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Title: Habitat type and complexity drive fish assemblages in a tropical seascape

Authors: April. E. Hall* and Michael, J. Kingsford

Affiliations: College of Science and Engineering and ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD, Australia

* **Corresponding author:** Dr April Hall; College of Science and Engineering, Building 34, James Cook University, 1 James Cook Drive, Douglas QLD 4811; april.hall@jcu.edu.au;

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ABSTRACT

Inshore marine seascapes support a diversity of interconnected habitats and are an important focus for biodiversity conservation. This study examines the importance of habitat attributes to fish assemblages across a mosaic of inshore habitats: coral reefs, rocky reefs, macroalgae beds, and sand/rubble beds. Fishes and benthic habitats were surveyed at thirty four sites around continental islands of the central Great Barrier Reef using Baited Remote Underwater Video Stations (BRUVS). Species richness was influenced foremost by habitat type, and also by structural complexity within habitat types. The most speciose assemblages occurred in coral and rocky reef habitats with high structural complexity, provided by the presence of coral bommies/overhangs, boulders, and rock crevices. However, macroalgae and sand/rubble beds also supported unique species, and so contributed to the overall richness of fish assemblages in the seascape. Most trophic groups had positive associations with complexity, which was the most important predictor for abundance of piscivorous fishes and mobile planktivores. There was significant differentiation of fish assemblages among habitats, with the notable exception of coral and rocky reefs. Species assemblages overlapped substantially between coral and rocky reefs, which had 60% common species, despite coral cover being lower on rocky reefs. This suggests that, for many species, rocky and coral substrates can provide equivalent habitat structure, emphasizing the importance of complexity in providing habitat refuges, and highlighting the contribution of rocky reefs to habitat provision within tropical seascapes. Our results support an emerging recognition of the collective value of habitat mosaics in inshore marine ecosystems.

Keywords

Baited Remote Underwater Video Stations, coral reefs, Great Barrier Reef, macroalgae, rocky reefs, rugosity

1 1. INTRODUCTION

2 The composition and complexity of marine habitats can have a strong influence on associated
3 fish assemblages. In tropical marine ecosystems, coral reefs often occur alongside a range of
4 adjacent interconnected habitat types, each providing unique ecological features, and
5 ecosystem services. In addition to coral reefs, inshore habitats include mangroves,
6 macroalgae beds, seagrass meadows, sand or rubble beds, and rocky reefs. These habitats
7 are often patchily distributed around inshore islands and coastal regions, and may contribute
8 uniquely to regional diversity by supporting distinct fish assemblages (Evans et al., 2014;
9 Wilson et al., 2010). Inshore tropical ecosystems consist of a mosaic of such habitats, and
10 there is an increasing recognition of the importance of this habitat heterogeneity for fishes
11 (Fulton et al., 2019; Sheaves, 2009; Sievers et al., 2020).

12

13 Non-reef habitats are often critical in supporting adjacent coral reefs, with high connectivity
14 amongst habitats, especially in inshore regions (Sheaves, 2009; Sievers et al., 2020). Many
15 “coral reef fish” species (e.g. Haemulidae, Labridae, Lutjanidae, Serranidae, , Siganidae) also
16 utilize habitats other than coral reefs as juvenile nursery habitats (Dahlgren & Eggleston,
17 2000; Nagelkerken et al., 2000; Tano et al., 2017), or have been recorded as adults in these
18 non-coral reef habitats (Sambrook et al., 2019). Adult reef fishes also commonly utilize a range
19 of habitat mosaics for foraging grounds, for example species of Haemulidae, Lutjanidae, and
20 Nemipteridae have been documented to reside on coral reefs, and undertake diel or tidal
21 migrations to adjacent sandy, seagrass, or rocky habitats to forage (Boaden & Kingsford, 2012;
22 Clark et al., 2009; Hitt et al., 2011; Unsworth et al., 2007). Given this, there is an emergent
23 interest in examining the value of such habitat mosaics, and their importance for reef fishes
24 (Olds et al., 2012; Sambrook et al., 2019; Sievers et al., 2020).

25

26 The structural complexity (or rugosity) of marine habitats can have a strong influence on fish
27 assemblages. Structurally complex habitats provide a greater availability of microhabitats for
28 fishes of a range of sizes to shelter in, and therefore positively influence both abundance and
29 species richness (Emslie et al., 2008; Friedlander et al., 2003; García-Charton & Pérez-Ruzafa,
30 2001; Graham et al., 2015; Nash et al., 2013). Structural complexity can vary greatly among
31 habitat types. Structured habitat types such as coral reefs or rocky reefs inherently have a
32 greater rugosity compared to unstructured habitats such as macroalgae beds or sand/rubble
33 beds. On coral reefs, corals form the dominant foundational architecture, and provide
34 essential refuges for juvenile and/ or adult fishes (Jones et al., 2004; Wilson, Burgess, et al.,
35 2008). The availability of live coral can be a critical determinant of species abundance and
36 influence the composition of fish assemblages (Coker et al., 2014; Emslie et al., 2008;
37 Friedlander et al., 2003; Komyakova et al., 2013; Nash et al., 2013). On rocky reefs, this
38 structure is provided by boulders of various sizes, as well as cracks and crevices, which provide
39 a variety of microhabitats (Kingsford, 1998, Jones 1988).

40

41

42 The structural complexity of reef architecture can also vary greatly within habitats, depending
43 on the underlying habitat matrix and the composition of the benthic substratum (Darling et
44 al., 2017; Dominici-Arosemena & Wolff, 2006; García-Charton & Pérez-Ruzafa, 2001; Nash et
45 al., 2013). For larger bodied fishes (e.g. Haemulidae, Serranidae, Lutjanidae), structurally
46 complex habitats and seascape features such as caves, boulders, and tabulate corals (Kerry &
47 Bellwood, 2012) form critical habitats, whereas smaller bodied fishes such as damselfishes
48 tend to utilize smaller microhabitats provided by branching corals, which offer shelter from
49 predators (Beukers & Jones, 1998; Boström-Einarsson et al., 2013; Wilson, Burgess, et al.,
50 2008). In habitats dominated by macroalgae, the composition and density of the canopy can

51 influence the structural complexity provided by the habitat, with canopy-forming genera such
52 as *Sargassum* providing important habitat structure, especially for juvenile fishes (Fulton et
53 al., 2019). Sand or rubble beds, by comparison, tend to have uniform low complexity, and
54 offer little structural habitat attributes for fishes.

55

56 Inshore marine habitats have unique conservation value, provide essential ecosystem
57 services, and are important economically, socially, and culturally (Hughes et al., 2015; Wenger
58 et al., 2018) . They are also highly responsive to human influences such as coastal runoff, and
59 are often key fishing areas, due to their close proximity to land (De'ath & Fabricius, 2010;
60 Webley et al., 2015). Given this, an understanding of the importance of habitat characteristics
61 for fishes on inshore marine habitats is critical for guiding conservation and management
62 practices. On the Great Barrier Reef (GBR), inshore regions support a range of diverse habitats
63 and associated fish fauna (GBRMPA, 2014). However, data on fish/habitat relationships on
64 inshore regions of the GBR are often lacking, especially for habitats in close proximity (i.e.
65 within a few kilometres) of the coast. Further, most research on fishes in these inshore regions
66 is focused solely on the coral reef component of the habitat mosaic (Ceccarelli et al., 2020;
67 Sambrook et al., 2019). Inshore regions are often highly turbid environments, where SCUBA
68 based monitoring and survey efforts may be hindered by poor visibility or the presence of
69 estuarine crocodiles (Bradley et al., 2017). As such, there is a need for greater understanding
70 of the key habitat attributes on inshore reefs, and how habitat mosaics support inshore fish
71 fauna.

72

73 The intent of this study was to examine the importance of habitat attributes across a mosaic
74 of inshore habitats in the central GBR. To address this, we examined the relative influence of

75 habitat characteristics and biophysical parameters on fish assemblages in two regions: the
76 Dunk Island and Hinchinbrook Island regions.

77

78 The aims of the study were as follows:

- 79 1. Determine how the composition and complexity of benthic substratum differed
80 amongst broad habitat types;
- 81 2. Describe the taxonomic and trophic composition of inshore fish fauna, and identify
82 the major processes driving species richness;
- 83 3. Evaluate the key habitat attributes and biophysical parameters driving abundance for
84 fish trophic groups; and
- 85 4. Examine the extent to which broad habitat types supported distinct fish assemblages.

86

87 2. MATERIALS AND METHODS

88 The care and use of experimental animals complied with Australian animal welfare laws,
89 guidelines and policies as approved by the James Cook University Animal Ethics Committee
90 #A2438.

91 2.1 Study area and sampling design

92 The study area comprised two inshore regions of the central GBR: the Hinchinbrook and Dunk
93 Island regions (Figure 1). Both regions contain a number of continental islands in close
94 proximity to the Queensland coast (16-28km for Hinchinbrook and 4-17km for Dunk Island
95 region), which are composed of granite, with a range of fringing habitats (Furnas, 2003). The
96 area is a popular area for fishing (primarily recreationally) and contains both fished
97 (Conservation Park) zones and No-take Marine Reserves (Figure 1). Fishing occurs in a
98 restricted manner in Conservation Park zones and is prohibited in No-Take Marine Reserves;

99 details of permitted activities in each zone are outlined in Hall et al. (2021).. To ensure that
100 the sampling design was not confounded by zone, and to allow broad inference about fish-
101 habitat relationships throughout the study area, we surveyed sites across both management
102 zones. The distribution of sites was chosen to optimally encompass the range of broad habitat
103 types present in each region; sampling occurred around multiple islands and management
104 zones within each region (Figure 1). Since the characterization of each site by broad habitat
105 types occurred after sampling (during video analysis), the number of sites was uneven among
106 habitat types, and was considered representative of the spatial arrangement of habitats
107 within each area sampled (Figure 1).

108

109 Baited Remote Underwater Video Stations (BRUVS) were used to survey fishes at 34 sites; 18
110 in the Dunk Island region and 16 in the Hinchinbrook Island region (Figure 1). Six replicate
111 deployments were made per site, with a total of 204 replicate BRUVS deployed within the
112 study area. Surveys occurred during two field trips: August/ October and June/September
113 2018 for the Hinchinbrook and Dunk Island regions respectively. Surveys were conducted
114 during the dry season and in neap tide periods, to ensure maximal water visibility and
115 minimize tidal effects on video footage. Each BRUVS had a deployment (soak) time of 60
116 minutes; replicates were placed along shallow fringing habitats around the edges of islands,
117 and the depth recorded (Table 1). To ensure sampling independence, each BRUVS was
118 dropped at least 250-350m apart, and for areas with limited spatial extent, separation was
119 achieved by alternating the placement of sites by field trip. In this manner, each site and
120 replicate was considered independent.

121

122

123

124 **2.2 BRUVS apparatus and deployment**

125 The use of BRUVS to effectively survey a fish assemblages has been well established (Cappo
126 et al., 2004; Cappo et al., 2011; Harvey et al., 2013), especially in inshore areas, where turbid
127 water and the presence of estuarine crocodiles prohibit in-water surveys (Bradley et al., 2017;
128 Donaldson et al., 2020). Baited techniques were chosen over unbaited video, since
129 comparative studies have shown that the use of bait provides better power to discriminate
130 fish assemblages amongst habitats (Harvey et al. 2007). The BRUVS apparatus and
131 deployment methods are described in detail by Stowar et al. (2008). Each BRUVS unit
132 consisted of a galvanized steel frame, onto which an underwater camera and housing and bait
133 arm were attached. The camera housing was secured to the frame, and oriented downwards
134 to capture the view of the bait bag, which was secured at the end of the one metre long PVC
135 bait arm, and contained approximately 1kg pilchards (*Sardinops* sp.). The apparatus was
136 attached to a rope with surface floats to facilitate deployment and retrieval. The camera
137 housing contained either Sony handycams, or GoPro Hero 4 cameras, which were adjusted to
138 maximize the focal range and video resolution.

139

140 **2.3 Video analysis**

141 Fishes and habitats were surveyed from video footage using a custom made database
142 developed by the Australian Institute of Marine Science, as described in Cappo et al. (2011).
143 All fish species that were large and conspicuous enough to accurately count and identify were
144 included (Supporting Information Table S1). A number of resources were used for fish
145 taxonomy and identification (Allen, 2009; Bray & Gomon, 2021; Froese & Pauly, 2021; Randall
146 et al., 1997). Initial analysis indicated that small fishes such as wrasses <5cm, damselfishes,
147 cardinalfishes, and gobies could not be accurately identified and recorded, especially in low
148 visibility replicates, so these species were excluded from the dataset to ensure accuracy.

149 Replicates were excluded from the analysis if the visibility was very poor (<1.5m), or if the
150 BRUVS were positioned such that the field of view was impaired. The resulting dataset for
151 video analysis was 160 of 204 replicates, which included a minimum of 4 replicates per survey
152 site. Fish abundance was recorded as MaxN, the maximum number of individuals of a given
153 species observed in a single video frame per 60 minutes of footage. MaxN is a well-accepted
154 and commonly used measure of abundance for BRUVS data, and the use of this metric
155 prevents over-counting of fishes that may move in and out of the field of view (Cappo et al.,
156 2007; Cappo et al., 2004). All fishes were identified to species level where possible, and to
157 genus where species could not be distinguished (Supporting Information Table S1).

