundant fish communities on pinnacles rich with large populations of
608 planktivores and piscivores perhaps reflects strong bio-physical coupling analogous to
609 seamounts (Genin 2004; Morato et al. 2010). Although the small scale of this study does not
610 fully capture the abundance and distribution of large mobile predators, sharks were only
611 observed in transects at pinnacle reefs. This could suggest that these habitats support higher
612 trophic levels and more complex food-webs than nearshore reefs at the same depth, which
613 may be lower-energy environments. Greater sampling effort and additional studies, however,
614 are needed to ascertain an accurate reflection of habitat use on pinnacle reefs by large
615 predatory fishes.

616

617 The hydrological-energy mechanisms we suggest as drivers of high diversity on pinnacles do
618 occur on emergent reefs but are largely focused on the shallow crests by surface waves and
619 upwellings travelling up the slope. As such, productivity, nutrient concentrations and larval
620 supply are again focused in this zone rather than the lower slopes (Wolanski and Delesalle
621 1995; Sponaugle et al. 2002; Leichter et al. 2005; James et al. 2020). Interactions between
622 hydrodynamics and reef topography clearly differ between reef zones but there have been
623 few comparisons between emergent reefs and submerged reefs. Despite the difference in
624 absolute crest depth between emergent and submerged reefs, the culmination of
625 hydrodynamics on the crest may lead to greater assemblage similarities in this zone between
626 reef morphologies, regardless of depth. Additionally, in terms of habitat, emergent reefs
627 typically have large areas of high coral cover on the crest, which is likely to concentrate the

628 majority of reef-associated individuals and species in shallower depths. It was notable in our
629 study how many species usually associated with shallow crests on emergent reefs were also
630 observed on the crests of submerged pinnacles, most likely a result of aspect and clear
631 offshore waters. A similar pattern was reported for corals on submerged reefs in the central
632 GBR, where similar reef crest/upper slope assemblages on emergent reefs are found at
633 greater depths on the crests of submerged pinnacles (Roberts et al. 2015). Comparative
634 investigations of patterns in reef zonation along depth gradients will help further explain how
635 communities change across the full range of available habitat on both emergent and
636 submerged reefs. Disentangling the relative effects of reef zone, depth and hydrodynamics on
637 submerged pinnacles will require fine-scale in-situ measurements of currents and associated
638 abiotic factors to reveal new information about these unusual habitats rather than relying on
639 generalised trends from shallow and mesophotic coral reef literature (Pearson and Stevens
640 2015).

641

642 As isolated but ubiquitous patch habitats, submerged pinnacles also present significant
643 opportunities to assess connectivity between emergent and deep reefs as well as the wider
644 pelagic environment. Just as seamounts are thought to act as steppingstones for dispersal in
645 the deep sea, pinnacles may play a significant role in connectivity across large scale coral
646 reef systems. The differing hydrodynamics on submerged pinnacles (e.g. lack of a reef flat to
647 dissipate currents and wave energy) likely result in a greater proportion of larvae being
648 exported to adjacent reefs than on emergent reefs, suggesting they may represent important
649 sources of propagules (Thomas et al. 2015). Multiple forms of submerged reef supporting
650 diverse marine ecosystems are widely distributed across the continental shelf of both north-
651 east and north-west Australia (Bridge et al. 2012, 2019; Roberts et al. 2015; Moore et al.
652 2017; Heyward and Radford 2019), but have largely been excluded from management and

653 monitoring efforts. Results from this study and others demonstrate that submerged reefs
654 warrant greater consideration in management plans. Although the locations of submerged
655 reefs in many regions may be poorly understood, precautionary management principles that
656 explicitly account for uncertainty regarding the locations of ecologically significant features
657 such as submerged reefs can be effective in protecting these types of features ‘incidentally’
658 (Bridge et al. 2015).

659

660 Our baseline assessment indicates that pinnacles represent a distinct form of submerged coral
661 reef that supports highly species rich and abundant fish communities. Assemblages here are
662 likely shaped by complex interactions of hydrology, physical structure and high levels of
663 pelagic influence, resulting from greater crest depth and offshore locations. These processes
664 are present on emergent, nearshore reefs, but largely only at shallow seaward edges, and their
665 effects may attenuate with depth as the reef structure changes. Further studies are required to
666 assess how the combination of pelagic and reef habitats on small submerged pinnacles
667 generate distinct abiotic and physical conditions and how they might enhance productivity
668 and the variety of available resources. Isolation by depth and offshore setting may also confer
669 aspects of natural resilience in addition to beneficial hydrodynamics. In a rapidly changing
670 marine environment, it is important to establish how distinct reef morphologies may respond
671 to climate change and the extent to which they may provide refuge to degrading shallow reef
672 organisms. As ubiquitous features across all low-latitude coastal shelves, deep and distinct
673 coral habitats are becoming increasingly important components of the future global coral reef
674 biome. Further work is warranted to quantify the spatial extent of these unique coral reef
675 habitats, characterise their ecological communities and understand their role in coral reef
676 ecosystems.

677

678 **Acknowledgements**

679 We are grateful to the traditional owners of the Tamare-Kilu reefs for access to their reefs
680 and thank Mahonia Na Dari Research Centre for field support, particularly Jerry and Nelson
681 Sikatua. Thanks to Walindi Plantation Resort and the Benjamin family for facilitating access
682 to offshore sites. Early drafts were greatly improved by comments and discussions with
683 T.Rüger, C.Macdonald, P.Smallhorn-West and S.Gordon. We thank P.Harris and R.Beaman
684 for guidance on forming definitions of pinnacle coral reefs, N.Peterson, A.Green and
685 S.Sheppard for advice on Kimbe Bay's bathymetry and two anonymous reviewers whose
686 comments helped improve this manuscript. Funding was provided by an ARC Discovery
687 Grant (DP190103056) to G.P.Jones and research allocation to M.I.McCormick from The
688 ARC Centre of Excellence for Coral Reef Studies. This paper is dedicated to the memory of
689 Lauia Keating; we'll see you when we're looking at you Lau.

690

691 **Conflict of interests statement**

692 On behalf of all authors, the corresponding author states that there is no conflict of interest.

693

694 **References**

695

- 696 Abbey E, Webster JM (2011) Submerged reefs. In: Hopley D. (eds) Encyclopedia of Modern
697 Coral Reefs. Springer Netherlands, pp 1058–1062
- 698 Ainsworth CH, Mumby PJ (2015) Coral-algal phase shifts alter fish communities and reduce
699 fisheries production. *Glob Chang Biol* 21:165–172
- 700 Akaike H, Petrov B, Csaki F (1973) Information theory as an extension of the maximum
701 likelihood principle. 267–281
- 702 Allen G., Steene R, Humann P, Deloach N (2003) Reef fish identification: tropical Pacific.
703 New World Publications, Jacksonville, FL,
- 704 Almany GR (2004) Differential effects of habitat complexity, predators and competitors on
705 abundance of juvenile and adult coral reef fishes. *Oecologia* 141:105–113
- 706 Almany GR, Planes S, Thorrold SR, Berumen ML, Bode M, Saenz-Agudelo P, Bonin MC,
707 Frisch AJ, Harrison HB, Messmer V, Nanninga GB, Priest MA, Srinivasan M, Sinclair-
708 Taylor T, Williamson DH, Jones GP (2017) Larval fish dispersal in a coral-reef
709 seascape. *Nat Ecol Evol* 1:148
- 710 Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance.
711 *Austral Ecol* 26:32–46

- 712 Anderson MJ (2006) Distance-Based Tests for Homogeneity of Multivariate Dispersions.
713 *Biometrics* 62:245–253
- 714 Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ for PRIMER: Guide to
715 Software and Statistical Methods. Plymouth: PRIMER-E Ltd.,
- 716 Anderson MJ, Walsh DCI (2013) PERMANOVA, ANOSIM, and the Mantel test in the face
717 of heterogeneous dispersions: What null hypothesis are you testing? *Ecol Monogr*
718 83:557–574
- 719 Auster PJ (2007) Linking deep-water corals and fish populations. In: George R., Cairns S..
720 (eds) Conservation and adaptive management of seamount and deep-sea coral
721 ecosystems. Rosenstiel School of Marine and Atmospheric Science, University of
722 Miami, pp 93–99
- 723 Baird A, Madin J, Álvarez-Noriega M, Fontoura L, Kerry J, Kuo C, Precoda K, Torres-
724 Pulliza D, Woods R, Zawada K, Hughes T (2018) A decline in bleaching suggests that
725 depth can provide a refuge from global warming in most coral taxa. *Mar Ecol Prog Ser*
726 603:257–264
- 727 Bak RPM, Nieuwland G, Meesters EH (2005) Coral reef crisis in deep and shallow reefs:
728 30 years of constancy and change in reefs of Curacao and Bonaire. *Coral Reefs* 24:475–
729 479
- 730 Baker EK, Puglise KA, Harris PT (2016) Mesophotic Coral Ecosystems A lifeboat for coral
731 reefs? United Nations Environ Program GRID-Arendal, Nairobi
- 732 Barreiros J., Santos R., de Borba AE (2002) Food habits, schooling and predatory behaviour
733 of the yellowmouth barracuda, *Sphyaena viridensis* (Perciformes: Sphyaenidae) in the
734 Azores. *French Ichthyol Soc - Cybium* 26:83–88
- 735 Bartoń K (2019) MuMIn: Multi-Model Inference.
- 736 Bates D, Maechler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models
737 Using lme4. *J Stat Softw* 67:1–48
- 738 Bell JD, Galzin R (1984) Influence of live coral cover on coral-reef fish communities. *Mar*
739 *Ecol Prog Ser* 15:265–274
- 740 Bellwood DR, Hughes TP (2001) Regional-Scale Assembly Rules and Biodiversity of Coral
741 Reefs. *Science* (80-) 292:1532–1535
- 742 Bennett S, Halford AR, Choat JH, Hobbs J-PA, Santana-Garcon J, Ayling AM, Harvey ES,
743 Newman SJ (2018) Geography and island geomorphology shape fish assemblage
744 structure on isolated coral reef systems. *Ecol Evol* 8:6242–6252
- 745 Beukers JS, Jones GP (1998) Habitat complexity modifies the impact of piscivores on a coral
746 reef fish population. *Oecologia* 114:50–59
- 747 Bode M, Leis JM, Mason LB, Williamson DH, Harrison HB, Choukroun S, Jones GP (2019)
748 Successful validation of a larval dispersal model using genetic parentage data. *PLOS*
749 *Biol* 17:e3000380
- 750 Boehlert GW (1988) Current-topography interactions at mid-ocean seamounts and the impact
751 on pelagic ecosystems. *GeoJournal* 16:45–52
- 752 Bongaerts P, Riginos C, Brunner R, Englebert N, Smith SR, Hoegh-guldberg O (2017) Deep
753 reefs are not universal refuges : Reseeding potential varies among coral species. *Sci Adv*
754 3:e1602373
- 755 Bongaerts P, Smith TB (2019) Beyond the ‘‘Deep Reef Refuge’’ Hypothesis: A Conceptual
756 Framework to Characterize Persistence at Depth. In: Loya Y., Puglise K.A., Bridge
757 T.C.L. (eds) *Mesophotic Coral Ecosystems*. Springer International Publishing, Cham, pp
758 881–895
- 759 Bonin MC, Almany GR, Jones GP (2011) Contrasting effects of habitat loss and
760 fragmentation on coral-associated reef fishes. *Ecology* 92:1503–1512

