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

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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. INTRODUCTION

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

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

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

The structural complexity of reef architecture can also vary greatly within habitats, depending on the underlying habitat matrix and the composition of the benthic substratum (Darling et al., 2017; Dominici-Arosemena & Wolff, 2006; García-Charton & Pérez-Ruzafa, 2001; Nash et al., 2013). For larger bodied fishes (e.g. Haemulidae, Serranidae, Lutjanidae), structurally complex habitats and seascape features such as caves, boulders, and tabulate corals (Kerry & Bellwood, 2012) form critical habitats, whereas smaller bodied fishes such as damselfishes tend to utilize smaller microhabitats provided by branching corals, which offer shelter from predators (Beukers & Jones, 1998; Boström-Einarsson et al., 2013; Wilson, Burgess, et al., 2008). In habitats dominated by macroalgae, the composition and density of the canopy can influence the structural complexity provided by the habitat, with canopy-forming genera such as *Sargassum* providing important habitat structure, especially for juvenile fishes (Fulton et al., 2019). Sand or rubble beds, by comparison, tend to have uniform low complexity, and offer little structural habitat attributes for fishes.

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

The intent of this study was to examine the importance of habitat attributes across a mosaic of inshore habitats in the central GBR. To address this, we examined the relative influence of habitat characteristics and biophysical parameters on fish assemblages in two regions: the Dunk Island and Hinchinbrook Island regions.

The aims of the study were as follows:

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

2. MATERIALS AND METHODS

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

2.1 Study area and sampling design

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

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

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

2.2 BRUVS apparatus and deployment

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

2.3 Video analysis

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

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

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

Visibility was also estimated for each video, and assigned a category of low, medium, or high, using the bait arm as a length reference (Table 1). Site-level habitat data was derived for use in multivariate statistical analyses (as outlined below), using site-averaged data for complexity (as a score), benthic cover, depth, and visibility (in metres). To determine site-level habitat type, each site was categorised by considering the suite of replicates within. Although habitats were distributed patchily within each region, each site tended to be spatially homogeneous in its broad habitat type, so categorization of habitat type at the site level was considered representative (Figure 1).

2.4 Fish trophic groups

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

2.5 Statistical analyses

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

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

The influence of habitat and other predictor variables on species richness was analysed to develop a Classification and Regression Tree (CART), fitted in R using the recursive partitioning (‘rpart’) package (R Core Team, 2018). This method is considered a flexible and robust approach, which is well suited for complex ecological datasets, and does not require balanced data (De'ath & Fabricius, 2000). The CART was used to model variation in species richness, by repeatedly splitting the full dataset into binary groups according to predictor variables. Initial input into the model included all predictor variables outlined in Table 1, as well as region and management zone. Each split in a CART aims to minimize the total sums of squares within the two nodes formed, and once splitting has produced a full tree, the tree is "pruned" to produce a CART that is the simplest but most effective representation of variation within the response variable (De'ath, 2002). Selection of the final CART for our model was made using 10-fold cross validation to select the tree with the minimum cross validation error; this method produces valid and clearly interpretable trees (Brieman et al., 1984; De'ath & Fabricius, 2000). The resulting CART only includes predictor variables that contributed to the final tree model.

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

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

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

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

3. RESULTS

3.1 Composition and structure of benthic habitats

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

The composition of benthic substrates differed among the four habitat types. With the exception of coral reef habitats, sites were clustered in the PCA according to habitat type (Figure 2). Coral reef sites were separated across PC1 according to complexity category and the dominant benthic substrate. Moderate complexity coral reefs clustered loosely with macroalgae beds, and had a higher cover of algae (relative to coral). High complexity coral reefs were more similar to rocky reefs, with a higher cover of hard and (to a lesser extent) soft coral cover (Figure 2). Rocky reefs had distinct benthic composition, and with the exception of a single site, were clustered in the PCA, with moderate and high complexity sites intermixed. Rocky reefs tended to occur in deeper sites, and were dominated by bedrock with scatterings of sponges, hydroids, and soft corals (Figure 2). Principle Component 2 (PC2) separated high complexity sites dominated by hard corals from low complexity sites with bare (sand/rubble) substrates. Sand / rubble beds were distinctly clustered within the PCA, and were dominated by bare substrates with scatterings of seagrass (Figure 2).