158

159 A number of habitat variables were recorded during the video analysis, using images of the
160 surrounding habitat from the video field of view (Table 1). The percentage cover of live coral,
161 algae, bare, and bedrock were estimated from the habitat visible in each video. A qualitative
162 index of topographic complexity was determined for each replicate based on the structural
163 features present in the field of view (Espinoza et al., 2014). Estimates of complexity were kept
164 broad (low, medium, and high), to ensure that habitats could accurately be assigned to a
165 complexity category (Table 1). Complexity categories, and categorization of broad habitat
166 types, occurred after the analysis of all videos had been completed, to allow comparison of
167 all sites and designation of sites into the various categories (Table 1). From this, four broad
168 habitat types were derived, as outlined in Table 1: coral reefs (underlying substrate of coral),
169 rocky reefs (underlying substrate of granite boulders), macroalgae bed (mostly *Sargassum*
170 spp.), and sand/rubble bed (Supporting Information Figure S1).

171 Visibility was also estimated for each video, and assigned a category of low, medium, or high,
172 using the bait arm as a length reference (Table 1). Site-level habitat data was derived for use
173 in multivariate statistical analyses (as outlined below), using site-averaged data for complexity

174 (as a score), benthic cover, depth, and visibility (in metres). To determine site-level habitat
175 type, each site was categorised by considering the suite of replicates within. Although habitats
176 were distributed patchily within each region, each site tended to be spatially homogeneous
177 in its broad habitat type, so categorization of habitat type at the site level was considered
178 representative (Figure 1).

179

180 **2.4 Fish trophic groups**

181 To evaluate variation in the functional composition of fish assemblages, each fish species was
182 categorised into a trophic grouping as follows: piscivores, carnivores, benthic foragers, mobile
183 planktivores, corallivores, and herbivores (Supporting Information Table S1). Trophic
184 groupings were based on published accounts of fish diets where possible, and/ or designation
185 of species by trophic group in prior publications (e.g. Emslie et al., 2015; Williamson et al.,
186 2019). Piscivores had a diet dominated by fishes ($\geq 50\%$), whereas carnivores ate a mix of
187 invertebrates ($< 50\%$) and fishes (10-50%), and benthic foragers ate only benthic invertebrates
188 (Farmer & Wilson, 2011; Kulbicki et al., 2005; Nakamura et al., 2003). Corallivores included
189 both facultative and obligate corallivores (Cole et al., 2008), and mobile planktivores were
190 species that foraged on the plankton in the water column (Froese & Pauly, 2021). To describe
191 in detail the trophic and taxonomic composition of assemblages, herbivores were further
192 categorised into sub-groups: grazers/detritivores, scrapers/excavators, and browsers (Green
193 & Bellwood, 2009). The combined category “herbivores” was used for all statistical analyses
194 for simplicity, and due to low abundances of some herbivore sub-groups. Species richness
195 was calculated as the number of species recorded per replicate, and to prevent over-
196 estimation, we only included taxa that were identified to species level (140 out of the 179
197 taxa).

198

199 **2.5 Statistical analyses**

200 The objective of the sampling design was to encompass the variation in habitat types
201 occurring within the study area. Since many predictor variables were unknown until after
202 video analysis, most predictor variables (e.g. complexity, habitat type) had an uneven sample
203 size amongst levels. Statistical measures were focused on approaches that determine the
204 relative importance of the predictors that occurred, and were robust to variation in sample
205 sizes (De'ath & Fabricius, 2000; Elith et al., 2008).

206

207 To determine how benthic composition varied among habitat types and complexity
208 categories, variation in benthic composition among sites was analysed using a Principle
209 Component Analysis (PCA) using the PRIMER statistical package (Clarke et al., 2014). To best
210 describe the unique substrate biota that occurred among habitat types, categories of benthic
211 cover were further separated. Substrate biota for the PCA were categorised as follows: live
212 hard coral, live soft coral, bedrock (bare rock), sponges, hydroids, seagrass, algae, and bare
213 (sand or rubble with no substrate biota). Along with the percentage cover of these substrate
214 biota, depth and complexity were also included in the PCA dataset. Data were averaged per
215 site and normalized prior to analysis (Clarke et al., 2014).

216

217 The influence of habitat and other predictor variables on species richness was analysed to
218 develop a Classification and Regression Tree (CART), fitted in R using the recursive partitioning
219 ('rpart') package (R Core Team, 2018). This method is considered a flexible and robust
220 approach, which is well suited for complex ecological datasets, and does not require balanced
221 data (De'ath & Fabricius, 2000). The CART was used to model variation in species richness, by
222 repeatedly splitting the full dataset into binary groups according to predictor variables. Initial
223 input into the model included all predictor variables outlined in Table 1, as well as region and

224 management zone. Each split in a CART aims to minimize the total sums of squares within
225 the two nodes formed, and once splitting has produced a full tree, the tree is “pruned” to
226 produce a CART that is the simplest but most effective representation of variation within the
227 response variable (De'ath, 2002). Selection of the final CART for our model was made using
228 10-fold cross validation to select the tree with the minimum cross validation error; this
229 method produces valid and clearly interpretable trees (Brieman et al., 1984; De'ath &
230 Fabricius, 2000). The resulting CART only includes predictor variables that contributed to the
231 final tree model.

232

233 Boosted Regression Trees (BRTs) were used to explore the key drivers of abundance for each
234 of the fish trophic groups, using the same suite of predictors described for the CART. Boosted
235 Regression Trees are a modelling approach whereby a succession of regression trees are
236 developed using machine learning models as described by Elith et al. (2008). The BRT models
237 were fitted using the ‘gbm’ package in R (R Core Team, 2018), with the following parameters:
238 learning rate (contribution of each tree to the final model) = 0.001, bag fraction (proportion
239 of data used in each step) = 0.5, and tree complexity (maximum nodes per tree) = 5 (Elith et
240 al., 2008). Fish abundance, pooled to the level of trophic group, was used as the response
241 variable, such that each trophic group had a unique fitted BRT.

242

243 To examine the influence of habitat type on fish species assemblages, we used Canonical
244 Analysis of Principle Coordinates (CAP), along with Bootstrapped metric Multidimensional
245 Scaling (mMDS). Site-averaged species abundance data were dispersion weighted and log
246 transformed to reduce the influence of highly abundant species, and the Bray Curtis similarity
247 matrix was used. The CAP method is described in detail in Anderson and Willis (2003), and
248 uses an ordination process constrained by *a priori* classifications (in this case, “habitat type”);

249 the resulting patterns are projected onto a 2D ordination (CAP) plot. This method is
250 considered a powerful approach that is useful for datasets with many rare species, such as
251 ours. The CAP approach provided a measure of “allocation success”, which indicates the
252 percentage of sites correctly classified by habitat type under permutation. Since there were
253 four habitat types, an allocation success of greater than 25% is considered greater than
254 expected by random chance. To test for significant differences in species assemblage amongst
255 habitat types, we used a CAP permutation test in conjunction with bootstrapped nMDS. The
256 CAP test p value (trace statistic) is obtained through 999 permutations, where group labels
257 are exchanged, to test the null hypothesis of no differences in species composition by habitat
258 type (Anderson & Willis, 2003).

259

260 To counter the possibility that the categorization of fish assemblages by habitat in the CAP
261 was influenced by variation in sample size, we performed bootstrapped mMDS. Bootstrap
262 resampling (with replacement) was applied to produce a total of 50 values per habitat type.
263 Bootstrapping was limited to $m = 6$ dimensions to reduce the likelihood of a high-d artefact
264 producing erroneous results, and this value was selected based on a Shephard diagram
265 (Clarke et al., 2014). To estimate confidence intervals for the bootstrapped regions, ellipses
266 representing 95% of the bootstrapped averages per habitat type were plotted, such that non-
267 overlapping ellipses in the mMDS are representative of distinct assemblages (Clarke et al.,
268 2014). The results of the bootstrapped MDS were then used in conjunction with the CAP
269 ordination and permutation test to infer variation in species composition amongst habitat
270 types.

271

272

273 3. RESULTS

274 3.1 Composition and structure of benthic habitats

275 Four broad habitat types occurred within the region: coral reefs (n= 14 sites), rocky reefs
276 (n=10 sites), macroalgae beds (n= 5 sites), and sand/ rubble beds (n=5 sites; Supporting
277 Information Figure S1 and Table 1). The distribution of habitat types differed among regions,
278 and was patchy within regions; many islands had more than one habitat type (Figure 1). Some
279 islands (e.g. Bedarra, Smith, Coombe) had both coral and rocky reef habitats, whereas others
280 had only coral reef (Brook Islands) or rocky reef (Eva Island) habitats. Both coral reefs and
281 rocky reefs had moderate or high complexity, but differed in the nature of the underlying
282 structure, which was composed of hard corals for coral reefs, and bedrock for rocky reefs
283 (Table 1). High complexity sites occurred on coral reefs that had large massive corals, along
284 with smaller hard and soft corals of a diverse range of morphologies. On rocky reefs, high
285 complexity sites had large granite boulders alongside smaller boulder structures and a range
286 of substrate biota including soft corals, hydroids and sponges (Supporting Information Figure
287 S1). Macroalgae beds were more prevalent in the Dunk Island region, whereas the
288 Hinchinbrook Island region had more sand/rubble beds (Figure 1). Macroalgae beds were
289 characterised by large stands of macroalgae (mostly *Sargassum* spp.), and these were found
290 on low or moderate complexity habitats. Sand/rubble beds were unstructured habitats, with
291 extensive cover of bare sand or rubble, and minimal substrate biota; they occurred as low
292 complexity habitats only (Supporting Information Figure S1).

293

294 The composition of benthic substrates differed among the four habitat types. With the
295 exception of coral reef habitats, sites were clustered in the PCA according to habitat type
296 (Figure 2). Coral reef sites were separated across PC1 according to complexity category and

297 the dominant benthic substrate. Moderate complexity coral reefs clustered loosely with
298 macroalgae beds, and had a higher cover of algae (relative to coral). High complexity coral
299 reefs were more similar to rocky reefs, with a higher cover of hard and (to a lesser extent)
300 soft coral cover (Figure 2). Rocky reefs had distinct benthic composition, and with the
301 exception of a single site, were clustered in the PCA, with moderate and high complexity sites
302 intermixed. Rocky reefs tended to occur in deeper sites, and were dominated by bedrock with
303 scatterings of sponges, hydroids, and soft corals (Figure 2). Principle Component 2 (PC2)
304 separated high complexity sites dominated by hard corals from low complexity sites with bare
305 (sand/rubble) substrates. Sand / rubble beds were distinctly clustered within the PCA, and
306 were dominated by bare substrates with scatterings of seagrass (Figure 2).

307

308 **3.2 Trophic and taxonomic structure of fish assemblages**

309 Fish assemblages in the Dunk and Hinchinbrook Island region were diverse, with 179 taxa
310 from 29 fish families identified. Of these taxa, 140 were identified to species level, and 39
311 identified to genera (see Supporting Information Table S1). Species richness and abundance
312 varied greatly amongst fish families and trophic groups (Figure 3). The most abundant families
313 consisted of schooling species such as Caesionidae (fusiliers), as well as Lutjanidae (snappers)
314 and Labridae (wrasses) which contain a diverse range of species from a variety of trophic
315 groups (Figure 3). Many species were rare and/ or patchy in their distributions; 162 species
316 ($\approx 90\%$) occurred in less than 20% of replicates, and 37 species ($\approx 21\%$) only recorded a single
317 individual throughout the study area (Supporting Information Table S1). Of the 29 families
318 recorded, nine of these included only a single species, whereas the most speciose family
319 (Labridae) comprised 25 species (Figure 3). Twelve elasmobranch species from five families
320 were recorded: nine species of sharks and three species of rays. Elasmobranchs were rare and
321 patchily distributed, only two species occurred in more than 5% of replicates: blacktip reef

322 shark, *Carcharhinus melanopterus* (15%), and tawny nurse shark, *Nebrius ferrugineus* (5.6%).
323 The most abundant trophic group was mobile planktivores, which were dominated by the
324 highly abundant Caesionidae. Benthic foragers were the most speciose trophic group, and
325 included a variety of species from 14 families. Corallivores, scapers/excavators, and browsers
326 recorded both low abundance and species richness (Figure 3).

327

328 **3.3 Factors influencing species richness**

329 Species richness was most strongly influenced by habitat type, with the initial split in the CART
330 separating coral and rocky reef habitats from macroalgae and sand/ rubble bed habitats
331 (Figure 4a). Coral and rocky reefs recorded higher species richness than macroalgae and sand/
332 rubble beds, particularly in the Dunk Island region (Figure 4b). Within coral and rocky reef
333 habitats, species richness was influenced by visibility, complexity, region, and then zone (in
334 order of importance). Low visibility replicates recorded fewer species, however these only
335 constituted 17% of the dataset; differentiation of the two regions occurred within low
336 visibility replicates, with Dunk Island having higher species richness (Figure 4a). Complexity
337 was a strong driver in coral and rocky reef habitats; there was separation between moderate
338 and high complexity replicates, with the latter supporting greater species richness (Figure 4a).
339 There were no low complexity replicates in coral or rocky reef habitats. The Dunk Island region
340 consistently supported greater species richness than the Hinchinbrook Island region in the
341 CART. The influence of zone on species richness was inconsistent in both direction and
342 magnitude. In macroalgae and sand/ rubble beds, the overall influence of zone was greater,
343 and marine reserves had higher species richness compared to fished zones. In coral and rocky
344 reef habitats, the opposite trend was evident; zone had comparatively little influence, and
345 fished zones supported greater species richness compared to marine reserves (Figure 4a).