761 Brock RE. A Critique of the Visual Census Method for Assessing Coral Reef Fish
762 Populations. University of Miami—Rosenstiel School of Marine and Atmospheric Science;
763 1982

764 Le Bourg B, Letourneur Y, Bănaru D, Blanchot J, Chevalier C, Mou-Tham G, Lebreton B,
765 Pagano M (2018) The same but different: Stable isotopes reveal two distinguishable, yet
766 similar, neighbouring food chains in a coral reef. *J Mar Biol Assoc United Kingdom*
767 98:1589–1597

768 Brewer TD, Cinner JE, Fisher R, Green A, Wilson SK (2012) Market access, population
769 density, and socioeconomic development explain diversity and functional group biomass
770 of coral reef fish assemblages. *Glob Environ Chang* 22:399–406

771 Bridge T, Beaman R, Done T, Webster J (2012) Predicting the Location and Spatial Extent of
772 Submerged Coral Reef Habitat in the Great Barrier Reef World Heritage Area,
773 Australia. *PLoS One* 7:e48203

774 Bridge TC, Hughes TP, Guinotte JM, Bongaerts P (2013) Call to protect all coral reefs. *Nat*
775 *Clim. Change* 3:528–530

776 Bridge TCL, Grech AM, Pressey RL (2015) Factors influencing incidental representation of
777 previously unknown conservation features in marine protected areas. *Conservation*
778 *Biology* 30: 154-165

779 Bridge TCL, Beaman RJ, Bongaerts P, Muir PR, Ekins M, Sih T (2019) The Great Barrier
780 Reef and Coral Sea. In: Loya Y., Puglise K.A., Bridge T.C.L. (eds) *Mesophotic Coral*
781 *Ecosystems*. Springer International Publishing, Cham, pp 351–367

782 Bridge TCL, Done TJ, Beaman RJ, Friedman A, Williams SB, Pizarro O, Webster JM
783 (2011a) Topography, substratum and benthic macrofaunal relationships on a tropical
784 mesophotic shelf margin, central Great Barrier Reef, Australia. *Coral Reefs* 30:143–153

785 Bridge TCL, Done TJ, Friedman A, Beaman RJ, Williams SB, Pizarro O, Webster JM
786 (2011b) Variability in mesophotic coral reef communities along the Great Barrier Reef,
787 Australia. *428:63–75*

788 Brokovich E, Baranes A, Goren M (2006) Habitat structure determines coral reef fish
789 assemblages at the northern tip of the Red Sea. *Ecol Indic* 6:494–507

790 Brokovich E, Einbinder S, Shashar N, Kiflawi M, Kark S (2008) Descending to the twilight-
791 zone: changes in coral reef fish assemblages along a depth gradient down to 65 m. *Mar*
792 *Ecol Prog Ser* 371:253–262

793 Caley MJ, John JS (1996) Refuge Availability Structures Assemblages of Tropical Reef
794 Fishes. *J Anim Ecol* 65:414

795 Caldwell, Z. R., Zgliczynski, B. J., Williams, G. J., & Sandin, S. A. (2016). Reef Fish Survey
796 Techniques: Assessing the Potential for Standardizing Methodologies. *PloS one*, 11(4),
797 e0153066.

798 Chong-Seng KM, Mannering TD, Pratchett MS, Bellwood DR, Graham NAJ (2012) The
799 Influence of Coral Reef Benthic Condition on Associated Fish Assemblages. *PLoS One*
800 7:e42167

801 Clarke K., Warwick R. (2001) Change in marine communities: an approach to statistical
802 analysis and interpretation. *PRIMER-E: Plymouth*,

803 Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure.
804 *Austral Ecol* 18:117–143

805 Coker DJ, Wilson SK, Pratchett MS (2014) Importance of live coral habitat for reef fishes.
806 *Rev Fish Biol Fish* 24:89–126

807 Connolly SR, Bellwood DR, Hughes TP (2003) Indo-Pacific biodiversity of coral reefs:
808 Deviations from a mid-domain model. *Ecology* 84:2178–2190

809 Cooper AM, MacDonald C, Roberts TE, Bridge TCL (2019) Variability in the functional
810 composition of coral reef fish communities on submerged and emergent reefs in the

811 central Great Barrier Reef, Australia. PLoS One 14:e0216785

812 Crosbie A, Bridge T, Jones G, Baird A (2019) Response of reef corals and fish at Osprey

813 Reef to a thermal anomaly across a 30 m depth gradient. *Mar Ecol Prog Ser* 622:93–102

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

815 structure between fished and unfished atolls in the northern Line Islands, central Pacific.

816 *Mar Ecol Prog Ser* 365:199–215

817 Done TJ (1983) Coral zonation, its nature and significance. *Perspectives on coral reefs.*

818 Australian Institute of Marine Science. pp 107–147

819 Eggertsen L, Hammar L, Gullström M (2016) Effects of tidal current-induced flow on reef

820 fish behaviour and function on a subtropical rocky reef. *Mar Ecol Prog Ser* 559:175–192

821 Fahrig L (2003) Effects of Habitat Fragmentation on Biodiversity. *Annu Rev Ecol Evol Syst*

822 34:487–515

823 Fagan WF, Cantrell RS, Cosner C (1999) How habitat edges change species interactions. *Am*

824 *Nat* 153:165–182

825 Fisher EE, Choat JH, McCormick MI, Cappo M (2018) Relative influence of environmental

826 factors on the timing and occurrence of multi-species coral reef fish aggregations. *PLoS*

827 *One* 13:1–23

828 Fonseca M. (2008) Edge Effects. In: Jorgensen S, Fath B (eds) *Encyclopedia of Ecology.*

829 Elsevier Science

830 Fox J, Weisberg S (2019) *An {R} Companion to Applied Regression.* Thousand Oaks CA:

831 Sage,

832 Fréon P, Dagorn L (2000) Review of fish associative behaviour: Toward a generalisation of

833 the meeting point hypothesis. *Rev Fish Biol Fish* 10:183–207

834 Fulton CJ, Bellwood DR (2005) Wave-induced water motion and the functional implications

835 for coral reef fish assemblages. *Limnol Oceanogr* 50:255–264

836 Fulton CJ, Bellwood DR, Wainwright PC (2005) Wave energy and swimming performance

837 shape coral reef fish assemblages. *Proc R Soc B Biol Sci* 272:827–832

838 García-Hernández JE, Sanchez PJ, Hammerman NM, Schizas N V. (2018) Fish, Coral, and

839 Sponge Assemblages Associated With Altiphotic and Mesophotic Reefs Along the

840 Guánica Biosphere Reserve Continental Shelf Edge, Southwest Puerto Rico. *Front Mar*

841 *Sci* 5:303

842 Gargan LM, Morato T, Pham CK, Finarelli JA, Carlsson JEL, Carlsson J (2017)

843 Development of a sensitive detection method to survey pelagic biodiversity using eDNA

844 and quantitative PCR: a case study of devil ray at seamounts. *Mar Biol* 164:112

845 Garrigue C, Clapham PJ, Geyer Y, Kennedy AS, Zerbini AN (2015) Satellite tracking reveals

846 novel migratory patterns and the importance of seamounts for endangered south pacific

847 humpback whales. *R Soc Open Sci* 2:150489

848 GEBCO Compilation Group (2019) GEBCO 2019 Grid (doi:10.5285/836f016a-33be-6ddc-

849 e053-6c86abc0788e) Accessed July 2019

850 Genin A (2004) Bio-physical coupling in the formation of zooplankton and fish aggregations

851 over abrupt topographies. *J Mar Syst* 50:3–20

852 Genin A, Dayton PK, Lonsdale PF, Spiess FN (1986) Corals on seamount peaks provide

853 evidence of current acceleration over deep-sea topography. *Nature* 322:59–61