3.2 Trophic and taxonomic structure of fish assemblages

Fish assemblages in the Dunk and Hinchinbrook Island region were diverse, with 179 taxa from 29 fish families identified. Of these taxa, 140 were identified to species level, and 39 identified to genera (see Supporting Information Table S1). Species richness and abundance varied greatly amongst fish families and trophic groups (Figure 3). The most abundant families consisted of schooling species such as Caesionidae (fusiliers), as well as Lutjanidae (snappers) and Labridae (wrasses) which contain a diverse range of species from a variety of trophic groups (Figure 3). Many species were rare and/ or patchy in their distributions; 162 species (≈90%) occurred in less than 20% of replicates, and 37 species (≈21%) only recorded a single individual throughout the study area (Supporting Information Table S1). Of the 29 families recorded, nine of these included only a single species, whereas the most speciose family (Labridae) comprised 25 species (Figure 3). Twelve elasmobranch species from five families were recorded: nine species of sharks and three species of rays. Elasmobranchs were rare and patchily distributed, only two species occurred in more than 5% of replicates: blacktip reef shark, *Carcharhinus melanopterus* (15%*)*, and tawny nurse shark, *Nebrius ferrugineus* (5.6%). The most abundant trophic group was mobile planktivores, which were dominated by the highly abundant Caesionidae. Benthic foragers were the most speciose trophic group, and included a variety of species from 14 families. Corallivores, scapers/excavators, and browsers recorded both low abundance and species richness (Figure 3).

3.3 Factors influencing species richness

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

3.4 Key drivers of abundance for fish trophic groups

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

3.5 Fish assemblages amongst habitat types

The composition of species assemblages varied according to habitat type. Of the 179 species observed, 67 occurred only in a single habitat (37%). Of these habitat-specific species, 35 occurred only on coral reefs, 12 occurred only on rocky reefs, 10 occurred only on macroalgae beds, and 10 occurred only in sand/ rubble beds (Supporting Information Table S1). The greatest overlap in occurrence was for coral and rocky reefs; 60% of species found on coral reefs also occurred on rocky reefs. The CAP ordination showed separation of assemblages into three distinct groups: (1) sand/rubble beds, (2) macroalgae beds, and (3) rocky reefs and coral reefs (Figure 7). The CAP permutation test showed a significant difference in the position of the four habitat centroids (trace test statistic, p = 0.017), and this was supported by non-overlapping confidence ellipsis in the bootstrapped MDS for all habitat types except coral and rocky reefs (Figure 7 and Supporting Information Figure S2).

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

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

4. DISCUSSION

Our results highlight the importance of inshore tropical seascapes in supporting a rich diversity of fish species. Collectively, the mosaic of coral reef, rocky reef, macroalgae, and sand/rubble habitats supported a functionally and taxonomically diverse fish assemblage. It is likely that many fishes recorded utilize multiple habitats within the seascape (Sambrook et al., 2019), however each habitat also supported unique species not recorded elsewhere, and so contributed uniquely to the overall species richness. Although the habitat relationships varied amongst the trophic groups considered, it was clear that broad habitat type strongly influenced the species richness and composition of fish assemblages. A notable exception to this outcome was the similarity of fish assemblages in rocky and coral reefs, which both supported higher species richness compared to macroalgae and sand/ rubble beds, most likely due to the provision of complex habitat architecture. Our results concur with and build upon a number of recent studies highlighting the role of habitat mosaics on inshore coastal ecosystems (e.g. Sambrook et al., 2019, Sievers et al., 2020), and further suggest that rocky reefs make a valuable and previously under-recognised contribution to the habitat mosaic.