346

347 **3.4 Key drivers of abundance for fish trophic groups**

348 Key drivers of abundance differed in their nature and magnitude for the six trophic groups
349 (Figure 5 and Table 2). Piscivores, corallivores, and to a lesser extent carnivores, were strongly
350 influenced by a single predictor. In contrast, for benthic foragers and mobile planktivores, the
351 influence of predictors on abundance was relatively even (Figure 5). Complexity was a very
352 strong predictor for piscivores (43.7% relative importance), and was also the most important
353 predictor for mobile planktivores (24.9%; Figure 5 and Table 2); both groups had markedly
354 higher abundance in high complexity compared to low or moderate complexity habitats
355 (Figure 6). For carnivores, benthic foragers, corallivores, and herbivores, abundance increased
356 with increasing complexity (Figure 6), but the relative importance of complexity as a predictor
357 was low (<10%; Figure 5). Corallivores and carnivores both had strong positive relationships
358 with coral cover, and for corallivores, this relationship overwhelmingly influenced abundance
359 (>61% relative importance, and all other predictors were comparatively unimportant (<6%;
360 Figure 5 and Table 2). For herbivores, both depth and algae were important, each contributing
361 ≈32% relative influence (Figure 5). Herbivores were most abundant at shallow depths, and
362 had a positive relationship with the cover of algae (Table 2).

363

364

365 **3.5 Fish assemblages amongst habitat types**

366 The composition of species assemblages varied according to habitat type. Of the 179 species
367 observed, 67 occurred only in a single habitat (37%). Of these habitat-specific species, 35
368 occurred only on coral reefs, 12 occurred only on rocky reefs, 10 occurred only on macroalgae
369 beds, and 10 occurred only in sand/ rubble beds (Supporting Information Table S1). The
370 greatest overlap in occurrence was for coral and rocky reefs; 60% of species found on coral
371 reefs also occurred on rocky reefs. The CAP ordination showed separation of assemblages

372 into three distinct groups: (1) sand/rubble beds, (2) macroalgae beds, and (3) rocky reefs and
373 coral reefs (Figure 7). The CAP permutation test showed a significant difference in the position
374 of the four habitat centroids (trace test statistic, $p = 0.017$), and this was supported by non-
375 overlapping confidence ellipsis in the bootstrapped MDS for all habitat types except coral and
376 rocky reefs (Figure 7 and Supporting Information Figure S2).

377 Rocky reef and coral reef habitats were not distinct from each other, and overlapping regions
378 occurred in both the CAP ordination, and MDS confidence ellipses (Figure 7 and Supporting
379 Information Figure S2). Fish assemblages were better characterised in the CAP analysis when
380 coral and rocky reefs were considered collectively rather than separately. The allocation
381 success of the CAP was 60% for rocky reefs and 61% for coral reefs when considered as
382 separate habitat types, but increased to 87% when analysed as a combined “reefs” habitat
383 type. Three rocky reef sites had very similar fish assemblages to coral reefs, and overlapped
384 closely with coral reef sites in the CAP (Figure 7). Of these rocky reefs sites, two were on
385 islands that also supported coral reef habitats (Bedarra and Goold Island), whereas the third
386 site (Cape Sandwich) had no coral reefs in close proximity based on our surveys (Figure 1 and
387 Figure 7). Rocky and coral reefs collectively supported a distinct suite of species, namely
388 species that were either only present on reefs, or were markedly more abundant on reefs
389 compared to other habitats. Coral and rocky reefs were comprised of more reef- associated
390 species, including various species of Chaetodontidae, Pomacanthidae, Lutjanidae and
391 Serranidae (Figure 7). For example, reef associated species *Chaetodon rainfordi* (Rainford’s
392 butterflyfish), *Cephalopholis boenak* (brown-barred rockcod), and *Lutjanus sebae* (red
393 emperor) only occurred in rocky or coral reef habitats, whereas *Pomacanthus sextriatus*
394 (sixbar angelfish) and *Lutjanus lemniscatus* (darktail snapper) were present but rare in
395 macroalgae and sand/ rubble beds, but much more abundant in coral or rocky reef habitats
396 (Figure 7).

397

398 Sand/ rubble beds supported the lowest species richness and abundance of the four habitats,
399 but did support some unique species not found elsewhere. Transient pelagic species such as
400 *Scomberomorus* spp. (mackerels), and *Sphyraena barracuda* (great barracuda) were only
401 detected in this habitat, and *Caesio lunaris* (lunar fusilier) was also unique to sand/rubble
402 beds. Sand/ rubble beds often contained groups of *Lutjanus vitta* (brownstripe snapper), and
403 were distinct due to the absence of tuskfish species such as *Choerodon graphicus* and
404 *C. cyanodus*, which were commonly encountered in other habitats, and particularly abundant
405 in macroalgae beds (Figure 7). Allocation success for sand/ rubble beds in the CAP analysis
406 was 60%; macroalgae beds were more distinct, with a high allocation success of 80%. A
407 number of species only occurred in macroalgae beds, including *Parupeneus spilurus* (black-
408 saddle goatfish), *Scarus forsteni* (whitespot parrotfish) and *Lethrinus obsoletus* (orange-
409 striped emperor; Figure 7).

410

411 4. DISCUSSION

412 Our results highlight the importance of inshore tropical seascapes in supporting a rich
413 diversity of fish species. Collectively, the mosaic of coral reef, rocky reef, macroalgae, and
414 sand/rubble habitats supported a functionally and taxonomically diverse fish assemblage. It
415 is likely that many fishes recorded utilize multiple habitats within the seascape (Sambrook et
416 al., 2019), however each habitat also supported unique species not recorded elsewhere, and
417 so contributed uniquely to the overall species richness. Although the habitat relationships
418 varied amongst the trophic groups considered, it was clear that broad habitat type strongly
419 influenced the species richness and composition of fish assemblages. A notable exception to
420 this outcome was the similarity of fish assemblages in rocky and coral reefs, which both
421 supported higher species richness compared to macroalgae and sand/ rubble beds, most

422 likely due to the provision of complex habitat architecture. Our results concur with and build
423 upon a number of recent studies highlighting the role of habitat mosaics on inshore coastal
424 ecosystems (e.g. Sambrook et al., 2019, Sievers et al., 2020), and further suggest that rocky
425 reefs make a valuable and previously under-recognised contribution to the habitat mosaic.

426

427 Species richness was principally influenced by the differences in structural complexity among
428 and within habitat types. The initial split in the CART separated the two unstructured habitats
429 (macroalgae and sand/rubble beds) from the two structured habitats (coral reefs and rocky
430 reefs), with the latter having higher species richness. The highest species richness also
431 occurred in high complexity replicates within these structured habitats. These results are
432 consistent with prior studies showing greater species richness in structured habitats in
433 tropical (Bradley et al., 2017; Gratwicke & Speight, 2005) sub-tropical (Gilby et al., 2016) and
434 temperate inshore regions (García-Charton & Pérez-Ruzafa, 2001). The abundance of all
435 trophic groups increased with complexity, especially for piscivores, for which complexity was
436 by far the most influential predictor in the BRTs. This result aligns with prior studies
437 emphasizing the importance of high rugosity habitats for large-bodied piscivores fishes
438 (Connell & Kingsford, 1998; Ferrari et al., 2018; Kerry & Bellwood, 2012). Unsurprisingly, there
439 was an effect of visibility on species richness, presumably because in low visibility replicates,
440 the detectability of cryptic species would be lower (Donaldson et al., 2020), however, even
441 within low visibility replicates, differences between regions were detected in the CART. There
442 was a lesser effect of visibility on the abundance of fish groups; visibility was not an important
443 BRT model predictor for the majority of trophic groups and therefore did not confound our
444 conclusions regarding the importance of habitat predictors. The explicit inclusion of a visibility
445 ranking enabled its effects to be disentangled from other factors of interest.

446

447 Reef habitats supported the greatest species richness and abundance of fishes, and both
448 rocky and coral reefs contributed to the provision of structurally complex habitats. High
449 complexity coral reef habitats had a variety of coral morphologies as well as large tabulate
450 corals and overhangs, whereas on rocky reefs high complexity habitats contained boulders of
451 a variety of sizes, with cracks and crevices providing additional microhabitats. The significance
452 of coral reefs as fish habitat in tropical systems is well documented (e.g. Coker et al., 2014;
453 Friedlander et al., 2003; Wilson, Fisher, et al., 2008), and there has been a similar focus on the
454 importance of rocky reefs in temperate regions, where they form important inshore and
455 coastal habitats (Jones, 1988; Kingsford, 1998; Trebilco et al., 2015). There is, however, a
456 notable absence of literature on rocky reefs in the tropical Indo-Pacific, and indeed little
457 known about their prevalence within these inshore habitats.

458

459 In temperate regions, rocky reefs (often associated with macroalgae) form the foundational
460 architecture over large areas, creating structurally complex habitats that can support diverse
461 and abundant fish assemblages (Connell & Jones, 1991; García-Charton & Pérez-Ruzafa, 2001;
462 Jones, 1988; Kingsford & Carlson, 2010). In our study area, rocky and coral reefs were
463 intermixed patchily at small spatial scales, and many fish species utilised both reef habitats.
464 The overlap of species occurrences within coral and rocky reefs was substantial (60%), despite
465 the fact that coral cover was usually much lower on rocky reefs. Furthermore, the overlap in
466 species composition from both the CAP and MDS analysis suggest that, at least for some
467 species, these two habitats are equivalent in habitat provision. It is notable that two of the
468 three rocky reef sites that were most similar to coral reefs occurred on islands which had both
469 reef habitats. This suggests that proximity to coral reefs may influence the composition of fish
470 assemblages on rocky reefs, however more detailed spatial resolution on habitat distributions
471 would be required to explore this hypothesis. An important follow on from this study would

472 be to examine the connectivity between rocky and coral reef habitats, using detailed habitat
473 mapping.

474

475 The extent to which species utilised coral and rocky reef habitats may depend on their habitat
476 and dietary requirements. For example, *C. rainfordi* (Chaetodontidae) occurred in both
477 habitats, but was more abundant on coral reefs, whereas *Chelmon rostratus*
478 (Chaetodontidae) utilised both habitats in equal abundance. This difference is likely related
479 to the differing habitat specialisation and dietary requirements of the two species. *Chaetodon*
480 *rainfordi* is a habitat specialist and obligate corallivore that is strongly reliant on the cover of
481 hard coral (Cole et al., 2008; Pratchett & Berumen, 2008). In contrast, *C. rostratus* is a habitat
482 generalist, whose diet is primarily derived from benthic organisms (Pratchett, 2005). Both of
483 the commonly encountered lutjanid species: *Lutjanus carponotatus*, and *L. lemniscatus*, were
484 recorded in all four habitats, but their abundance patterns varied. *Lutjanus carponotatus*
485 was equally abundant in coral and rocky reefs, with lower abundances in macroalgae and
486 sand/rubble beds, whereas *L. lemniscatus* was much more abundant on rocky reefs compared
487 to all other habitats. Both species are piscivores characteristic of inshore regions; *L.*
488 *carponotatus* is generally considered a coral-reef associated species (Kingsford, 2009; Wen et
489 al., 2013), although no prior studies have considered their associations with rocky reefs. There
490 are few data on habitat associations for *L. lemniscatus*, although a study by Newman and
491 Williams (1996) noted their prevalence on rocky headlands. Our study excluded small fishes
492 such as damselfishes (Pomacentridae), which include many species with a strong reliance on
493 live coral, and would likely be more specific to coral reef habitats (Coker et al., 2009; Pratchett
494 et al., 2012). Nevertheless, the equivalence of rocky and coral reefs for many species is
495 notable, as it suggests that for these species the structure itself is critical as a habitat refuge,
496 regardless of the nature of the substrate (i.e. coral or rock).

497

498 The composition of the benthic substratum was not a consistent driver of abundance or
499 species richness. The cover of live coral had a strong influence on the abundance of
500 corallivores and (to a lesser extent) carnivores, but was of minimal importance to other
501 trophic groups from the BRTs. Consistent with previous studies (Cole et al., 2008; Pratchett &
502 Berumen, 2008), corallivores had very strong associations with coral cover (>60% relative
503 influence from BRTs), however they constituted only a small proportion of overall fish
504 abundance and species richness. Coral cover was also an important predictor for carnivores,
505 which included abundant species such as *Epinephelus quoyanus* and *Thalassoma lunare*,
506 which are typically reef-associated carnivores (Connell, 1998; Connell & Kingsford, 1998; Wen
507 et al., 2013), although it is notable that both species were also recorded in other habitats. The
508 cover of algae was an important predictor for herbivores, which favoured shallow algal-
509 dominated sites, which would provide opportunities for algal browsing/grazing (Green &
510 Bellwood, 2009).

511

512 We found a number of species unique to each of the unstructured habitats (macroalgae and
513 sand/rubble beds), indicating their unique role in contributing to the local diversity of fish
514 fauna. It is possible that with further sampling in macroalgae and sand/rubble beds, we may
515 have uncovered additional unique species, and such targeted surveys in unstructured habitats
516 in the region would be an interesting follow up study. There were ten species unique to
517 macroalgae beds, including *P. spilurus* (Mullidae), *S.forsteni* (Scaridae), and *L. obsoletus*
518 (Lethrinidae), as well as a number of additional taxa (e.g. tuskfishes; *Choerodon* spp.) that
519 were markedly more abundant in macroalgae beds compared to other habitats. These results
520 concur with a recent review (Fulton et al., 2020) highlighting the unique role of macroalgae
521 habitats in supporting distinct fish assemblages; indeed we found overlap between our study

522 and this review in the taxa considered “macroalgal residents” (e.g. *Choerodon*, and *Lethrinus*
523 spp.). Sand and rubble beds had the lowest species richness and abundance of all habitats, as
524 would be expected due to the lack of habitat features and low complexity (Lefcheck et al.,
525 2019). Sand /rubble beds did support unique species, including transient pelagic taxa such as
526 mackerels (*Scomberomorus* spp.) and great barracuda (*S. barracuda*). Since sand/rubble beds
527 are lacking in structural features, it is likely that many fishes detected were moving through
528 this habitat, possibly attracted from open pelagic areas by the bait. As such, the importance
529 of this habitat to these species is less evident. However, it is notable that sand/ rubble beds
530 also supported unique species of threadfin breams (*Pentapodus nagasakiensis* and *P.*
531 *paradiseus*), which are known forage over sandy habitats, and so may have stronger habitat
532 associations within sand/rubble areas (Quimpo et al., 2019).