854 Genin A, Dower JF (2007) Seamount plankton dynamics. In: Pitcher T.J., Morato T., Clark

855 M.R. (eds) *Seamounts: Ecology, Fisheries & Conservation.* Blackwell Publishing Ltd,

856 Graham NAJ, Wilson SK, Jennings S, Polunin NVC, Bijoux JP, Robinson J (2006) Dynamic

857 fragility of oceanic coral reef ecosystems. *Proc Natl Acad Sci U S A* 103:8425–8429

858 Gratwicke B, Speight MR (2005) The relationship between fish species richness, abundance

859 and habitat complexity in a range of shallow tropical marine habitats. *J Fish Biol*

860 66:650–667

861 Green A, Smith SE, Lipsett-Moore G, Groves C, Peterson N, Sheppard S, Lokani P,
862 Hamilton R, Almany J, Aitsi J, Bualia L (2009) Designing a resilient network of marine
863 protected areas for Kimbe Bay, Papua New Guinea. *Oryx* 43:488–498
864 Halekoh U, Højsgaard S (2014). “A Kenward-Roger Approximation and Parametric
865 Bootstrap Methods for Tests in Linear Mixed Models – The R Package
866 pbkrtest.” *Journal of Statistical Software*, 59(9), 1–30. <http://www.jstatsoft.org/v59/i09/>.
867 Harris PT, Bridge TCL, Beaman RJ, Webster JM, Nichol SL, Brooke BP (2013) Submerged
868 banks in the Great Barrier Reef, Australia, greatly increase available coral reef habitat.
869 *ICES J Mar Sci* 70:284–293
870 Harvey BJ, Nash KL, Blanchard JL, Edwards DP (2018) Ecosystem-based management of
871 coral reefs under climate change. *Ecol Evol* 8:6354–6368
872 Hearn CJ (2011) Hydrodynamics of coral reef systems. *Encyclopedia of Earth Sciences*
873 *Series*. Springer Netherlands, pp 563–573
874 Heyward A, Radford B (2019) Northwest Australia. In: Loya Y., Puglise K.A., Bridge T.C.L.
875 (eds) *Mesophotic Coral Ecosystems*. Springer International Publishing, Cham, pp 337–
876 349
877 Hinderstein LM, Marr JCA, Martinez FA, Dowgiallo MJ, Puglise KA, Pyle RL, Zawada DG,
878 Appeldoorn R (2010) Theme section on “Mesophotic Coral Ecosystems:
879 Characterization, Ecology, and Management.” *Coral Reefs* 29:247–251
880 Hixon MA, Beets JP (1993) Predation, Prey Refuges, and the Structure of Coral-Reef Fish
881 Assemblages. *Ecol Monogr* 63:77–101
882 Hobbs J-PA, Jones GP, Munday PL, Connolly SR, Srinivasan M (2012) Biogeography and
883 the structure of coral reef fish communities on isolated islands. *J Biogeogr* 39:130–139
884 Hobson E. (1991) Trophic relationships of fishes specialized to feed on zooplankters above
885 coral reefs. In: Sale P.F. (eds) *The Ecology of Fishes on Coral Reefs*. Academic Press,
886 San Diego., pp 69–95
887 Holland KN, Dean Grubbs R (2007) Fish Visitors to Seamounts: Tunas and Bill Fish at
888 Seamounts. In: Pitcher T.J., Morato T., Clark M.R. (eds) *Seamounts: Ecology, Fisheries*
889 *& Conservation*. Blackwell Publishing Ltd, pp 189–201
890 Hopley D (2011) *Encyclopedia of Modern Coral Reef: Structure, Form and Process*.
891 Hopley D, Smithers SG, Parnell K (2007) *The Geomorphology of the Great Barrier Reef:*
892 *Development, Diversity and Change*. Cambridge University Press,
893 Horowitz J, Cowman PF, Brugler M, Bridge TCL (2020) Morphological and molecular
894 description of a new genus and species of black coral from the mesophotic reefs of
895 Papua New Guinea (Cnidaria: Anthozoa: Hexacorallia: Antipatharia: Antipathidae:
896 *Blastopathes*). *Zootaxa*, 4821 (3): 553–569
897 Hughes TP (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean
898 coral reef. *Science* (80-) 265:1547–1551
899 IHO (2008) *Standardization of Undersea Feature Names: Guidelines Proposal form*
900 *Terminology*.
901 James AK, Washburn L, Gotschalk C, Maritorena S, Alldredge A, Nelson CE, Hench JL,
902 Leichter JJ, Wyatt ASJ, Carlson CA (2020) An Island Mass Effect Resolved Near
903 Mo’orea, French Polynesia. *Front Mar Sci* 7:16
904 Jones GP, McCormick MI, Srinivasan M, Eagle J V (2004) Coral decline threatens fish
905 biodiversity in marine reserves. *Proc Natl Acad Sci* 101:8251–8253
906 Jones GP, Syms C (1998) Disturbance, habitat structure and the ecology of fishes on coral
907 reefs. *Austral Ecol* 23:287–297
908 Jorgensen SJ, Klimley AP, Muhlia-Melo A, Morgan SG (2016) Seasonal changes in fish
909 assemblage structure at a shallow seamount in the Gulf of California. *PeerJ* 4:e2357
910 Kahng S, Copus JM, Wagner D (2017) *Mesophotic Coral Ecosystems*. Marine Animal

911 Forests. Springer International Publishing, Cham, pp 185–206

912 Kahng S, Hochberg E, Apprill A, Wagner D, Luck D, Perez D, Bidigare R (2012) Efficient
913 light harvesting in deep-water zooxanthellate corals. *Mar Ecol Prog Ser* 455:65–77

914 Kane CN, Tissot BN (2017) Trophic designation and live coral cover predict changes in reef-
915 fish community structure along a shallow to mesophotic gradient in Hawaii. *Coral Reefs*
916 36:891–901

917 Kattan A, Coker DJ, Berumen ML (2017) Reef fish communities in the central Red Sea show
918 evidence of asymmetrical fishing pressure. *Mar Biodivers* 47:1227–1238

919 Kerry JT, Bellwood DR (2015) Do tabular corals constitute keystone structures for fishes on
920 coral reefs? *Coral Reefs* 34:41–50

921 Knudby A, Kenchington E, Murillo FJ (2013) Modeling the Distribution of *Geodia* Sponges
922 and Sponge Grounds in the Northwest Atlantic. *PLoS One* 8:e82306

923 Komyakova V, Jones GP, Munday PL (2018) Strong effects of coral species on the diversity
924 and structure of reef fish communities: A multi-scale analysis. *PLoS One* 13:e0202206

925 Komyakova V, Munday PL, Jones GP (2013) Relative Importance of Coral Cover, Habitat
926 Complexity and Diversity in Determining the Structure of Reef Fish Communities.
927 *PLoS One* 8:e83178

928 Koslow JA, Auster P, Bergstad OA, Roberts JM, Rogers A, Vecchione M, Harris P, Rice J,
929 Bernal P (2016) Biological Communities on Seamounts and Other Submarine Features
930 Potentially Threatened by Disturbance. In: Inniss L., Simcock A. (eds) *The First*
931 *Integrated Marine Assessment: World Ocean Assessment*. United Nations General
932 Assembly, New York, pp 26

933 Kulbicki M, Parravicini V, Bellwood DR, Arias-González E, Chabanet P, Floeter SR,
934 Friedlander A, McPherson J, Myers RE, Vigliola L, Mouillot D (2013) Global
935 Biogeography of Reef Fishes: A Hierarchical Quantitative Delineation of Regions. *PLoS*
936 *One* 8:e81847

937 Lavelle JW, Mohn C (2010) Motion, Commotion, and Biophysical Connections at Deep
938 Ocean Seamounts. *Oceanography* 23:90–103

939 Laverick JH, Andradi-brown DA, Exton DA, Bongaerts P, Bridge TCL, Lesser MP, Pyle RL,
940 Slattery M, Wagner D, Rogers AD (2016) To what extent do mesophotic coral
941 ecosystems and shallow reefs share species of conservation interest? 5:

942 Legendre P, Gallagher ED (2001) Ecologically meaningful transformations for ordination of
943 species data. *Oecologia* 129:271–280

944 Leichter JJ, Deane GB, Stokes MD (2005) Spatial and temporal variability of internal wave
945 forcing on a coral reef. *J Phys Oceanogr* 35:1945–1962

946 Lenth RL (2019) emmeans: Estimated Marginal Means, aka Least-Squares Means.

947 Lesser MP, Slattery M (2018) Sponge density increases with depth throughout the Caribbean.
948 *Ecosphere* 9:e02525

949 Lesser MP, Slattery M, Leichter JJ (2009) Ecology of mesophotic coral reefs. *J Exp Mar Biol*
950 375:1–8

951 Letessier TB, Mouillot D, Bouchet PJ, Vigliola L, Fernandes MC, Thompson C, Boussarie G,
952 Turner J, Juhel J-B, Maire E, Caley MJ, Koldewey HJ, Friedlander A, Sala E, Meeuwig
953 JJ (2019) Remote reefs and seamounts are the last refuges for marine predators across
954 the Indo-Pacific. *PLOS Biol* 17:e3000366

955 Lindfield SJ, Harvey ES, Halford AR, McIlwain JL (2016) Mesophotic depths as refuge
956 areas for fishery-targeted species on coral reefs. *Coral Reefs* 35:125–137