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

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

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

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

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

We found a number of species unique to each of the unstructured habitats (macroalgae and sand/rubble beds), indicating their unique role in contributing to the local diversity of fish fauna. It is possible that with further sampling in macroalgae and sand/rubble beds, we may have uncovered additional unique species, and such targeted surveys in unstructured habitats in the region would be an interesting follow up study. There were ten species unique to macroalgae beds, including *P. spilurus* (Mullidae), *S.forsteni* (Scaridae), and *L. obsoletus* (Lethrinidae), as well as a number of additional taxa (e.g. tuskfishes; *Choerodon* spp.) that were markedly more abundant in macroalgae beds compared to other habitats. These results concur with a recent review (Fulton et al., 2020) highlighting the unique role of macroalgae habitats in supporting distinct fish assemblages; indeed we found overlap between our study and this review in the taxa considered “macroalgal residents” (e.g. *Choerodon,* and *Lethrinus* spp.). Sand and rubble beds had the lowest species richness and abundance of all habitats, as would be expected due to the lack of habitat features and low complexity (Lefcheck et al., 2019). Sand /rubble beds did support unique species, including transient pelagic taxa such as mackerels (*Scomberomorus* spp.) and great barracuda (*S. barracuda*). Since sand/rubble beds are lacking in structural features, it is likely that many fishes detected were moving through this habitat, possibly attracted from open pelagic areas by the bait. As such, the importance of this habitat to these species is less evident. However, it is notable that sand/ rubble beds also supported unique species of threadfin breams (*Pentapodus nagasakiensis* and *P. paradiseus*), which are known forage over sandy habitats, and so may have stronger habitat associations within sand/rubble areas (Quimpo et al., 2019).

Baited Remote Underwater Video Stations are an effective technique for surveying a range of fishes, however, as with any survey approach, there are inherent biases and limitations to the BRUVS technique. The use of bait may disproportionately attract predatory species compared to unbaited techniques (i.e. RUVS), and the use of underwater video of any kind precludes accurate assessment of very small fishes (Cappo et al., 2004; Harvey et al., 2007). These limitations did not bias our interpretation of fish/habitat relationships, however, since any bias would be consistent amongst habitats, and small fishes were excluded from video analysis. Furthermore, since many analyses were considered at the site level, and sites were separated by at least 2km during each sampling event, there was little risk of species moving among sites and confounding interpretation of fish/habitat relationships. A study by Harvey et al. (2007) demonstrated that the use of bait in underwater video surveys allows for better discrimination of fish assemblages amongst habitats compared to unbaited video. Our results are consistent with this, since we were able to detect distinct fish assemblages in the habitats we surveyed. The dominant habitats in the study area were structured (either coral or rocky reefs), and these habitats therefore had greater sampling effort. The difference in sample size amongst habitats did not confound our interpretations of the factors influencing species richness, since the CART model used replicate level species richness, and survey effort was consistent for each replicate. Furthermore, both the CAP and bootstrapped MDS separated fish assemblages into the same three habitat groups: reef (coral and rocky), macroalgae bed, and sand/rubble bed, which indicates the CAP results were robust despite variation in sample size.

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

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

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CONTRIBUTIONS

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

REFERENCES

Allen, G. R. (2009). *Field guide to marine fishes of tropical Australia and South-east Asia* (4th ed.). Welshpool, Western Australia: Western Australian Museum.

Anderson, M. J., & Willis, T. J. (2003). Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. *Ecology, 84*(2), 511-525. doi:10.1890/0012-9658(2003)084[0511:caopca]2.0.co;2

Beukers, J. S., & Jones, G. P. (1998). Habitat complexity modifies the impact of piscivores on a coral reef fish population. *Oecologia, 114*(1), 50-59. doi:10.1007/s004420050419

Boaden, A. E., & Kingsford, M. J. (2012). Diel behaviour and trophic ecology of *Scolopsis bilineatus* (Nemipteridae). *Coral Reefs, 31*, 871-883. doi:10.1007/s00338-012-0903-2

Boström-Einarsson, L., Bonin, M. C., Munday, P. L., & Jones, G. P. (2013). Strong intraspecific competition and habitat selectivity influence abundance of a coral-dwelling damselfish. *Journal of Experimental Marine Biology and Ecology, 448*, 85-92. doi:10.1016/j.jembe.2013.06.017

Bradley, M., Baker, R., & Sheaves, M. (2017). Hidden components in tropical seascapes: Deep-estuary habitats support unique fish assemblages. *Estuaries and Coasts, 40*(4), 1195-1206. doi:10.1007/s12237-016-0192-z

Bray, D. J., & Gomon, M. F. (2021). Fishes of Australia. Retrieved from http://fishesofaustralia.net.au/

Brieman, L., Friedman, J., Olshen, R., & Stone, C. (1984). *Classification and regression trees*. Pacific Grove, CA: Wadsworth.