533

534

535 Baited Remote Underwater Video Stations are an effective technique for surveying a range of
536 fishes, however, as with any survey approach, there are inherent biases and limitations to the
537 BRUVS technique. The use of bait may disproportionately attract predatory species compared
538 to unbaited techniques (i.e. RUVS), and the use of underwater video of any kind precludes
539 accurate assessment of very small fishes (Cappo et al., 2004; Harvey et al., 2007). These
540 limitations did not bias our interpretation of fish/habitat relationships, however, since any
541 bias would be consistent amongst habitats, and small fishes were excluded from video
542 analysis. Furthermore, since many analyses were considered at the site level, and sites were
543 separated by at least 2km during each sampling event, there was little risk of species moving
544 among sites and confounding interpretation of fish/habitat relationships. A study by Harvey
545 et al. (2007) demonstrated that the use of bait in underwater video surveys allows for better
546 discrimination of fish assemblages amongst habitats compared to unbaited video. Our results

547 are consistent with this, since we were able to detect distinct fish assemblages in the habitats
548 we surveyed. The dominant habitats in the study area were structured (either coral or rocky
549 reefs), and these habitats therefore had greater sampling effort. The difference in sample size
550 amongst habitats did not confound our interpretations of the factors influencing species
551 richness, since the CART model used replicate level species richness, and survey effort was
552 consistent for each replicate. Furthermore, both the CAP and bootstrapped MDS separated
553 fish assemblages into the same three habitat groups: reef (coral and rocky), macroalgae bed,
554 and sand/rubble bed, which indicates the CAP results were robust despite variation in sample
555 size.

556

557 An interesting outcome from the CART analysis was the difference amongst habitats in how
558 species richness varied according to management zones (i.e. whether or not fishing was
559 permitted). Zoning only had a strong influence on species richness in unstructured habitats
560 (macroalgae and sand/rubble beds), where richness was greater in marine reserves compared
561 to fished zones. In contrast, zoning was unimportant in influencing species richness in
562 structured habitats (coral and rocky reefs), although the opposite trend was observed
563 (richness greater in fished zones). Zoning also had minimal effect on the abundance of most
564 trophic groups, as observed in the BRTs. These results largely concur with a previously study
565 in the region (Hall et al., 2021) , which found a significant reduction in abundances of primary
566 target species in fished versus marine reserve zones, but no effect of zone on non-target fish
567 abundance, or on overall species richness. The majority of species targeted by fishers in the
568 region are either piscivores or carnivores (Hall & Kingsford, 2016), however these trophic
569 groups also contained a large number of non-target species, and the remaining trophic groups
570 were comprised of non-target species. As such, it is unsurprising that zoning had minimal
571 influence on trophic group abundance. The lack of a fishing effect in structured habitats,

572 however, is surprising, since anecdotally most fishers tend to target structure when selecting
573 fishing sites.

574

575 Our results are consistent with the emerging recognition of the importance of the seascape
576 mosaic in tropical inshore ecosystems (Sambrook et al., 2019; Sheaves, 2009; Sievers et al.,
577 2020). Of particular note is the role of structural complexity, and the potential for rocky reefs
578 to provide significant habitat architecture within the seascape mosaic, rivaling the diversity
579 and function of nearby coral-dominated reefs. Since rock-based substrates would be less
580 vulnerable to impacts such as bleaching, storms, or coastal run-off, these habitats may form
581 important refuges for a number of fish species in impacted regions. Future research
582 examining the spatial configuration and connectivity of habitats within this mosaic would aid
583 greatly in understanding the relative importance of each habitat type to species assemblages
584 in the region. Consideration of the individual and collective contribution of habitats to
585 ecosystem function is critical for conservation planning, especially given the range of threats
586 that inshore habitats now face.

587

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596

597 CONTRIBUTIONS

598 This manuscript describes original research and is not submitted elsewhere. Both authors
599 have agreed to be listed, and approve the submitted version of the manuscript. Both authors
600 contributed to collection of provision of funding, the sampling design, collection of data, and
601 writing of the manuscript, with A.E.H taking a lead role and M.J.K in a supporting role. A.E.H.
602 conceived of the project and performed the data analysis. We declare no conflict of interest.

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Table 1: Habitat and biophysical variables measured during video analysis and their overall range, mean, and definitions. Values for range and mean are based on total pooled replicates. FOV = field of view, SEM = standard error of the mean.

Variable	Type	Estimation method	Range	Mean \pm SEM	Definition
Depth (m)	Continuous	Measured in field	2-17	6.25 \pm 0.25	Water depth from surface to seafloor at location of BRUVS deployment
Visibility (m)	Categorical	Estimated (in metres) during video analysis, based on the visible FOV. Categorised into low, medium, and high after video analysis.	1.5-5m	2.43m \pm 0.07	Defined as the horizontal distance that could be seen in the FOV of each video; estimated using the bait arm as a reference. Low: 2m, Medium: 2-4m, High >4m
Topographic complexity score	Categorical	Categorised during video analysis, based on the habitat structure in the FOV. Score derived to assign complexity into categories.	NA	NA	<u>Low</u> : essentially a flat surface, with little or no structural features <u>Medium</u> : moderate complexity structural features such as coral and/or bedrock present <u>High</u> : high relief habitats, with a range of structural features such as coral and/or bedrock, forming diverse habitat features
Habitat type	Categorical	Categorised during video analysis, and based on the underlying habitat structure in the FOV	NA	NA	<u>Coral reef</u> : reefs with coral as the underlying substrate- has a range of % live coral and other benthic substrates <u>Rocky reef</u> : reefs with bedrock (granite boulder) as the underlying substrate- often with scattered coral (mostly soft coral), sponges, and hydroids <u>Macroalgae beds</u> : dominated by macroalgae (mostly <i>Sargassum</i> spp.) growing on sandy substrates <u>Sand/ rubble bed</u> : underlying substrate of sand, with >90% bare (sand or rubble) cover
% coral	Continuous	Estimated during video analysis, by dividing the FOV into quadrants, and visually estimating the % cover of each substrate component	0-80	23.18 \pm 1.91	Combined percentage of live hard and live soft corals
% algae			0-100	24.91 \pm 2.41	Percentage cover of all visible algae, including turf, coralline, and macroalgae
% bare			0-100	35.11 \pm 2.63	Percentage cover of bare sand or rubble, with no substrate biota
% bedrock			0-90	15.88 \pm 2.14	Percentage cover of bedrock, with no substrate biota

Table 2: Top three ranked predictors from Boosted Regression Tress, showing the percentage relative importance, and relationship between each predictor variable and fish trophic groups.

Trophic group	Top ranked predictor		2 nd ranked predictor		3 rd ranked predictor	
	Variable	% relative importance (direction of relationship)	Variable	% relative importance (direction of relationship)	Variable	% relative importance (direction of relationship)
Piscivores	Complexity	43.7 (+)	% coral	11.4(+)	Depth	9.3 (+)
Carnivores	% coral	33.5 (+)	Depth	17.4 (↑↓)	Algae	10.6 (-)
Benthic foragers	% algae	16.2 (-)	Visibility	14.5 (+)	Depth	13.9 (↑↓)
Corallivores	% coral	61.45 (+)	Complexity	7.7 (+)	Algae	5.1 (-)
Herbivores	Depth	32.6 (-)	Algae	32.2 (+)	Bare	6.3 (-)
Mobile planktivores	Complexity	24.9 (+)	Bedrock	16.4 (+)	Location	13.2 (Dunk)

Direction of relationships shown in parentheses: (+) = positive relationship, (-) = negative relationship, (↑↓) = varying response: positive, then negative relationship of abundance with predictor. For categorical variables, the category with the maximum abundance value is indicated

Figure captions

Figure 1: Map showing the location of BRUVS survey sites in A) the Dunk Island and B) the Hinchinbrook Island region. Sites are coded by habitat type and indicate the central position of an array of 6 replicate BRUVS which were placed per site. Colours indicate the Great Barrier Reef Marine Park management zones.

Figure 2: Principle Component Analysis (PCA) of the benthic composition, depth, and complexity of habitats amongst sites. Sites are coloured by habitat type, with different symbols representing complexity categories within each habitat type. Vectors show the corresponding strength and direction of variables from Pearson correlations

Figure 3: Abundance by trophic group and family, numbers above bars indicate total species richness within each trophic group or family

Figure 4: (a) Classification and Regression Tree (CART), showing the key modelled drivers of species richness. At each terminal branch, numbers shown in boxes indicate mean species richness estimates, and percentages below indicate the percentage of replicates grouped within each branch. (b) Boxplot (Tukey) showing species richness amongst the four habitat types in the Dunk and Hinchinbrook Island region; dots are individual replicates.

Figure 5: Results from Boosted Regression Trees (BRTs) showing the percent relative importance of each predictor variable in the BRT model, amongst the six trophic groups. Predictor variables along the x axis are ordered by relative importance for each trophic group.

Figure 6: Abundance (mean MaxN \pm SEM) of each trophic group according to low, moderate, and high complexity categories.

Figure 7: Canonical Analysis of Principle Coordinates (CAP) of fish assemblages amongst sites according to habitat type. Vectors show the influence of species on differences amongst habitats; only species with Pearson correlations of >0.4 are shown. Species images show species that only occurred in the corresponding habitat

Supporting Information

Figure S1: Photographs showing examples of the four habitat types according to complexity categories. "Not present" indicates that a habitat type was not observed within a given complexity category.

Figure S2: Metric Multidimensional Scaling (mMDS) plot of fish assemblages showing bootstrapped averages ($n=50$) according to habitat type. Coloured symbols indicate bootstrapped averages, and black symbols show the overall average per habitat type. Coloured ellipses represent the regions encompassing 95% of bootstrapped averages for each habitat type such that non-overlapping ellipses indicate distinct separation of habitats.

Figure 1

- Survey sites**
- ▼ Coral reef
 - ▲ Rocky reef
 - Sand/rubble bed
 - Macroalgae bed
- Zoning in map extent**
- General Use Zone
 - Conservation Park Zone
 - No-Take Marine Reserve
 - Special Management Area
 - Great Barrier Reef Marine Park boundary
 - Indicative Reef boundary
 - Mainland and Islands