957 Linklater M, Jordan AR, Carroll AG, Neilson JM, Gudge S, Brooke BP, Nichol SL (2019)
958 Mesophotic corals on the subtropical shelves of Lord Howe Island and Balls Pyramid,
959 south-western Pacific Ocean Publication Details. *Mar Freshw Res* 70:43–61

960 Litvinov F (2007) Fish Visitors to Seamounts: Aggregations of Large Pelagic Sharks Above

- 961 Seamounts. In: Pitcher T.J., Morato T., Hart P.J., Clark M.R., Haggan N., Santos R.S.
 962 (eds) *Seamounts: Ecology, Fisheries & Conservation*. Blackwell Publishing Inc, pp 202–
 963 206
- 964 Locker SD, Armstrong RA, Battista TA, Rooney JJ, Sherman C, Zawada DG (2010)
 965 Geomorphology of mesophotic coral ecosystems: Current perspectives on morphology,
 966 distribution, and mapping strategies. *Coral Reefs* 29:329–345
- 967 Longenecker K, Roberts TE, Colin PL (2019) Papua New Guinea. In: Loya Y., Puglise K.A.,
 968 Bridge T.C.L. (eds) *Mesophotic Coral Ecosystems*. Springer International Publishing,
 969 Cham, pp 321–336
- 970 Lueck RG, Mudge TD (1997) Topographically induced mixing around a shallow seamount.
 971 *Science* (80-) 276:1831–1833
- 972 MacArthur RH, Wilson EO (1967) *The theory of island biogeography*. Princeton University
 973 Press, New Jersey
- 974 Macdonald C, Bridge TCL, Jones GP (2016) Depth, bay position and habitat structure as
 975 determinants of coral reef fish distributions: Are deep reefs a potential refuge? *Mar Ecol*
 976 *Prog Ser* 561:217–231
- 977 Macdonald C, Jones GP, Bridge T (2018) Marginal sinks or potential refuges? Costs and
 978 benefits for coral-obligate reef fishes at deep range margins. *Proc R Soc B Biol Sci*
 979 285:20181545
- 980 Malcolm HA, Jordan A, Smith SDA (2010) Biogeographical and cross-shelf patterns of reef
 981 fish assemblages in a transition zone. *Mar Biodivers* 40:181–193
- 982 Mellin C, Huchery C, Caley MJ, Meekan MG, Bradshaw CJA (2010) Reef size and isolation
 983 determine the temporal stability of coral reef fish populations. *Ecology* 91:3138–3145
- 984 Messmer V, Jones GP, Munday PL, Holbrook SJ, Schmitt RJ, Brooks AJ (2011) Habitat
 985 biodiversity as a determinant of fish community structure on coral reefs. *Ecology*
 986 92:2285–2298
- 987 Moore C, Cappo M, Radford B, Heyward A (2017) Submerged oceanic shoals of north
 988 Western Australia are a major reservoir of marine biodiversity. *Coral Reefs* 36:719–734
- 989 Mora C, Chittaro PM, Sale PF, Kritzer JP, Ludsin SA (2003) Patterns and processes in reef
 990 fish diversity. *Nature* 421:933–936
- 991 Morais RA, Bellwood DR (2019) Pelagic Subsidies Underpin Fish Productivity on a
 992 Degraded Coral Reef. *Curr Biol* 29:1521-1527.e6
- 993 Morato T, Bulman C, Pitcher TJ (2009) Modelled effects of primary and secondary
 994 production enhancement by seamounts on local fish stocks. *Deep Res Part II Top Stud*
 995 *Oceanogr* 56:2713–2719
- 996 Morato T, Clark MR (2007) Seamount fishes: ecology and life histories. In: Pitcher T.J.,
 997 Morato T., Hart P.J.B., Clark M.R., Haggan N., Santos R.S. (eds) *Seamounts: Ecology,*
 998 *Fisheries & Conservation*. Blackwell Publishing Ltd, pp 170–188
- 999 Morato T, Hoyle SD, Allain V, Nicol SJ (2010) Seamounts are hotspots of pelagic
 1000 biodiversity in the open ocean. *Proc Natl Acad Sci U S A* 107:9707–9711
- 1001 Mosquera Giménez Á, Vélez-Belchí P, Rivera J, Piñeiro S, Fajar N, Caínzos V, Balbín R,
 1002 Jiménez Aparicio JA, Dominguez-Carrió C, Blasco-Ferre J, Carreiro-Silva M, Morato T,
 1003 Puerta P, Orejas C (2019) Ocean Circulation Over North Atlantic Underwater Features
 1004 in the Path of the Mediterranean Outflow Water: The Ormonde and Formigas
 1005 Seamounts, and the Gazul Mud Volcano. *Front Mar Sci* 6:702
- 1006 Moura RL, Amado-Filho GM, Moraes FC, Brasileiro PS, Salomon PS, Mahiques MM,
 1007 Bastos AC, Almeida MG, Silva JM, Araujo BF, Brito FP, Rangel TP, Oliveira BCV,
 1008 Bahia RG, Paranhos RP, Dias RJS, Siegle E, Figueiredo AG, Pereira RC, Leal C V.,
 1009 Hajdu E, Asp NE, Gregoracci GB, Neumann-Leitão S, Yager PL, Francini-Filho RB,
 1010 Fróes A, Campeão M, Silva BS, Moreira APB, Oliveira L, Soares AC, Araujo L,

1011 Oliveira NL, Teixeira JB, Valle RAB, Thompson CC, Rezende CE, Thompson FL
1012 (2016) An extensive reef system at the Amazon River mouth. *Sci Adv* 2:e1501252
1013 Munday PL (2000) Interactions between habitat use and patterns of abundance in coral-
1014 dwelling fishes of the genus *Gobiodon*. *Environ Biol Fishes* 58:355–369
1015 Munday PL (2004) Habitat loss, resource specialization, and extinction on coral reefs. *Glob*
1016 *Chang Biol* 10:1642–1647
1017 Nakagawa S, Johnson PCD, Schielzeth H (2017) The coefficient of determination R^2 and
1018 intra-class correlation coefficient from generalized linear mixed-effects models revisited
1019 and expanded. *J R Soc Interface* 14:20170213
1020 Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R^2 from
1021 generalized linear mixed-effects models. *Methods Ecol Evol* 4:133–142
1022 Oksanen JF, Blanchet G, Friendly M, Kindt R, Legendre P, McGlenn D, Minchin PR, O’Hara
1023 RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2019) *vegan*:
1024 *Community Ecology Package*.
1025 Paliy O, Shankar V (2016) Application of multivariate statistical techniques in microbial
1026 ecology. *Mol Ecol* 25:1032–1057
1027 Papastamatiou YP, Meyer CG, Kosaki RK, Wallsgrove NJ, Popp BN (2015) Movements and
1028 foraging of predators associated with mesophotic coral reefs and their potential for
1029 linking ecological habitats. *Mar Ecol Prog Ser* 521:155–170
1030 Paterson SE (1998) Group occurrence of Great Barracuda (*Sphraena barracuda*) in the Turks
1031 and Caicos Islands. *Bull Mar Sci* 63:633–638
1032 Pearson R, Stevens T (2015) Distinct cross-shelf gradient in mesophotic reef fish
1033 assemblages in subtropical eastern Australia. *Mar Ecol Prog Ser* 532:185–196
1034 Pereira-Filho GH, Amado-Filho GM, P B Guimarães SM, Moura RL, G Sumida PY,
1035 Abrantes DP, Bahia RG, Güth AZ, Jorge RR, Bastos Francini Filho R (2011) Reef fish
1036 and benthic assemblages of the Trindade and Martin Vaz island group, southwest
1037 Atlantic. *Brazilian J Oceanogr* 59:201–212
1038 Pinheiro HT, Mazzei E, Moura RL, Amado-filho GM, Ferreira CEL, Floeter SR, Francini-
1039 filho RB (2015) Fish Biodiversity of the Vitória-Trindade Seamount Chain ,
1040 Southwestern Atlantic : An Updated Database. *PLoS One* 10:e0118180
1041 Pitcher TJ, Bulman C (2007) Raiding the larder: a quantitative evaluation framework and
1042 trophic signature for seamount food webs. In: Pitcher T.J., Morato T., Hart P.J.B., Clark
1043 M.R., Haggan N., Santos R.S. (eds) *Seamounts: Ecology, Fisheries & Conservation*.
1044 Blackwell Publishing Ltd, pp 282–295
1045 Pratchett MS (2014) Feeding preferences and dietary specialisation among obligate coral-
1046 feeding butterflyfishes. In: Pratchett M.S., Berumen M.L., Kapoor B.. (eds) *Biology of*
1047 *Butterflyfishes*. Raton, FL, USA, pp 140–179
1048 Pratchett MS, Munday PL, Wilson SK, Graham NAJ, Cinner JE, Bellwood DR, Jones GP,
1049 Polunin NVC, McClanahan TR (2008) Effects of climate -induced coral bleaching on
1050 coral -reef fishes — ecological and economic consequences. In: Gibson R.N., Atkinson
1051 R.J.A., Gordon J.D.M. (eds) *Oceanography and Marine Biology: an annual review*. CRC
1052 Press, pp 257–302
1053 Du Preez C, Curtis JMR, Clarke ME (2016) The Structure and Distribution of Benthic
1054 Communities on a Shallow Seamount (Cobb Seamount, Northeast Pacific Ocean). *PLoS*
1055 *One* 11:e0165513
1056 Quimbayo JP, Dias MS, Kulbicki M, Mendes TC, Lamb RW, Johnson AF, Aburto-Oropeza
1057 O, Alvarado JJ, Bocos AA, Ferreira CEL, Garcia E, Luiz OJ, Mascareñas-Osorio I,
1058 Pinheiro HT, Rodriguez-Zaragoza F, Salas E, Zapata FA, Floeter SR (2018)
1059 Determinants of reef fish assemblages in tropical Oceanic islands. *Ecography (Cop)*
1060 41:1–11