Cappo, M., De'ath, G., & Speare, P. (2007). Inter-reef vertebrate communities of the Great Barrier Reef Marine Park determined by baited remote underwater video stations. *Marine Ecology Progress Series, 350*, 209-221.

Cappo, M., Speare, P., & De'ath, G. (2004). Comparison of baited remote underwater video stations (BRUVS) and prawn (shrimp) trawls for assessments of fish biodiversity in inter-reefal areas of the Great Barrier Reef Marine Park. *Journal of Experimental Marine Biology and Ecology, 302*(2), 123-152. doi:10.1016/j.jembe.2003.10.006

Cappo, M., Stowar, M., Syms, C., Johansson, C., & Cooper, T. (2011). Fish-habitat associations in the region offshore from James Price Point – a rapid assessment using Baited Remote Underwater Video Stations (BRUVS). *Journal of the Royal Society of Western Australia, 94*, 303-321.

Ceccarelli, D. M., Evans, R. D., Logan, M., Mantel, P., Puotinen, M., Petus, C., Russ, G. R., & Williamson, D. H. (2020). Long-term dynamics and drivers of coral and macroalgal cover on inshore reefs of the Great Barrier Reef Marine Park. *Ecological Applications, 30*(1), e02008. doi:10.1002/eap.2008

Clark, R. D., Pittman, S., Caldow, C., Christensen, J., Roque, B., Appeldoorn, R. S., & Monaco, M. E. (2009). Nocturnal fish movement and trophic flow across habitat boundaries in a coral reef ecosystem (SW Puerto Rico). *Caribbean Journal of Science, 45*(2-3), 282-303.

Clarke, K. R., Gorley, R. N., Somerfield, R. N., & Warwick, R. M. (2014). Change in marine communities: an approach to statistical analysis and interpretation: 3rd Edition. In. Plymouth.

Coker, D. J., Pratchett, M. S., & Munday, P. L. (2009). Coral bleaching and habitat degradation increase susceptibility to predation for coral-dwelling fishes. *Behavioral Ecology, 20*(6), 1204-1210. doi:10.1093/beheco/arp113

Coker, D. J., Wilson, S. K., & Pratchett, M. S. (2014). Importance of live coral habitat for reef fishes. *Reviews in Fish Biology and Fisheries, 24*(1), 89-126. doi:10.1007/s11160-013-9319-5

Cole, A., Pratchett, M., & Jones, G. (2008). Diversity and functional importance of coral-feeding fishes on tropical coral reefs. *Fish and Fisheries, 9*, 286-307. doi:10.1111/j.1467-2979.2008.00290.x

Connell, S. D. (1998). Patterns of piscivory by resident predatory reef fish at One Tree Reef, Great Barrier Reef. *Marine and Freshwater Research, 49*, 25-30.

Connell, S. D., & Jones, G. P. (1991). The influence of habitat complexity on postrecruitment processes in a temperate reef fish population. *Journal of Experimental Marine Biology and Ecology, 151*(2), 271-294.

Connell, S. D., & Kingsford, M. J. (1998). Spatial, temporal and habitat related variation in the abundance of large predatory fish at One Tree Reef, Australia. *Coral Reefs, 17*(1), 49-57. doi:10.1007/s003380050094

Dahlgren, C. P., & Eggleston, D. B. (2000). Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. *Ecology, 81*(8), 2227-2240. doi:10.1890/0012-9658(2000)081

Darling, E. S., Graham, N. A. J., Januchowski-Hartley, F. A., Nash, K. L., Pratchett, M. S., & Wilson, S. K. (2017). Relationships between structural complexity, coral traits, and reef fish assemblages. *Coral Reefs, 36*(2), 561-575. doi:10.1007/s00338-017-1539-z

De'ath, G. (2002). Multivariate regression trees: A new technique for modeling species–environment relationships. *Ecology, 83*(4), 1105-1117. doi:10.1890/0012-9658(2002)083[1105:mrtant]2.0.co;2

De'ath, G., & Fabricius, K. (2010). Water quality as a regional driver of coral biodiversity and macroalgae on the Great Barrier Reef. *Ecological Applications, 20*(3), 840-850. doi:https://doi.org/10.1890/08-2023.1