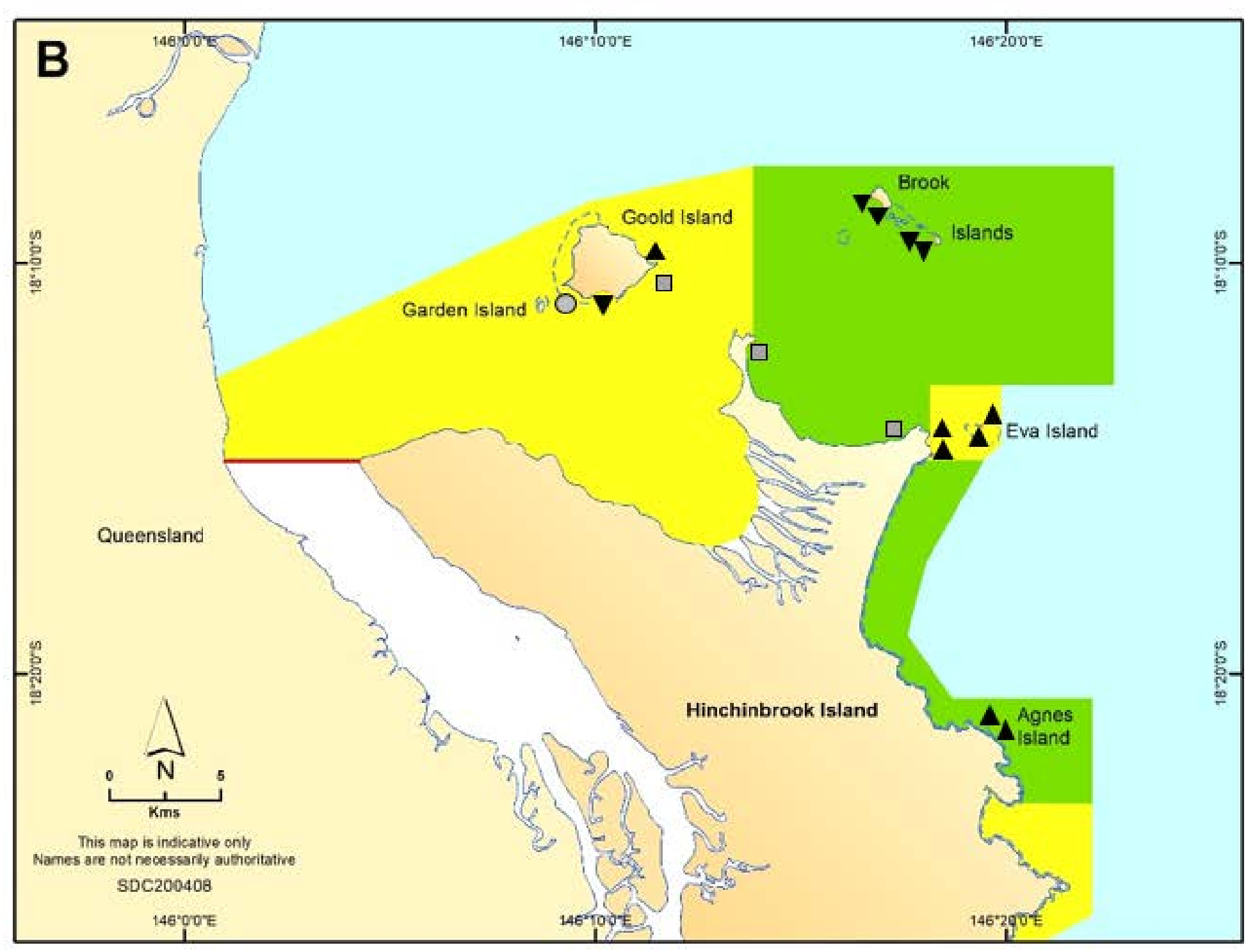
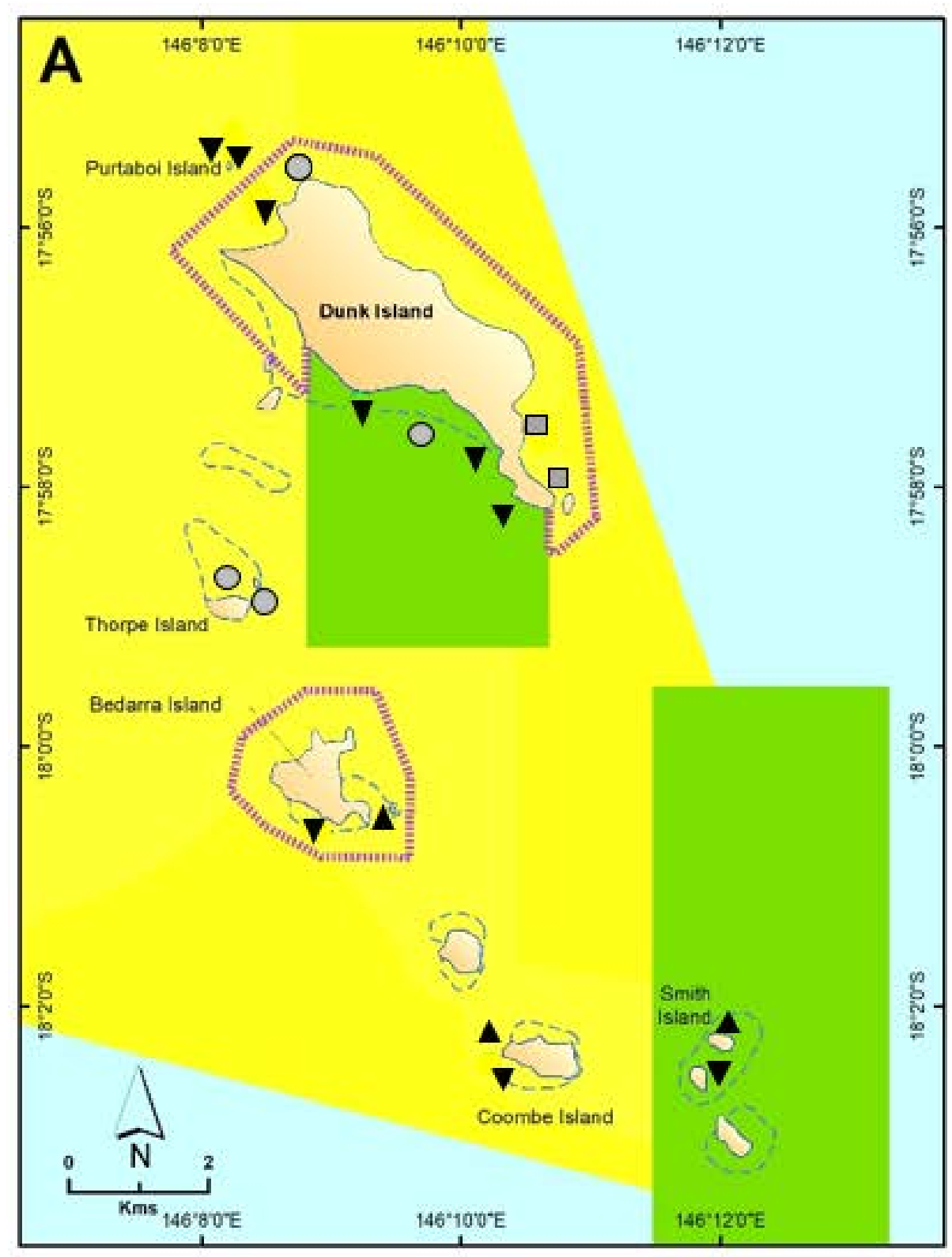


Figure 2

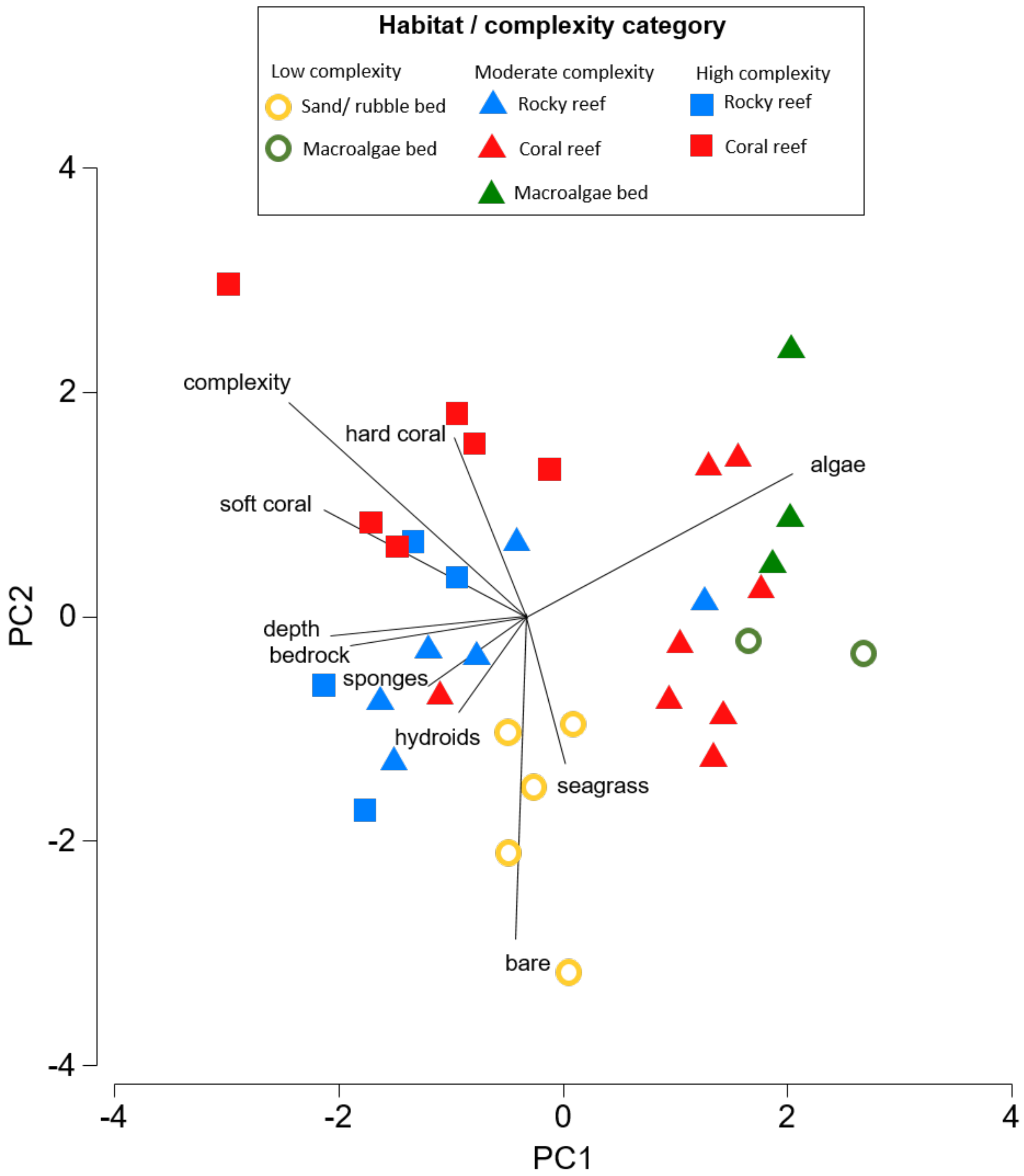
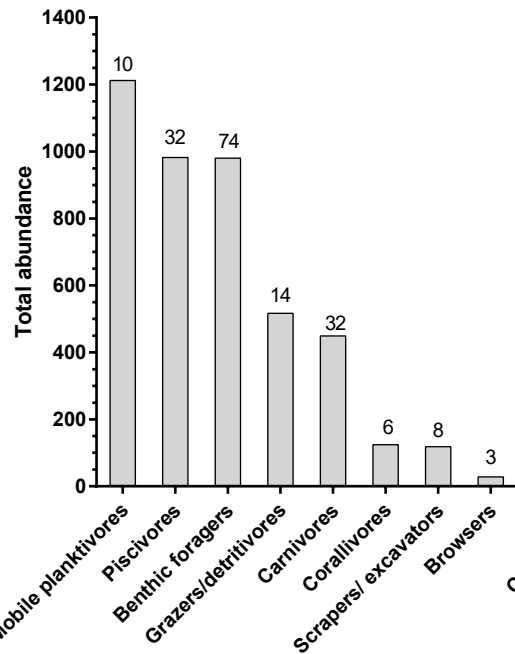
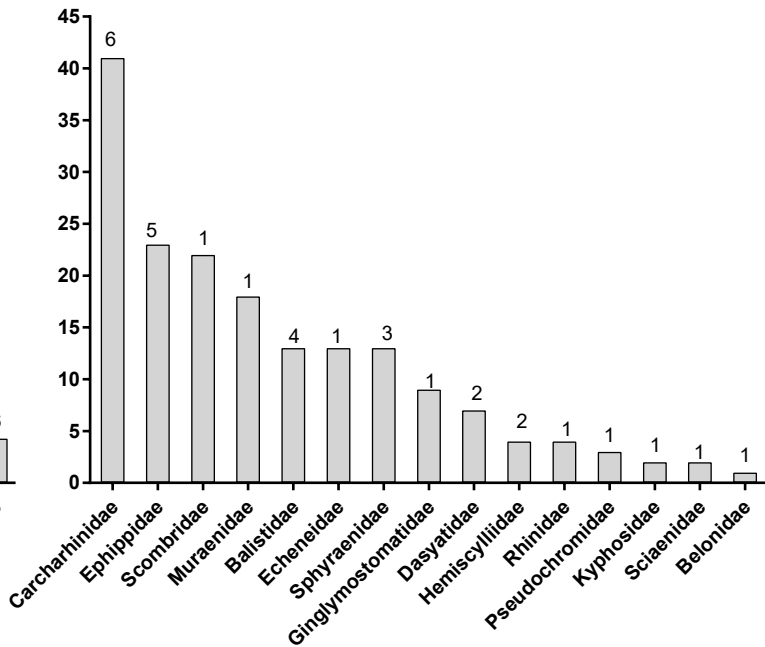
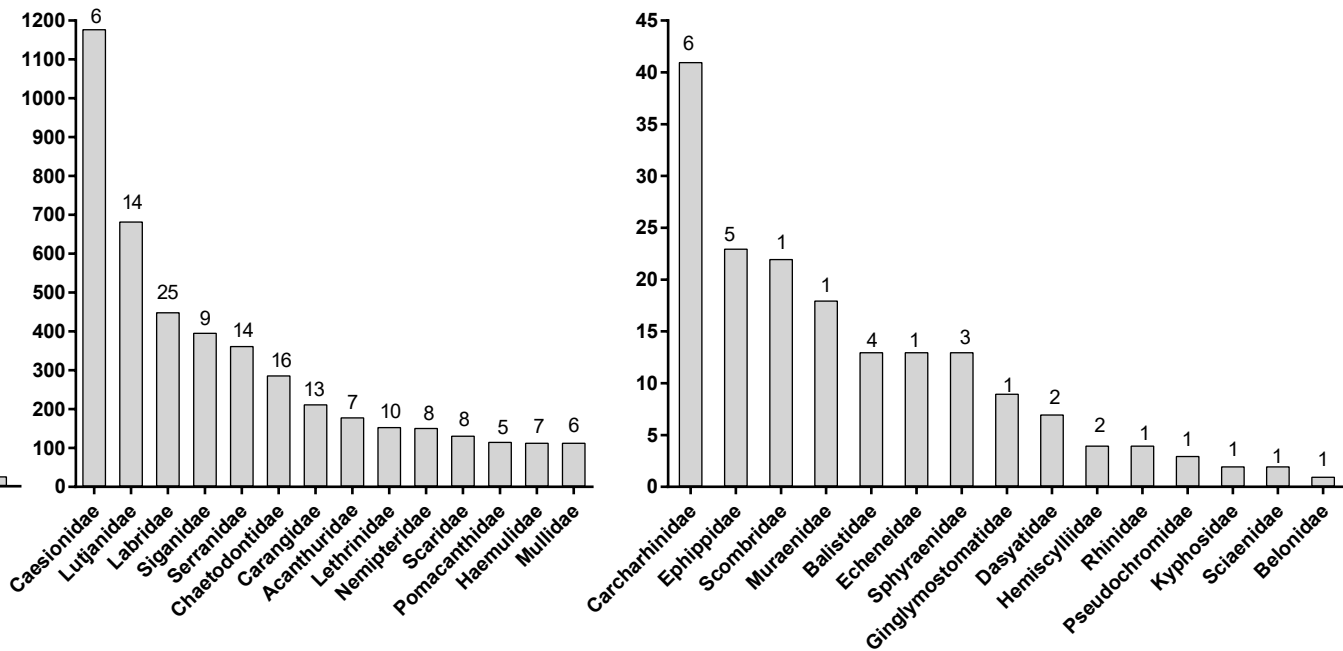