1061 Quimpo TJR, Cabaitan PC, Olavides RDD, Dumalagan Jr. EE, Munar J, Siringan FP (2018)
1062 Spatial variability in reef-fish assemblages in shallow and upper mesophotic coral
1063 ecosystems in the Philippines. *J Fish Biol* 94:17–28

1064 R Core Development Team (2018) R: A language and environment for statistical computing.
1065 Richert J, Jorgensen SJ, Ketchum JT, Mohajerani L, Klimley P (2017) The Importance of
1066 Pinnacles and Seamounts to Pelagic Fishes and Fisheries off the Southern Baja
1067 California Peninsula. *Oceanogr Fish* 4:555644

1068 Roberts C, Ormond R (1987) Habitat complexity and coral reef fish diversity and abundance
1069 on Red Sea fringing reefs. *Mar Ecol Prog Ser* 41:1–8

1070 Roberts T., Moloney J., Sweatman HPA, Bridge TCL (2015) Benthic community
1071 composition on submerged reefs in the central Great Barrier Reef. *Coral Reefs* 34:569–
1072 580

1073 Roberts TE, Bridge TCL, Caley MJ, Madin JS, Baird AH (2019) Resolving the depth
1074 zonation paradox in reef-building corals. *Ecology* 100:e02761

1075 Rogers AD (2004) The Biology, Ecology and Vulnerability of Seamount Communities.
1076 Roth F, Saalman F, Thomson T, Coker DJ, Villalobos R, Jones BH, Wild C, Carvalho S
1077 (2018) Coral reef degradation affects the potential for reef recovery after disturbance.
1078 *Mar Environ Res* 48–58

1079 Russ G (1984) Distribution and abundance of herbivorous grazing fishes in the central Great
1080 Barrier Reef. 11. Patterns of zonation of mid-shelf and outershelf reefs*. *Mar Ecol Prog*
1081 *Ser* 20:35–44

1082 Russ GR (2003) Grazer biomass correlates more strongly with production than with biomass
1083 of algal turfs on a coral reef. *Coral Reefs* 22:63–67

1084 Sambrook K, Jones G, Bonin M (2016) Life on the edge: Coral reef fishes exhibit strong
1085 responses to a habitat boundary. *Mar Ecol Prog Ser* 561:203–215

1086 Samoily MA, Halford A, Osuka K (2019) Disentangling drivers of the abundance of coral
1087 reef fishes in the Western Indian Ocean. *Ecol Evol* 9:4149–4167

1088 Sandin S., Vermeij MJ., Hurlbert A. (2008) Island biogeography of Caribbean coral reef fish.
1089 *Glob Ecol Biogeogr* 17:770–777

1090 Simpson GL (2019) ggvegan: “ggplot2” Plots for the “vegan” Package.

1091 Slattery M, Lesser MP, Brazeau D, Stokes MD, Leichter JJ (2011) Connectivity and stability
1092 of mesophotic coral reefs. *J Exp Mar Bio Ecol* 408:32–41

1093 Smallhorn-West PF, Bridge TCL, Munday PL, Jones GP (2017) Depth distribution and
1094 abundance of a coral-associated reef fish: roles of recruitment and post-recruitment
1095 processes. *Coral Reefs* 36:157–166

1096 Smith T., Hindell J., Jenkins G., Connolly R. (2007) Edge effects on fish associated with
1097 seagrass and sand patches. *Mar Ecol Prog Ser* 359:203–213

1098 Spalding HL, Amado-Filho GM, Bahia RG, Ballantine DL, Fredericq S, Leichter JJ, Nelson
1099 WA, Slattery M, Tsuda RT (2019) Macroalgae. Springer, Cham, pp 507–536

1100 Spalding MD, Grenfell AM (1997) New estimates of global and regional coral reef areas.
1101 *Coral Reefs* 16:225–230

1102 Sponaugle S, Cowen RK, Shanks A, Morgan SG, Leis JM, Pineda J, Boehlert GW, Kingsford
1103 MJ, Lindeman KC, Grimes C, Munro JL (2002) Predicting self-recruitment in marine
1104 populations: Biophysical correlates and mechanisms. *Bull Mar Sci* 70:341–375

1105 Stallings CD (2009) Fishery-Independent Data Reveal Negative Effect of Human Population
1106 Density on Caribbean Predatory Fish Communities. *PLoS One* 4:e5333

1107 Stoddart DR (1969) Ecology and Morphology of Recent Coral Reefs. *Biol Rev* 44:433–498

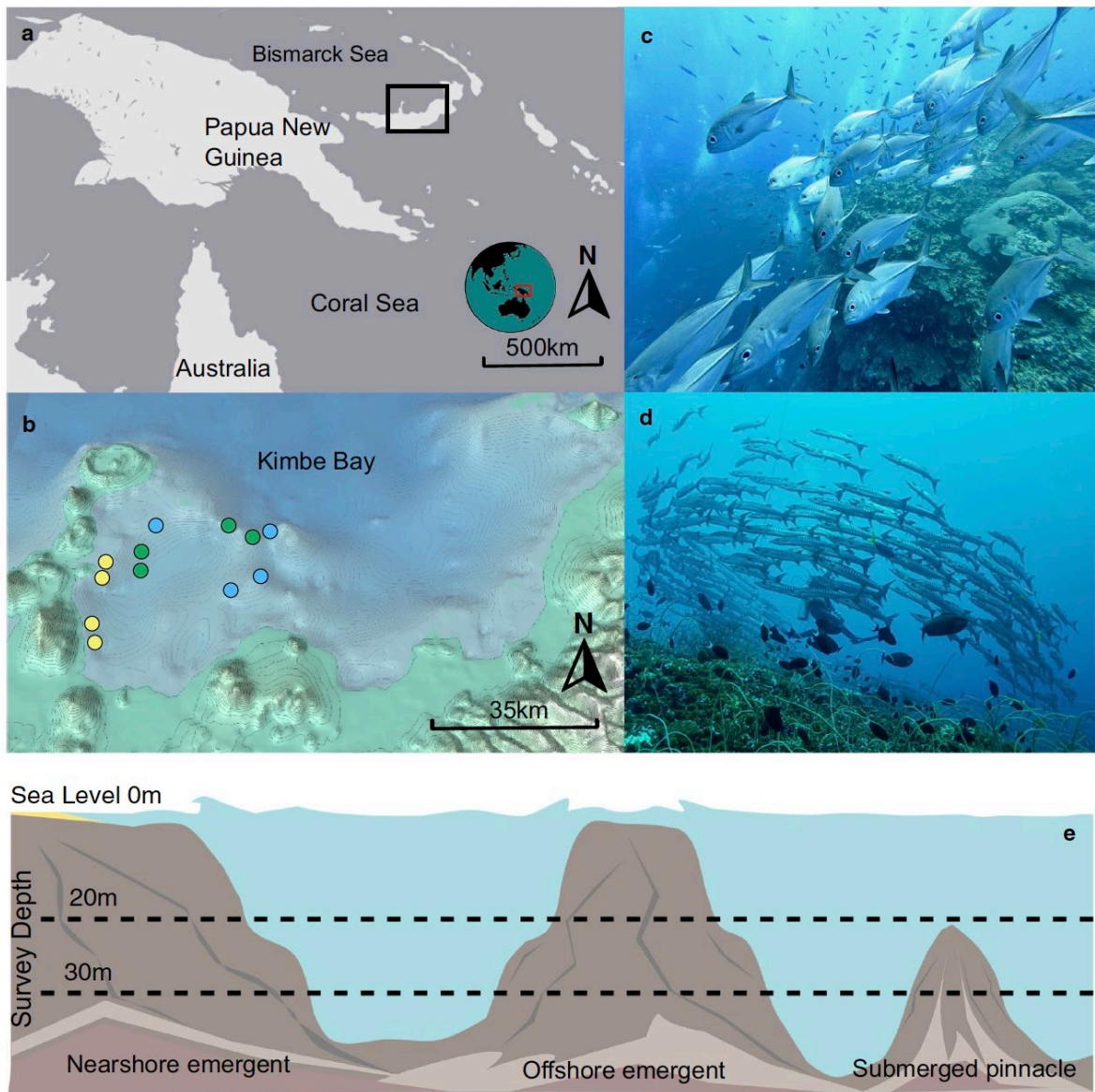
1108 Thomas CJ, Bridge TCL, Figueiredo J, Deleersnijder E, Hanert E (2015) Connectivity
1109 between submerged and near-sea-surface coral reefs: can submerged reef populations
1110 act as refuges? *Divers Distrib* 21:1254–1266