De'ath, G., & Fabricius, K. E. (2000). Classification and regression trees: A powerful yet simple technique for ecological data analysis. *Ecology, 81*(11), 3178-3192. doi:https://doi.org/10.1890/0012-9658(2000)081[3178:CARTAP]2.0.CO;2

De'ath, G., Fabricius, K. E., Sweatman, H., & Puotinen, M. (2012). The 27-year decline of coral cover on the Great Barrier Reef and its causes. *Proceedings of the National Academy of Sciences, 109*, 17995-17999.

Dominici-Arosemena, A., & Wolff, M. (2006). Reef fish community structure in the Tropical Eastern Pacific (Panama): living on a relatively stable rocky reef environment. *Helgoland Marine Research, 60*(4), 287-305. doi:10.1007/s10152-006-0045-4

Donaldson, J. A., Drews Jr, P., Bradley, M., Morgan, D. L., Baker, R., & Ebner, B. C. (2020). Countering low visibility in video survey of an estuarine fish assemblage. *Pacific Conservation Biology, 26*(2), 190-200. doi:https://doi.org/10.1071/PC19019

Elith, J., Leathwick, J. R., & Hastie, T. (2008). A working guide to boosted regression trees. *Journal of Animal Ecology, 77*(4), 802-813. doi:10.1111/j.1365-2656.2008.01390.x

Emslie, M., Cheal, A., Sweatman, H., & Delean, S. (2008). Recovery from disturbance of coral and reef fish communities on the Great Barrier Reef, Australia. *Marine Ecology Progress Series, 371*, 177-190. doi:10.3354/meps07657

Emslie, M. J., Logan, M., & Cheal, A. J. (2019). The distribution of planktivorous damselfishes (Pomacentridae) on the Great Barrier Reef and the relative influences of habitat and predation. *Diversity, 11*(3), 33.

Emslie, M. J., Logan, M., Williamson, D. H., Ayling, A. M., MacNeil, M. A., Ceccarelli, D., Cheal, A. J., Evans, R. D., Johns, K. A., Jonker, M. J., Miller, I. R., Osborne, K., Russ, G. R., & Sweatman, H. P. A. (2015). Expectations and outcomes of reserve network performance following re-zoning of the Great Barrier Reef Marine Park. *Current Biology, 25*(8), 983-992. doi:10.1016/j.cub.2015.01.073

Espinoza, M., Cappo, M., Heupel, M. R., Tobin, A. J., & Simpfendorfer, C. A. (2014). Quantifying shark distribution patterns and species-habitat associations: Implications of Marine Park zoning. *PLoS ONE, 9*(9), e106885. doi:10.1371/journal.pone.0106885

Evans, R. D., Wilson, S. K., Field, S. N., & Moore, J. A. Y. (2014). Importance of macroalgal fields as coral reef fish nursery habitat in north-west Australia. *Marine Biology, 161*(3), 599-607. doi:10.1007/s00227-013-2362-x

Farmer, B. M., & Wilson, S. K. (2011). Diet of finfish targeted by fishers in North West Australia and the implications for trophic cascades. *Environmental Biology of Fishes, 91*(1), 71-85. doi:10.1007/s10641-010-9761-3

Ferrari, R., Malcolm, H. A., Byrne, M., Friedman, A., Williams, S. B., Schultz, A., Jordan, A. R., & Figueira, W. F. (2018). Habitat structural complexity metrics improve predictions of fish abundance and distribution. *Ecography, 41*(7), 1077-1091. doi:https://doi.org/10.1111/ecog.02580

Friedlander, A. M., Brown, E. K., Jokiel, P. L., Smith, W. R., & Rodgers, K. S. (2003). Effects of habitat, wave exposure, and marine protected area status on coral reef fish assemblages in the Hawaiian archipelago. *Coral Reefs, 22*(3), 291-305. doi:10.1007/s00338-003-0317-2