Figure 3

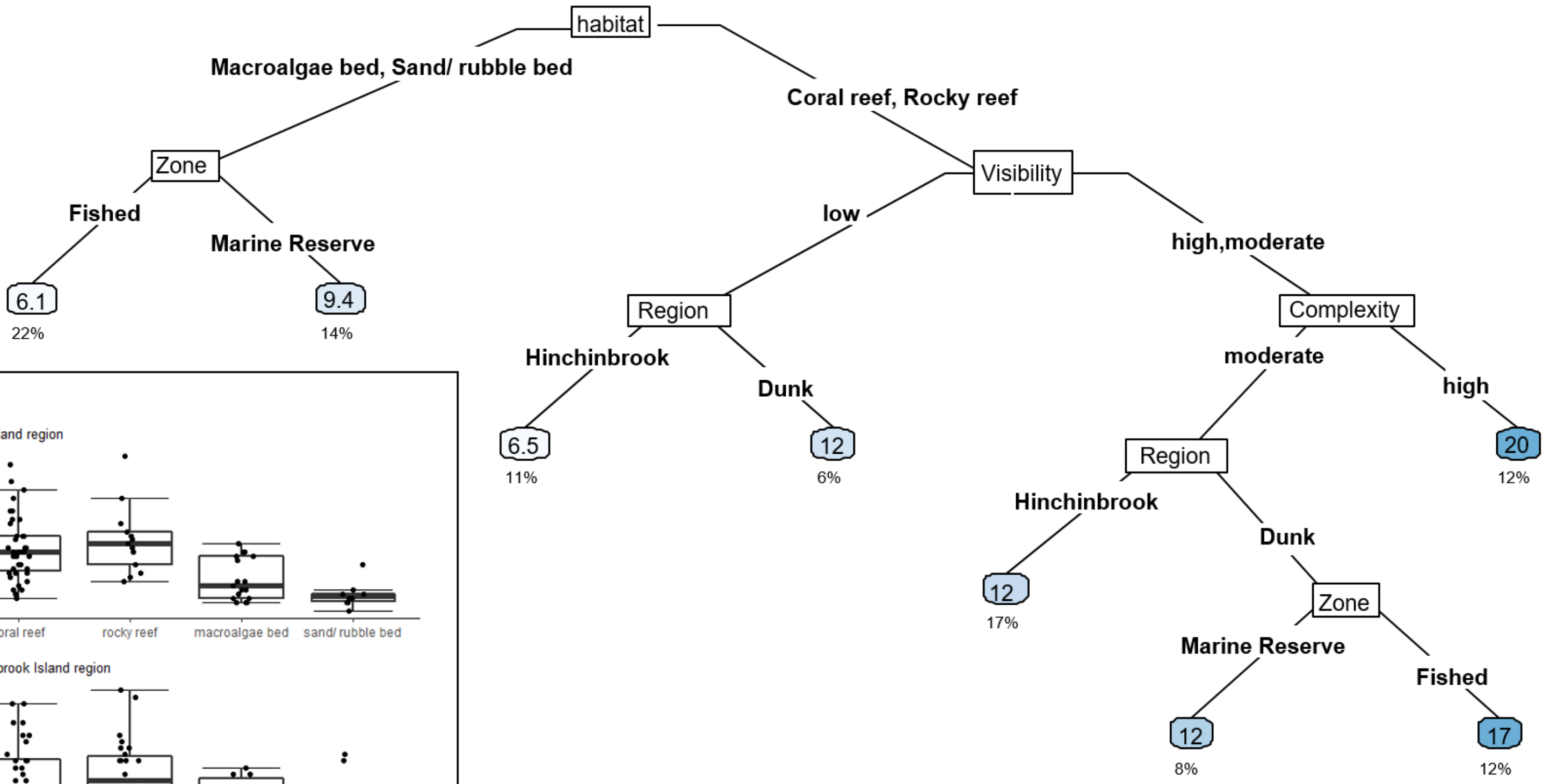
Abundance by trophic group



Abundance by family



(a)



(b)

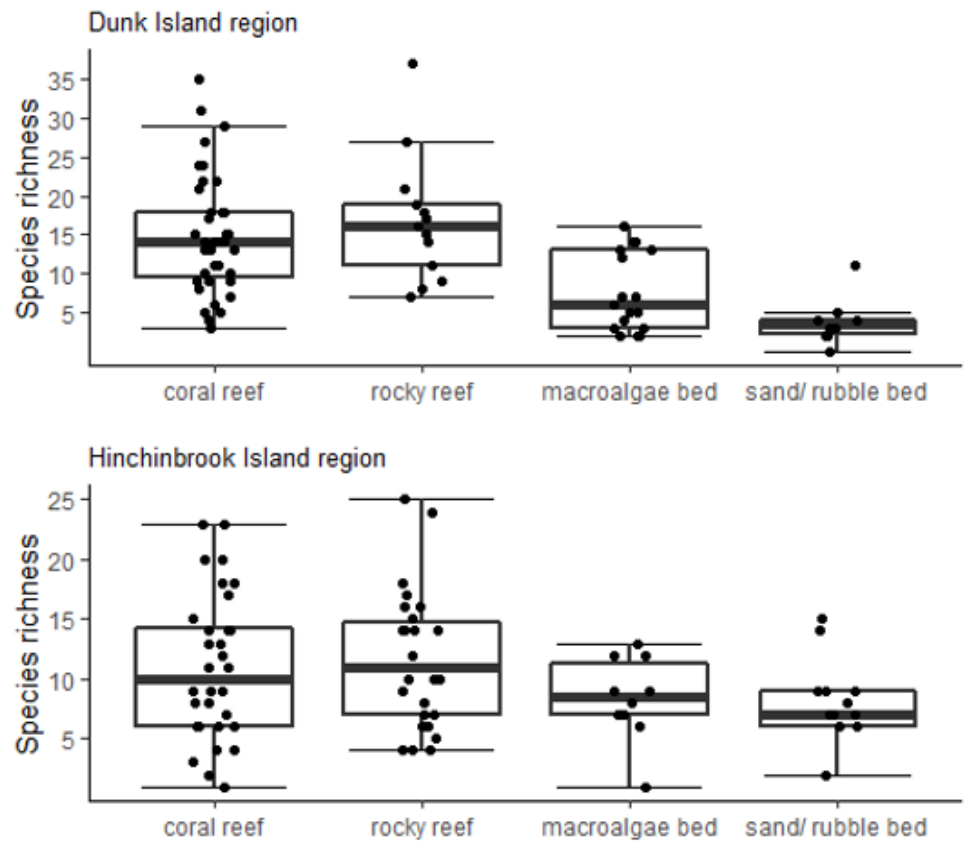


Figure 5

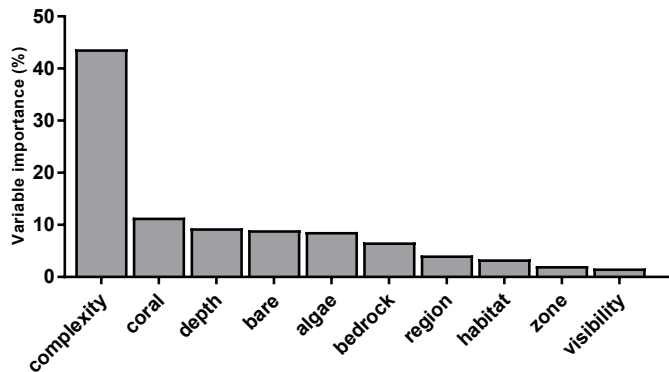
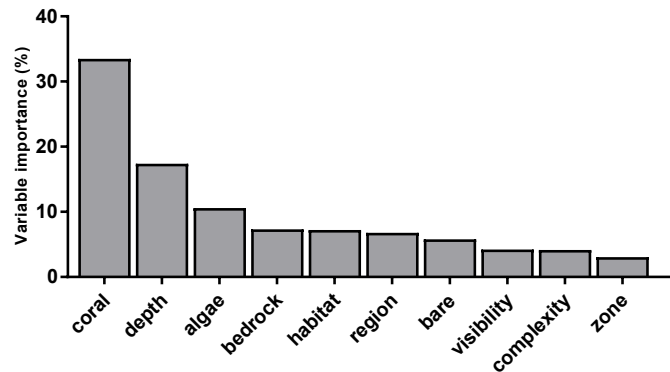
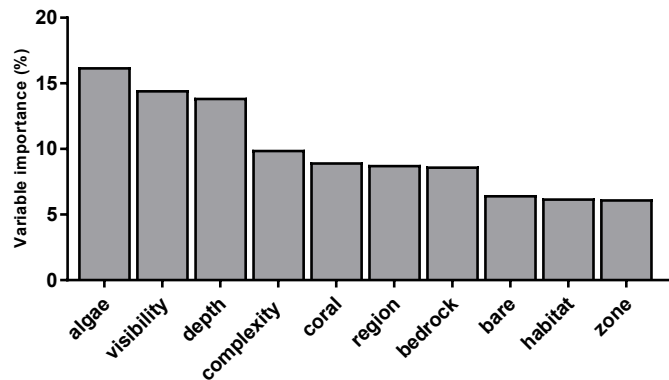
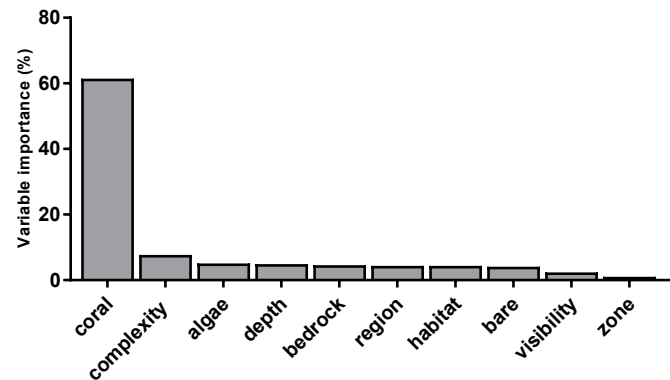
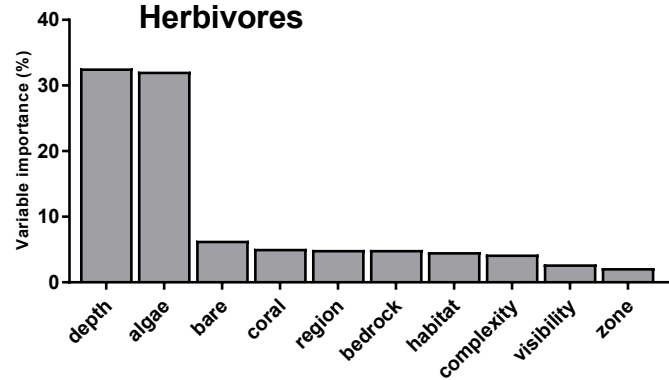
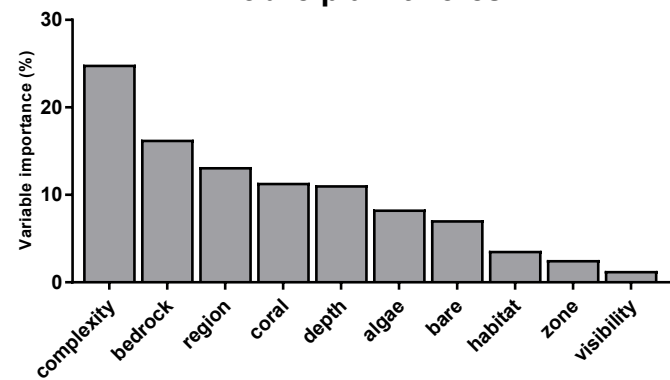
Piscivores**Carnivores****Benthic foragers****Corallivores****Herbivores****Mobile planktivores**