- 1111 Thresher R., Colin P. (1986) Trophic structure, diversity and abundance of fishes of the deep
1112 reef. *Bull Mar Sci* 38:253–272
- 1113 Venables WN, Ripley BD (2002) *Modern Applied Statistics with S*. Fourth Edition. Springer,
1114 New York,
- 1115 Venn A., Weber F., Loram J., Jones R. (2009) Deep zooxanthellate corals at the high latitude
1116 Bermuda Seamount. *Coral Reefs* 28:135
- 1117 Veron JEN, Done T (1979) Corals and coral communities of Lord Howe Island. *Aust J Mar*
1118 *Freshw Res* 30:203–236
- 1119 Vora K., Almeida F (1990) Submerged reef systems on the central western continental shelf
1120 of India. *Mar Geol* 91:255–262
- 1121 White M, Bashmachnikov I, Arístegui J, Martins A (2007) Physical processes and seamount
1122 productivity. In: Pitcher T.J., Morato T., Clark M.R. (eds) *Seamounts: Ecology,*
1123 *Fisheries & Conservation*. Blackwell Publishing Ltd, pp 65–84
- 1124 Wickham H (2016) *ggplot2: Elegant Graphics for Data Analysis*.
- 1125 Williams GJ, Graham NAJ, Jouffray J-B, Norström A V., Nyström M, Gove JM, Heenan A,
1126 Wedding LM (2019) Coral reef ecology in the Anthropocene. *Funct Ecol* 33:1014–1022
- 1127 Williams ID, Baum JK, Heenan A, Hanson KM, Nadon MO, Brainard RE (2015) Human,
1128 Oceanographic and Habitat Drivers of Central and Western Pacific Coral Reef Fish
1129 Assemblages. *PLoS One* 10:e0120516
- 1130 Williams ID, Richards BL, Sandin SA, Baum JK, Schroeder RE, Nadon MO, Zgliczynski B,
1131 Craig P, McIlwain JL, Brainard RE (2011) Differences in Reef Fish Assemblages
1132 between Populated and Remote Reefs Spanning Multiple Archipelagos Across the
1133 Central and Western Pacific. *J Mar Biol* 2011:1–14
- 1134 Wolanski E, Delesalle B (1995) Upwelling by internal waves , Tahiti , French Polynesia.
1135 *Cont Shelf Res* 15:357–368
- 1136 Wright DH (1983) Species-Energy Theory: An Extension of Species-Area Theory. *Oikos*
1137 41:496
- 1138 Wyatt ASJ, Waite AM, Humphries S (2012) Stable isotope analysis reveals community-level
1139 variation in fish trophodynamics across a fringing coral reef. *Coral Reefs* 31:1029–1044
- 1140
- 1141

1142 **Figure legends**

1143

1144



1145

1146

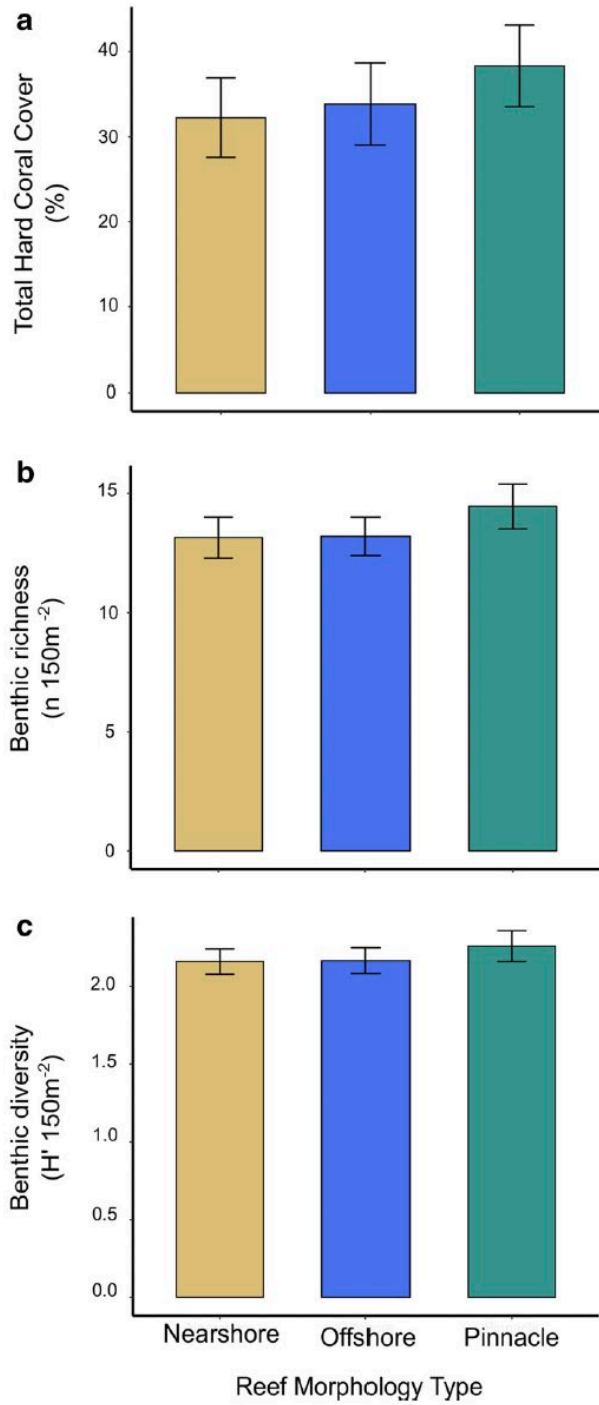
1147

1148

1149

1150

Figure 1. Study area locations, Kimbe Bay, Papua New Guinea. (a) Papua New Guinea and Kimbe Bay (b) Kimbe Bay bathymetry with location of pinnacle (green), offshore (blue) and nearshore (yellow) reefs (c) Schools of *Caranx sexfasciatus* at Joelles Reef (pinnacle) (d) *Sphyraena qenie* at Bradford Shoals (pinnacle) (e) Schematic of reef morphologies surveyed



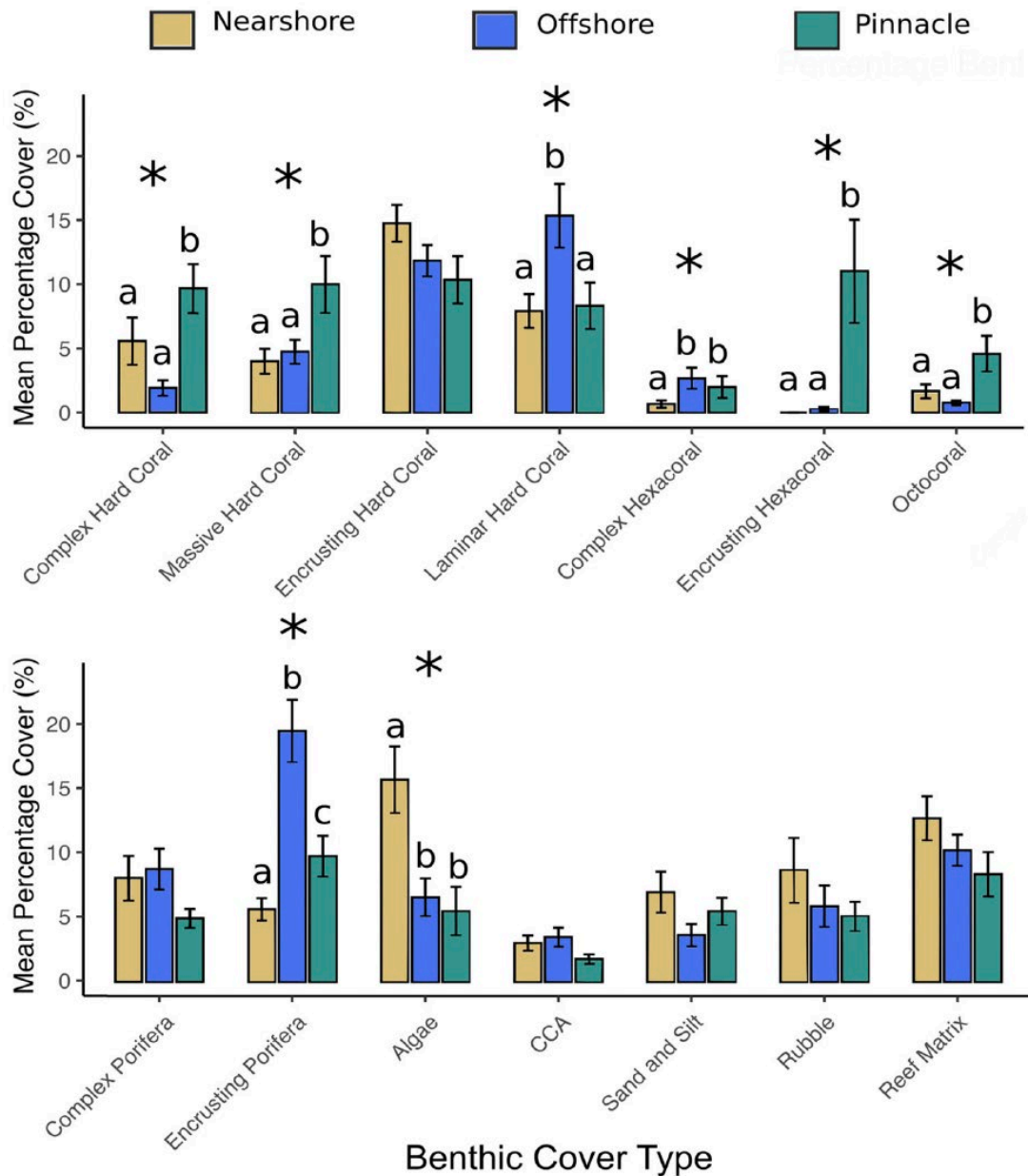
1151

1152 **Figure 2.** Mean \pm SE of three benthic complexity metrics for each reef morphologies (a) total
 1153 hard coral cover % (b) richness of benthic cover types (c) diversity of benthic cover types.