Figure 6

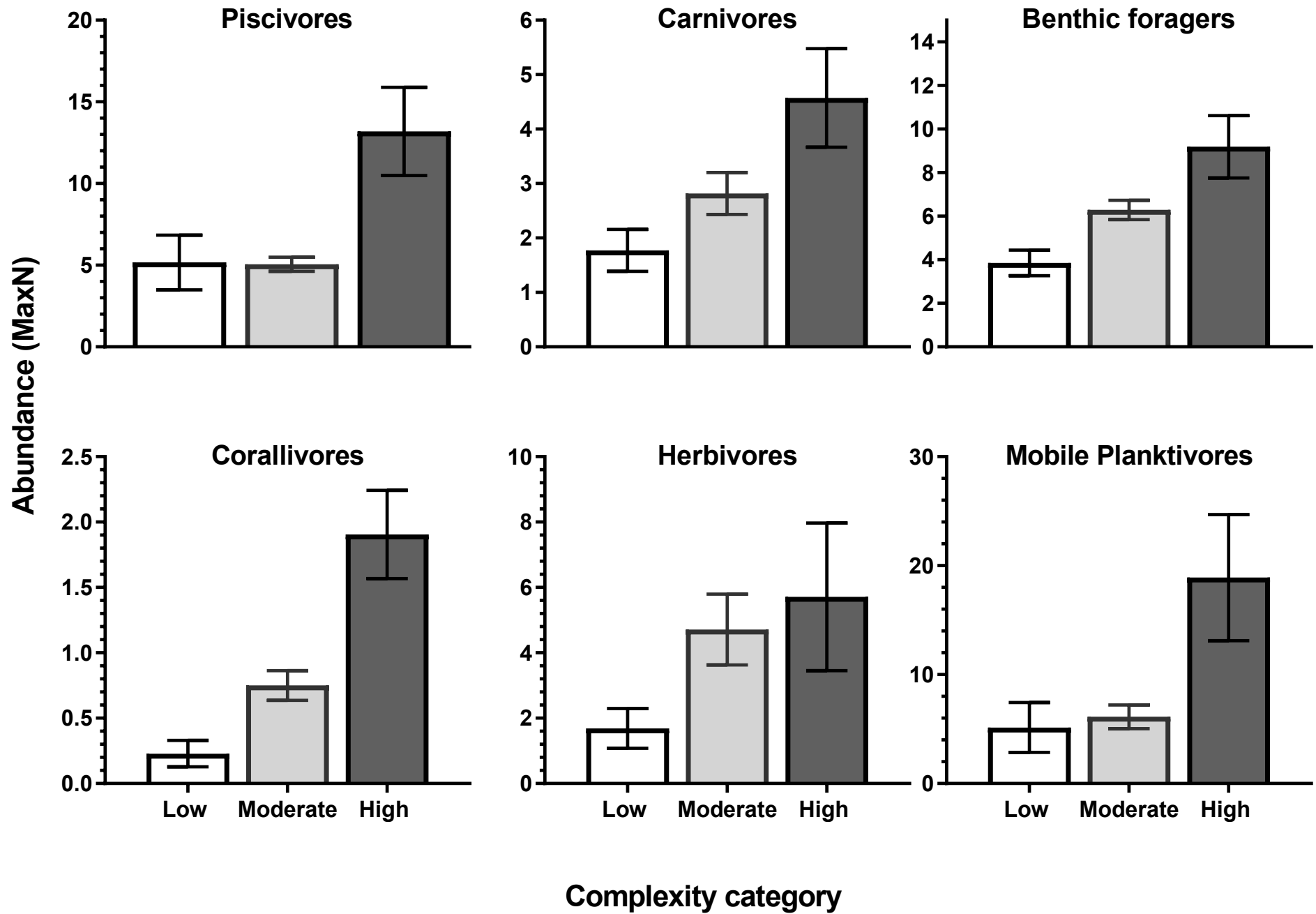


Figure 7

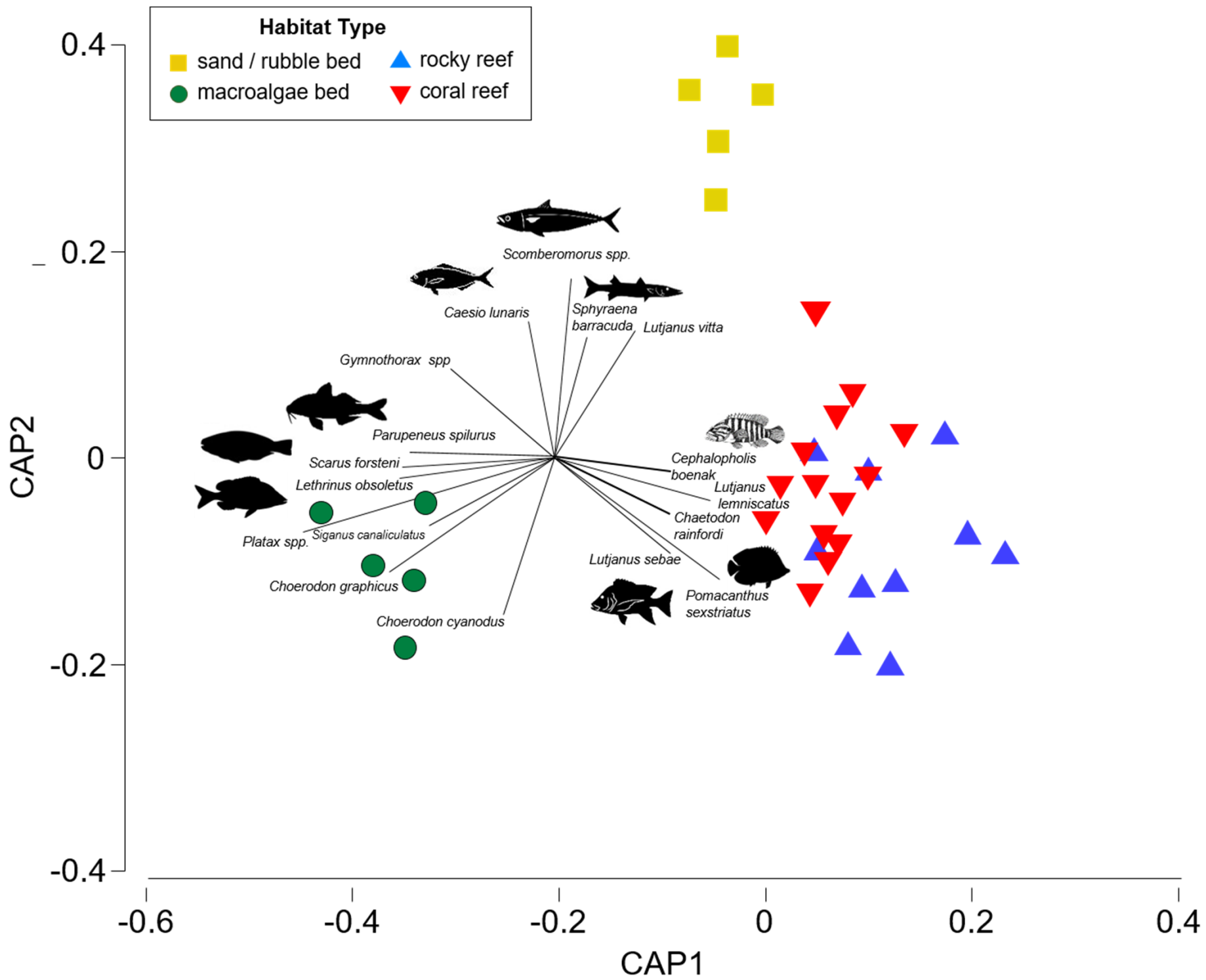


Table S1: List of 179 taxa recorded during the study, with trophic group, occurrence by habitat type, and overall total MaxN values. R = rocky reef, C = coral reef, S = sand/rubble bed, M = macroalgae bed

Family	Genus	Species	Trophic group	Occurrence by habitat type				Total Max N
				R	C	S	M	
Acanthuridae	<i>Acanthurus</i>	<i>blochii</i>	Herbivore (grazer / detritivore)	X	X	X	X	103
Acanthuridae	<i>Acanthurus</i>	<i>dussumieri</i>	Herbivore (grazer / detritivore)	X				1
Acanthuridae	<i>Acanthurus</i>	<i>grammoptilus</i>	Herbivore (grazer / detritivore)	X			X	4
Acanthuridae	<i>Acanthurus</i>	<i>spp.</i>	Herbivore (grazer / detritivore)	X	X		X	29
Acanthuridae	<i>Ctenochaetus</i>	<i>spp.</i>	Herbivore (grazer / detritivore)	X	X			5
Acanthuridae	<i>Naso</i>	<i>spp.</i>	Herbivore (browser)	X	X	X	X	25
Acanthuridae	<i>Naso</i>	<i>unicornis</i>	Herbivore (browser)	X	X			3
Balistidae	<i>Abalistes</i>	<i>spp.</i>	Benthic forager	X	X	X	X	8
Balistidae	<i>Pseudobalistes</i>	<i>flavimarginatus</i>	Benthic forager	X			X	2
Balistidae	<i>Pseudobalistes</i>	<i>spp.</i>	Benthic forager			X		1
Balistidae	<i>Sufflamen</i>	<i>spp.</i>	Benthic forager		X			1
Belonidae	<i>Tylosurus</i>	<i>spp.</i>	Piscivore			X		1
Caesionidae	<i>Caesio</i>	<i>caeruleaurea</i>	Mobile planktivore	X	X			96
Caesionidae	<i>Caesio</i>	<i>cuning</i>	Mobile planktivore	X	X	X	X	819
Caesionidae	<i>Caesio</i>	<i>lunaris</i>	Mobile planktivore			X		40
Caesionidae	<i>Caesio</i>	<i>spp.</i>	Mobile planktivore	X	X	X	X	113
Caesionidae	<i>Pterocaesio</i>	<i>marri</i>	Mobile planktivore	X				1
Caesionidae	<i>Pterocaesio</i>	<i>spp.</i>	Mobile planktivore				X	45
Carangidae	<i>Atule</i>	<i>mate</i>	Mobile planktivore	X	X	X		57
Carangidae	<i>Carangoides</i>	<i>ferdau</i>	Benthic forager	X	X		X	8
Carangidae	<i>Carangoides</i>	<i>fulvoguttatus</i>	Piscivore				X	1
Carangidae	<i>Carangoides</i>	<i>gymnostethus</i>	Carnivore		X	X		42
Carangidae	<i>Carangoides</i>	<i>oblongus</i>	Carnivore		X			1
Carangidae	<i>Carangoides</i>	<i>plagiotaenia</i>	Carnivore	X				1
Carangidae	<i>Carangoides</i>	<i>spp.</i>	Carnivore	X	X	X	X	6
Carangidae	<i>Caranx</i>	<i>ignobilis</i>	Piscivore			X	X	4
Carangidae	<i>Caranx</i>	<i>lugubris</i>	Piscivore		X		X	2
Carangidae	<i>Caranx</i>	<i>melampygus</i>	Piscivore	X	X	X	X	47
Carangidae	<i>Caranx</i>	<i>papuensis</i>	Piscivore			X	X	14
Carangidae	<i>Caranx</i>	<i>spp.</i>	Piscivore	X	X			4
Carangidae	<i>Pseudocaranx</i>	<i>dentex</i>	Benthic forager			X	X	3
Carcharhinidae	<i>Carcharhinus</i>	<i>amblyrhynchos</i>	Piscivore	X			X	2
Carcharhinidae	<i>Carcharhinus</i>	<i>leucas</i>	Piscivore		X			1
Carcharhinidae	<i>Carcharhinus</i>	<i>limbatus</i>	Piscivore		X			1
Carcharhinidae	<i>Carcharhinus</i>	<i>melanopterus</i>	Piscivore	X	X	X	X	27




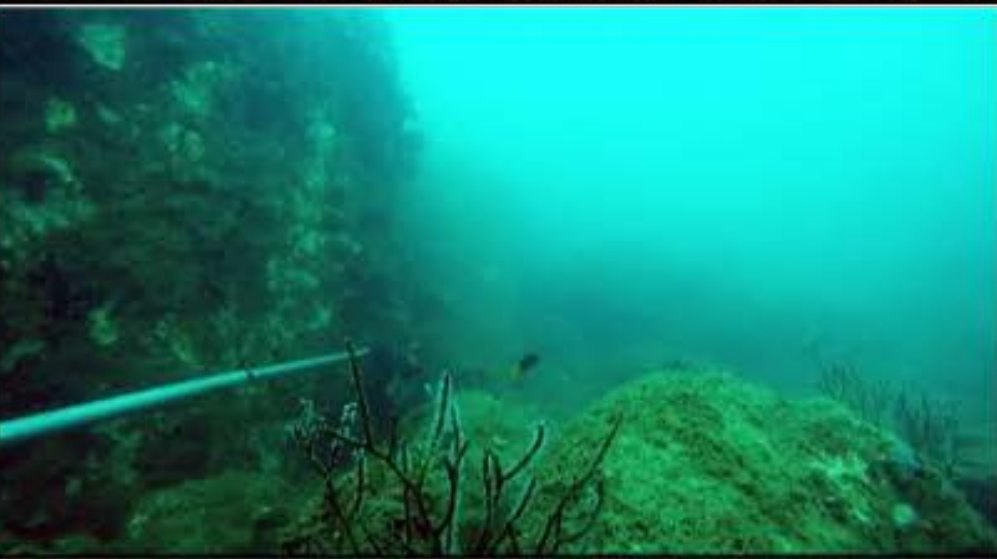



Family	Genus	Species	Trophic group	Occurrence by habitat type				Total Max N
				R	C	S	M	
Carcharhinidae	<i>Carcharhinus</i>	<i>spp.</i>	Piscivore		X	X	X	6
Carcharhinidae	<i>Triaenodon</i>	<i>obesus</i>	Piscivore		X			4
Chaetodontidae	<i>Chaetodon</i>	<i>aureofasciatus</i>	Corallivore	X	X	X	X	87
Chaetodontidae	<i>Chaetodon</i>	<i>auriga</i>	Benthic forager		X		X	6
Chaetodontidae	<i>Chaetodon</i>	<i>baronessa</i>	Corallivore		X			2
Chaetodontidae	<i>Chaetodon</i>	<i>lineolatus</i>	Benthic forager	X	X	X	X	23
Chaetodontidae	<i>Chaetodon</i>	<i>lunula</i>	Corallivore		X			2
Chaetodontidae	<i>Chaetodon</i>	<i>ocellicaudus</i>	Corallivore		X			2
Chaetodontidae	<i>Chaetodon</i>	<i>rainfordi</i>	Corallivore	X	X			21
Chaetodontidae	<i>Chaetodon</i>	<i>spp.</i>	Corallivore	X	X	X		12
Chaetodontidae	<i>Chaetodon</i>	<i>vagabundus</i>	Benthic forager	X	X	X	X	22
Chaetodontidae	<i>Chelmon</i>	<i>muelleri</i>	Benthic forager	X	X			5
Chaetodontidae	<i>Chelmon</i>	<i>rostratus</i>	Benthic forager	X	X		X	61
Chaetodontidae	<i>Chelmon</i>	<i>spp.</i>	Benthic forager	X				1
Chaetodontidae	<i>Coradion</i>	<i>altivelis</i>	Benthic forager	X				1
Chaetodontidae	<i>Coradion</i>	<i>spp.</i>	Benthic forager		X			1
Chaetodontidae	<i>Heniochus</i>	<i>acuminatus</i>	Mobile planktivore	X	X	X		26
Chaetodontidae	<i>Heniochus</i>	<i>spp.</i>	Mobile planktivore		X			2
Dasyatidae	<i>Taeniura</i>	<i>lymma</i>	Benthic forager			X	X	2
Dasyatidae	<i>Urogymnus</i>	<i>granulatus</i>	Benthic forager			X		2
Echeneidae	<i>Echeneis</i>	<i>naucrates</i>	Mobile planktivore		X	X	X	12
Ephippidae	<i>Platax</i>	<i>batavianus</i>	Benthic forager		X	X	X	3
Ephippidae	<i>Platax</i>	<i>orbicularis</i>	Benthic forager	X	X			8
Ephippidae	<i>Platax</i>	<i>pinnatus</i>	Benthic forager		X		X	4
Ephippidae	<i>Platax</i>	<i>spp.</i>	Benthic forager		X		X	5
Ephippidae	<i>Platax</i>	<i>teira</i>	Benthic forager		X			1
Ginglymostomatidae	<i>Nebrius</i>	<i>ferrugineus</i>	Benthic forager	X	X		X	9
Haemulidae	<i>Diagramma</i>	<i>pictum</i>	Carnivore	X	X	X	X	57
Haemulidae	<i>Plectorhinchus</i>	<i>albovittatus</i>	Benthic forager	X	X			11
Haemulidae	<i>Plectorhinchus</i>	<i>chaetodonoides</i>	Benthic forager		X			1
Haemulidae	<i>Plectorhinchus</i>	<i>flavomaculatus</i>	Benthic forager		X			3
Haemulidae	<i>Plectorhinchus</i>	<i>gibbosus</i>	Benthic forager	X	X	X	X	15
Haemulidae	<i>Plectorhinchus</i>	<i>picus</i>	Benthic forager	X	X		X	12
Haemulidae	<i>Plectorhinchus</i>	<i>spp.</i>	Benthic forager	X	X	X	X	10
Hemiscyllidae	<i>Chiloscyllium</i>	<i>punctatum</i>	Carnivore		X	X		3
Hemiscyllidae	<i>Chiloscyllium</i>	<i>spp.</i>	Carnivore			X		1
Kyphosidae	<i>Kyphosus</i>	<i>spp.</i>	Herbivore (browser)	X	X			2
Labridae	<i>Bodianus</i>	<i>axillaris</i>	Benthic forager		X			1
Labridae	<i>Cheilinus</i>	<i>chlorourus</i>	Benthic forager		X			1

Family	Genus	Species	Trophic group	Occurrence by habitat type				Total Max N
				R	C	S	M	
Labridae	<i>Cheilinus</i>	<i>fasciatus</i>	Benthic forager	x	x		x	7
Labridae	<i>Cheilinus</i>	<i>trilobatus</i>	Benthic forager		x			2
Labridae	<i>Cheilio</i>	<i>inermis</i>	Benthic forager				x	1
Labridae	<i>Choerodon</i>	<i>anchorago</i>	Benthic forager		x		x	16
Labridae	<i>Choerodon</i>	<i>cephalotes</i>	Benthic forager	x	x	x		5
Labridae	<i>Choerodon</i>	<i>cyanodus</i>	Benthic forager	x	x		x	30
Labridae	<i>Choerodon</i>	<i>fasciatus</i>	Benthic forager	x	x	x	x	48
Labridae	<i>Choerodon</i>	<i>graphicus</i>	Benthic forager	x	x		x	11
Labridae	<i>Choerodon</i>	<i>rubescens</i>	Benthic forager	x				1
Labridae	<i>Choerodon</i>	<i>schoenleinii</i>	Benthic forager	x	x	x	x	70
Labridae	<i>Choerodon</i>	<i>spp.</i>	Benthic forager	x	x	x	x	25
Labridae	<i>Choerodon</i>	<i>venustus</i>	Benthic forager		x	x		5
Labridae	<i>Choerodon</i>	<i>vitta</i>	Benthic forager	x	x	x	x	66
Labridae	<i>Coris</i>	<i>batuensis</i>	Benthic forager		x			1
Labridae	<i>Epibulus</i>	<i>insidiator</i>	Carnivore		x			1
Labridae	<i>Hemigymnus</i>	<i>fasciatus</i>	Benthic forager	x	x			5
Labridae	<i>Hemigymnus</i>	<i>melapterus</i>	Benthic forager	x	x	x	x	18
Labridae	<i>Novaculichthys</i>	<i>taeniourus</i>	Benthic forager		x			1
Labridae	<i>Oxycheilinus</i>	<i>spp.</i>	Carnivore	x	x	x		4
Labridae	<i>Thalassoma</i>	<i>lunare</i>	Carnivore	x	x	x	x	54
Labridae	<i>Thalassoma</i>	<i>lutescens</i>	Carnivore		x			1
Labridae	<i>Thalassoma</i>	<i>purpureum</i>	Carnivore		x			2
Labridae	<i>Thalassoma</i>	<i>spp.</i>	Carnivore	x	x		x	7
Lethrinidae	<i>Gymnocranius</i>	<i>spp.</i>	Carnivore	x		x		2
Lethrinidae	<i>Lethrinus</i>	<i>amboinensis</i>	Benthic forager	x				2
Lethrinidae	<i>Lethrinus</i>	<i>atkinsoni</i>	Carnivore		x		x	2
Lethrinidae	<i>Lethrinus</i>	<i>harak</i>	Benthic forager	x	x	x	x	33
Lethrinidae	<i>Lethrinus</i>	<i>laticaudis</i>	Piscivore	x	x	x	x	65
Lethrinidae	<i>Lethrinus</i>	<i>lentjan</i>	Carnivore	x	x			18
Lethrinidae	<i>Lethrinus</i>	<i>nebulosus</i>	Benthic forager	x		x		6
Lethrinidae	<i>Lethrinus</i>	<i>obsoletus</i>	Benthic forager				x	6
Lethrinidae	<i>Lethrinus</i>	<i>ornatus</i>	Benthic forager		x		x	2
Lethrinidae	<i>Lethrinus</i>	<i>spp.</i>	Benthic forager	x	x	x	x	16
Lutjanidae	<i>Lutjanus</i>	<i>argentimaculatus</i>	Carnivore	x				8
Lutjanidae	<i>Lutjanus</i>	<i>bohar</i>	Piscivore	x				1
Lutjanidae	<i>Lutjanus</i>	<i>carponotatus</i>	Piscivore	x	x	x	x	170
Lutjanidae	<i>Lutjanus</i>	<i>erythropterus/ malabaricus</i>	Piscivore	x	x	x		87
Lutjanidae	<i>Lutjanus</i>	<i>fulviflamma</i>	Carnivore		x			8

Family	Genus	Species	Trophic group	Occurrence by habitat type				Total Max N
				R	C	S	M	
Lutjanidae	<i>Lutjanus</i>	<i>fulvus</i>	Carnivore	x	x			3
Lutjanidae	<i>Lutjanus</i>	<i>lemniscatus</i>	Carnivore	x	x	x	x	93
Lutjanidae	<i>Lutjanus</i>	<i>lutjanus</i>	Carnivore		x	x		2
Lutjanidae	<i>Lutjanus</i>	<i>monostigma</i>	Carnivore		x			1
Lutjanidae	<i>Lutjanus</i>	<i>russelli</i>	Piscivore	x	x	x		43
Lutjanidae	<i>Lutjanus</i>	<i>sebae</i>	Piscivore	x	x			12
Lutjanidae	<i>Lutjanus</i>	<i>spp.</i>	Carnivore	x	x	x	x	14
Lutjanidae	<i>Lutjanus</i>	<i>vitta</i>	Piscivore	x	x	x	x	222
Lutjanidae	<i>Symphorus</i>	<i>nematophorus</i>	Carnivore	x	x	x		9
Mullidae	<i>Parupeneus</i>	<i>barberinus</i>	Benthic forager				x	2
Mullidae	<i>Parupeneus</i>	<i>ciliatus</i>	Benthic forager	x				1
Mullidae	<i>Parupeneus</i>	<i>indicus</i>	Benthic forager	x	x	x	x	96
Mullidae	<i>Parupeneus</i>	<i>spilurus</i>	Benthic forager				x	4
Mullidae	<i>Parupeneus</i>	<i>spp.</i>	Benthic forager		x			1
Mullidae	<i>Upeneus</i>	<i>tragula</i>	Benthic forager		x			4
Muraenidae	<i>Gymnothorax</i>	<i>spp.</i>	Carnivore	x	x	x	x	18
Nemipteridae	<i>Pentapodus</i>	<i>nagasakiensis</i>	Benthic forager			x		2
Nemipteridae	<i>Pentapodus</i>	<i>paradiseus</i>	Benthic forager			x		1
Nemipteridae	<i>Pentapodus</i>	<i>porosus</i>	Benthic forager		x			2
Nemipteridae	<i>Pentapodus</i>	<i>spp.</i>	Benthic forager			x		1
Nemipteridae	<i>Scolopsis</i>	<i>bilineatus</i>	Benthic forager		x			2
Nemipteridae	<i>Scolopsis</i>	<i>margaritifer</i>	Benthic forager				x	1
Nemipteridae	<i>Scolopsis</i>	<i>monogramma</i>	Benthic forager	x	x	x	x	132
Nemipteridae	<i>Scolopsis</i>	<i>spp.</i>	Benthic forager	x	x	x		3
Pomacanthidae	<i>Chaetodontoplus</i>	<i>duboulayi</i>	Benthic forager	x	x	x		20
Pomacanthidae	<i>Chaetodontoplus</i>	<i>meredithi</i>	Benthic forager	x	x			5
Pomacanthidae	<i>Pomacanthus</i>	<i>semicirculatus</i>	Benthic forager	x	x		x	17
Pomacanthidae	<i>Pomacanthus</i>	<i>sexstriatus</i>	Benthic forager	x	x	x	x	70
Pomacanthidae	<i>Pomacanthus</i>	<i>spp.</i>	Benthic forager	x	x			3
Pseudochromidae	<i>Pseudochromis</i>	<i>spp.</i>	Benthic forager		x	x		2
Rhinidae	<i>Rhynchobatus</i>	<i>australiae</i>	Benthic forager		x	x		4
Scaridae	<i>Chlorurus</i>	<i>spilurus</i>	Herbivore (excavator)	x	x			4
Scaridae	<i>Scarus</i>	<i>dimidiatus</i>	Herbivore (scraper)				x	1
Scaridae	<i>Scarus</i>	<i>forsteni</i>	Herbivore (scraper)				x	3
Scaridae	<i>Scarus</i>	<i>niger</i>	Herbivore (scraper)		x			1
Scaridae	<i>Scarus</i>	<i>oviceps</i>	Herbivore (scraper)		x			8
Scaridae	<i>Scarus</i>	<i>rivulatus</i>	Herbivore (scraper)	x	x		x	18
Scaridae	<i>Scarus</i>	<i>schlegeli</i>	Herbivore (scraper)	x	x			14
Scaridae	<i>Scarus</i>	<i>spp.</i>	Herbivore (scraper)	x	x	x	x	71

Family	Genus	Species	Trophic group	Occurrence by habitat type				Total Max N
				R	C	S	M	
Sciaenidae	<i>Protonibea</i>	<i>diacanthus</i>	Carnivore		X			2
Scombridae	<i>Scomberomorus</i>	<i>spp.</i>	Piscivore			X		18
Serranidae	<i>Cephalopholis</i>	<i>argus</i>	Piscivore		X		X	3
Serranidae	<i>Cephalopholis</i>	<i>boenak</i>	Piscivore	X	X			11
Serranidae	<i>Cephalopholis</i>	<i>cyanostigma</i>	Piscivore		X			1
Serranidae	<i>Cephalopholis</i>	<i>microprion</i>	Piscivore	X	X			10
Serranidae	<i>Cephalopholis</i>	<i>spp.</i>	Piscivore	X	X		X	44
Serranidae	<i>Diploprion</i>	<i>bifasciatum</i>	Piscivore	X	X		X	9
Serranidae	<i>Epinephelus</i>	<i>coioides</i>	Carnivore	X	X	X		15
Serranidae	<i>Epinephelus</i>	<i>lanceolatus</i>	Carnivore			X		1
Serranidae	<i>Epinephelus</i>	<i>merra</i>	Carnivore	X	X		X	7
Serranidae	<i>Epinephelus</i>	<i>ongus</i>	Carnivore	X				2
Serranidae	<i>Epinephelus</i>	<i>quoyanus</i>	Carnivore	X	X	X	X	51
Serranidae	<i>Epinephelus</i>	<i>spp.</i>	Carnivore		X	X		9
Serranidae	<i>Epinephelus</i>	<i>tauvina</i>	Piscivore		X			1
Serranidae	<i>Plectropomus</i>	<i>spp.</i>	Piscivore	X	X	X	X	185
Siganidae	<i>Siganus</i>	<i>argenteus</i>	Herbivore (grazer / detritivore)		X			22
Siganidae	<i>Siganus</i>	<i>canaliculatus</i>	Herbivore (grazer / detritivore)	X			X	81
Siganidae	<i>Siganus</i>	<i>doliatus</i>	Herbivore (grazer / detritivore)	X	X	X	X	128
Siganidae	<i>Siganus</i>	<i>guttatus</i>	Herbivore (grazer / detritivore)	X		X		10
Siganidae	<i>Siganus</i>	<i>javus</i>	Herbivore (grazer / detritivore)	X				4
Siganidae	<i>Siganus</i>	<i>lineatus</i>	Herbivore (grazer / detritivore)	X	X		X	48
Siganidae	<i>Siganus</i>	<i>punctatus</i>	Herbivore (grazer / detritivore)		X			2
Siganidae	<i>Siganus</i>	<i>spp.</i>	Herbivore (grazer / detritivore)	X	X		X	75
Siganidae	<i>Siganus</i>	<i>virgatus</i>	Herbivore (grazer / detritivore)		X			5
Sphyraenidae	<i>Sphyraena</i>	<i>barracuda</i>	Piscivore	X		X		5
Sphyraenidae	<i>Sphyraena</i>	<i>qenie</i>	Piscivore				X	6
Sphyraenidae	<i>Sphyraena</i>	<i>spp.</i>	Piscivore		X	X		2

* *Lutjanus erythropterus* and *L. malabaricus* were grouped, as they often schooled together, making individual fish difficult to identify to species level.

Coral reef	Not present		
Rocky Reef	Not present		
Macroalgae bed			Not present
Sand / rubble bed		Not present	Not present
	Low complexity	Moderate complexity	High complexity