1154 Full LMM results Table T2

1155

1156



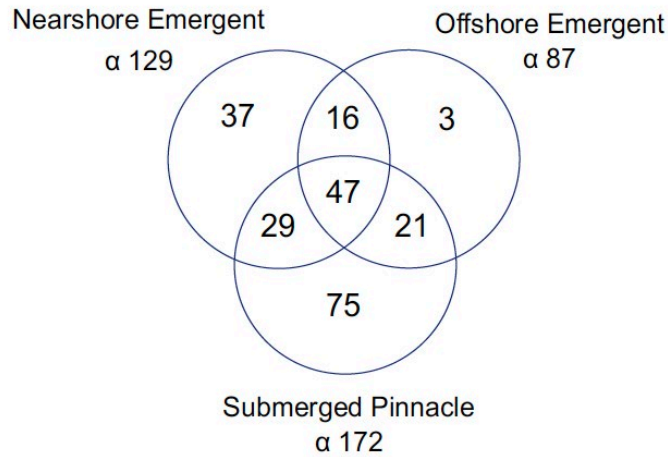
1157

1158 **Figure 3.** Differences in mean percent cover per transect \pm SE of 14 benthic cover types
 1159 across the three reef habitat types (n=20 per reef morphology). Significant differences are
 1160 represented by * and letters indicate statistically similar pairwise means ($p < 0.05$, Tukey
 1161 HSD). Full GLMM results Table S6

1162

1163

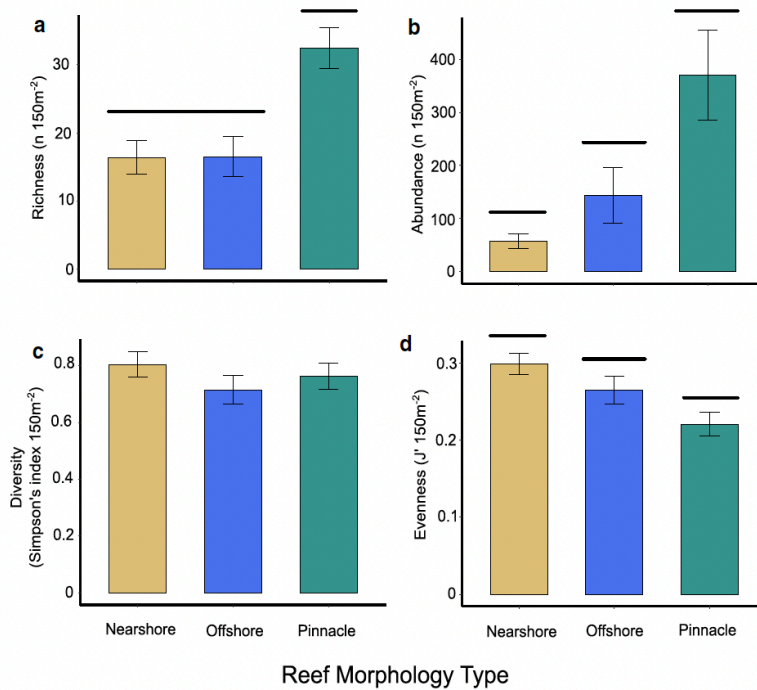
1164



1165

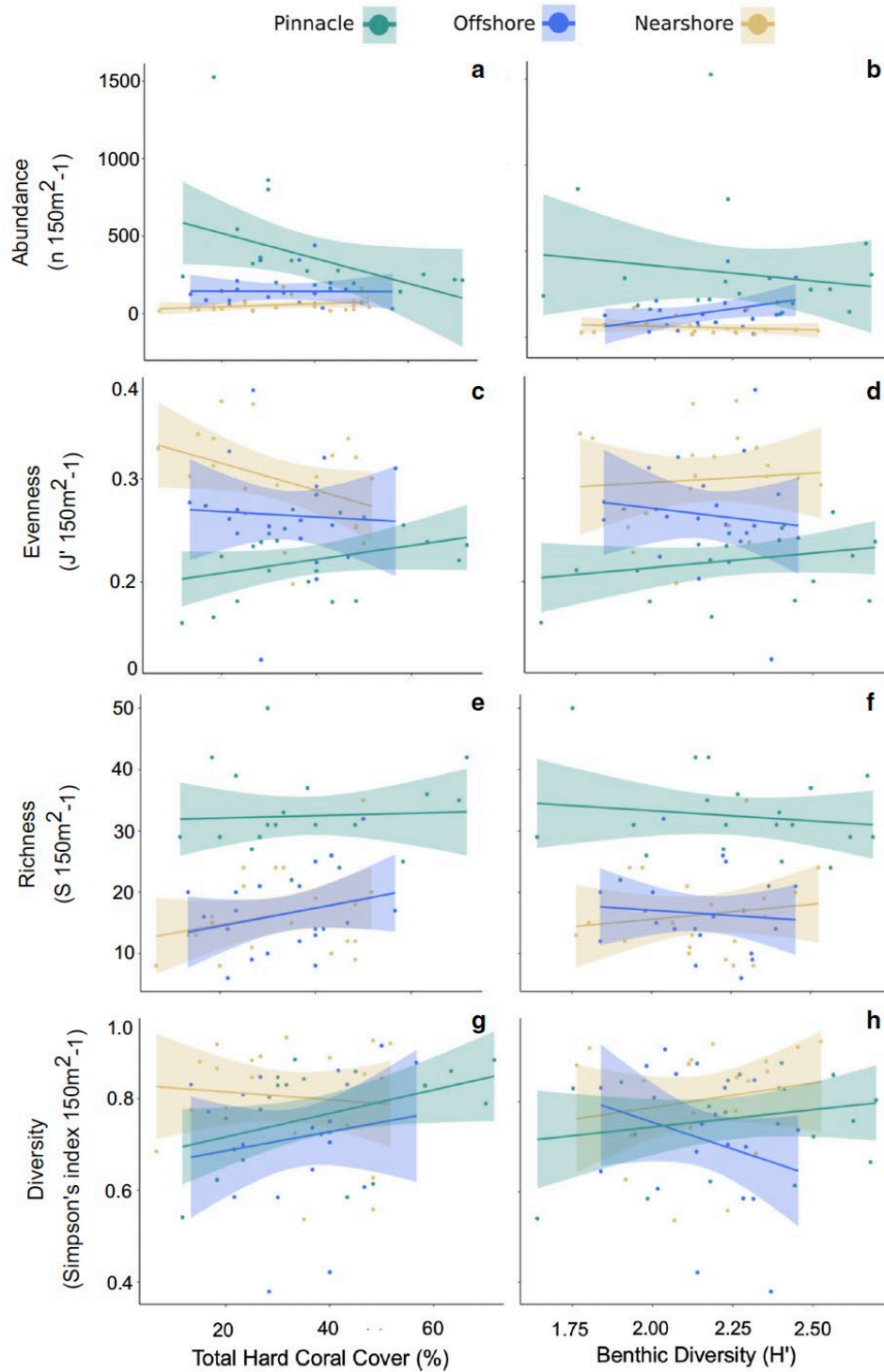
1166 **Figure 4.** Alpha and beta diversity for each reef morphology. Number of unique species at
 1167 each reef type are located in sectors of circles with no overlap

1168



1169

1170 **Figure 5.** Differences in fish community metrics between reef morphologies. Mean per
 1171 150m² transect ± SE bars (a) fish species richness (b) Total abundance of individuals (c)
 1172 Simpson's diversity (d) Community evenness Pielou's J'. Significant pair-wise differences
 1173 (p < 0.05, Tukey HSD) are indicated by grouping lines above. Full GLMM results Tables S1
 1174 and S5



1175

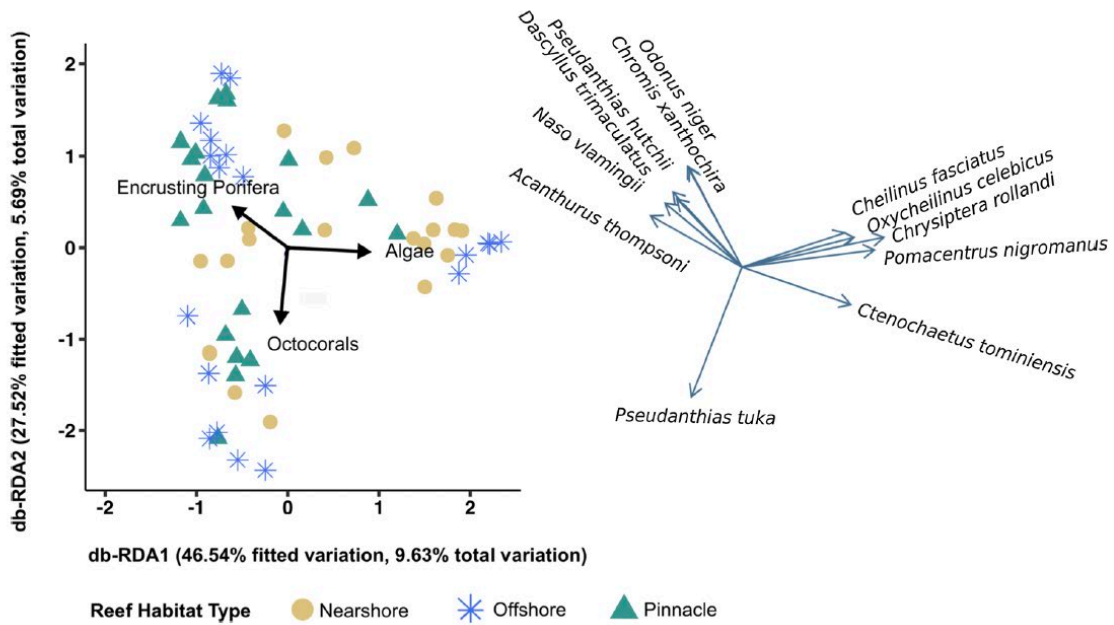
1176 **Figure 6.** Relationships between fish community metrics and benthic complexity variables

1177 for each reef type. Shaded areas depict 95 % confidence intervals from mixed effects

1178 models. Full summary of coefficients in models a-h in Table S9

1179

1180



1181

1182 **Figure 7.** (a) Distance-based redundancy analysis (db-RDA) plot of the ordiR2step model
 1183 based on benthic variables that better explained variability among fish communities across
 1184 reef habitat types (n=20 for each reef type). Significant benthic variables are overlaid as a
 1185 vector and fish species most correlated with each axis are presented to the right of the main
 1186 plot (b) Vector length and direction of the arrow represents the size and direction of the
 1187 relationships

1188

1189

1190

1191

1192

1193

1194

1195

1196

1197 **Table 1.** Summary of SIMPER results showing top five fish species and benthic cover
 1198 categories that contributed most to overall dissimilarity between assemblages for pair-wise
 1199 comparisons between reef types

Species reef type contrast	% Contribution	Mean abundance/ 150 m ²		Benthic habitat reef type contrast	% Contribution	Mean percentage cover	
		Pinnacle	Offshore			Pinnacle	Offshore
Pinnacle offshore overall dissimilarity 74.5%				Pinnacle offshore overall dissimilarity 38%			
<i>Pseudanthias tuka</i>	6.84	32.40	51.85	Complex Hard Coral	9.54	9.67	1.92
<i>Caesio cuning</i>	6.08	8.70	28.95	Encrusting Hexacoral	9.32	11.0	0.25
<i>Acanthurus thompsoni</i>	5.63	72.60	11.45	Laminar Hard Coral	9.15	8.33	15.33
<i>Pterocaesio tile</i>	2.95	11.60	14.85	Algae	8.94	5.92	7.08
<i>Chromis amboinensis</i>	2.77	8.40	4.90	Encrusting Porifera	7.77	10.5	21.0
Pinnacle–nearshore overall dissimilarity 87.8%				Pinnacle–nearshore overall dissimilarity 40%			
<i>Acanthurus thompsoni</i>	5.70	72.60	4.75	Algae	12.15	5.92	16.92
<i>Pomacentrus nigromanus</i>	5.48	0.00	7.60	Complex Hard Coral	9.16	9.67	5.58
<i>Pseudanthias tuka</i>	4.08	32.40	4.95	Encrusting Hexacoral	9.04	11.0	0
<i>Caesio cuning</i>	3.35	8.70	9.00	Rubble	8.44	5.5	9.33
<i>Ctenochaetus tominiensis</i>	3.09	0.45	3.00	Massive Hard Coral	8.33	10.0	4.00
Offshore– nearshore overall dissimilarity 79.5%				Offshore–nearshore overall dissimilarity 34%			
<i>Pseudanthias tuka</i>	9.05	51.85	4.95	Algae	11.99	7.08	16.92
<i>Caesio cuning</i>	6.86	28.95	9.00	Encrusting Porifera	11.01	21.0	6.08
<i>Pomacentrus nigromanus</i>	6.53	3.00	2.60	Rubble	9.64	6.33	9.33
<i>Acanthurus thompsoni</i>	3.86	11.45	4.75	Sand and Silt	8.69	3.91	7.50
<i>Chrysiptera anarzae</i>	3.09	1.05	2.30	Laminar Hard Coral	8.41	15.33	7.90

1200
 1201
 1202
 1203
 1204
 1205
 1206
 1207
 1208
 1209
 1210
 1211

1212 **Table 2.** Analysis of deviance or variance tables for main effects in all fish-benthic mixed
 1213 effects models. For GLMMs (total fish abundance and species richness), Likelihood-ratio
 1214 tests were used to test main effects. For LMMs (diversity and evenness) Wald-F tests with
 1215 Kenward-Rogers df were used. All main effects and interactions (“:”) are shown. Significant
 1216 results ($p < 0.05$) in bold

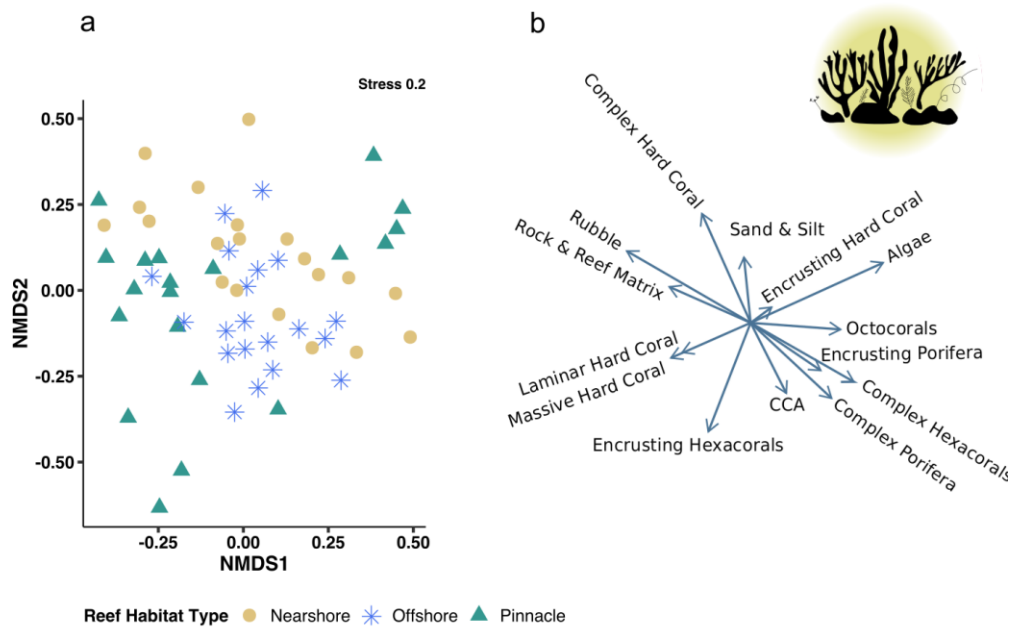
Variable	Df	Total abundance/150 m ²		Simpson diversity		Species richness		Species evenness	
		LRT	<i>p</i> value	<i>F</i>	<i>p</i> value	LRT	<i>p</i> value	<i>F</i>	<i>p</i> value
Total hard coral %	2	0.81	0.37	1.94	0.17	2.35	0.13	0.42	0.52
Reef type	1	49.58	< 0.001	1.69	0.20	65.50	< 0.001	1.11	0.34
Total hard coral: reef type	1	2.35	0.31	1.42	0.25	2.19	0.33	1.11	0.34
Benthic diversity (H')	2	1.25	0.26	0.11	0.74	0.03	0.85	0.19	0.67
Reef Type	1	28.87	< 0.001	0.95	0.40	65.54	< 0.001	0.17	0.84
Benthic diversity: reef type	1	5.03	0.08	1.21	0.31	1.03	0.60	0.19	0.83

Significant results ($p < 0.05$) in bold

1217

1218

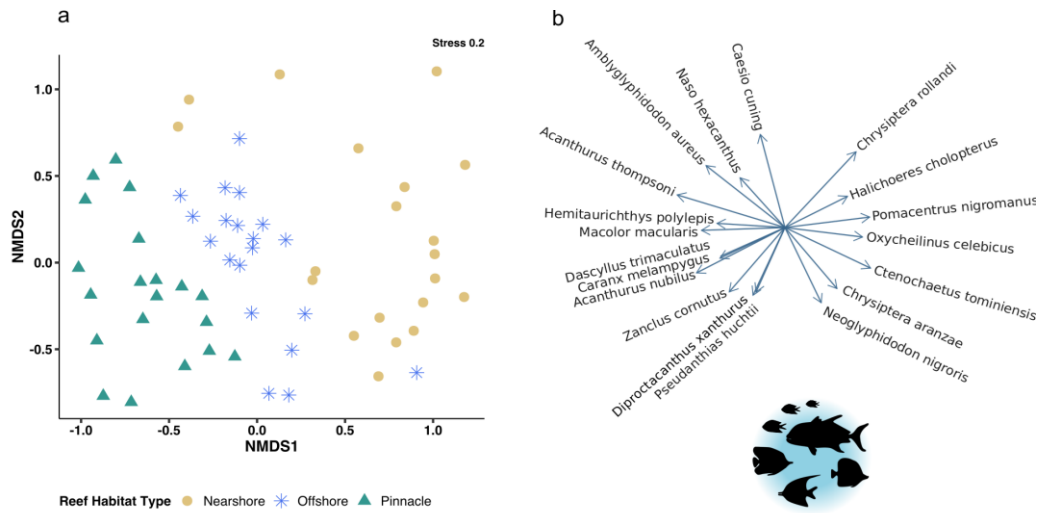
1219 **Supplementary Information Figures**



1220

1221 **Figure S1.** (a) nMDS of benthic communities aggregated by reef morphology (b) Vector plot
 1222 showing strength and direction of relationship between benthic category and nMDS axes

1223



1224

1225 **Figure S2.** (a) nMDS of fish communities aggregated by reef morphology (b) Vector plot

1226 showing the strength and direction of relationship between fish species and nMDS axes

1227

1228

1229

1230

1231

1232

1233

1234