Froese, R., & Pauly, D. (2021). Fishbase. Retrieved from http://www.fishbase.org

Fulton, C. J., Abesamis, R. A., Berkström, C., Depczynski, M., Graham, N. A. J., Holmes, T. H., Kulbicki, M., Noble, M. M., Radford, B. T., Tano, S., Tinkler, P., Wernberg, T., & Wilson, S. K. (2019). Form and function of tropical macroalgal reefs in the Anthropocene. *Functional Ecology, 33*(6), 989-999. doi:https://doi.org/10.1111/1365-2435.13282

Fulton, C. J., Berkström, C., Wilson, S. K., Abesamis, R. A., Bradley, M., Åkerlund, C., Barrett, L. T., Bucol, A. A., Chacin, D. H., Chong-Seng, K. M., Coker, D. J., Depczynski, M., Eggertsen, L., Eggertsen, M., Ellis, D., Evans, R. D., Graham, N. A. J., Hoey, A. S., Holmes, T. H., Kulbicki, M., Leung, P. T. Y., Lam, P. K. S., van Lier, J., Matis, P. A., Noble, M. M., Pérez-Matus, A., Piggott, C., Radford, B. T., Tano, S., & Tinkler, P. (2020). Macroalgal meadow habitats support fish and fisheries in diverse tropical seascapes. *Fish and Fisheries, 21*(4), 700-717. doi:https://doi.org/10.1111/faf.12455

García-Charton, J. A., & Pérez-Ruzafa, Á. (2001). Spatial pattern and the habitat structure of a Mediterranean rocky reef fish local assemblage. *Marine Biology, 138*(5), 917-934. doi:10.1007/s002270000524

GBRMPA. (2014). *Great Barrier Reef outlook report 2014*. Retrieved from Townsville:

Gilby, B. L., Tibbetts, I. R., Olds, A. D., Maxwell, P. S., & Stevens, T. (2016). Seascape context and predators override water quality effects on inshore coral reef fish communities. *Coral Reefs, 35*(3), 979-990. doi:10.1007/s00338-016-1449-5

Graham, N. A. J., Jennings, S., MacNeil, M. A., Mouillot, D., & Wilson, S. K. (2015). Predicting climate-driven regime shifts versus rebound potential in coral reefs. *Nature, 518*(7537), 94-97. doi:10.1038/nature14140

Gratwicke, B., & Speight, M. R. (2005). The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. *Journal of Fish Biology, 66*(3), 650-667. doi:https://doi.org/10.1111/j.0022-1112.2005.00629.x

Green, A., & Bellwood, D. R. (2009). *Monitoring functional groups of herbivorous reef fishes as indicators of coral reef resilience- a practical guide for coral reef managers in the Asia Pacific region*. Retrieved from Gland, Switzerland:

Hall, A. E., Cameron, D. S., & Kingsford, M. J. (2021). Partially protected areas as a management tool on inshore reefs. *Reviews in Fish Biology and Fisheries*. doi:10.1007/s11160-021-09654-y

Hall, A. E., & Kingsford, M. J. (2016). Variation in the population demographics of Scolopsis bilineatus in response to predators. *Coral Reefs, 35*(4), 1173-1185. doi:10.1007/s00338-016-1486-0

Harvey, E. S., Cappo, M., Butler, J. J., Hall, N., & Kendrick, G. A. (2007). Bait attraction affects the performance of remote underwater video stations in assessment of demersal fish community structure. *Marine Ecology Progress Series, 350*, 245-254.

Harvey, E. S., McLean, D. L., Frusher, S., Haywood, M. D. D., Newman, S. J., & Williams, A. (2013). *The use of BRUVs as a tool for assessing marine fisheries and ecosystems: a review of the hurdles and potential*. Retrieved from Perth, Australia:

Hitt, S., Pittman, S. J., & Nemeth, R. S. (2011). Diel movements of fishes linked to benthic seascape structure in a Caribbean coral reef ecosystem. *Marine Ecology Progress Series, 427*, 275-292.

Hughes, T. P., Day, J. C., & Brodie, J. (2015). Securing the future of the Great Barrier Reef. *Nature Climate Change, 5*(6), 508-511. doi:10.1038/nclimate2604

Jones, G. (1988). Ecology of rocky reef fish of north-eastern New Zealand: A review. *New Zealand Journal of Marine and Freshwater Research, 22*, 445-462. doi:10.1080/00288330.1988.9516315

Jones, G. P., McCormick, M. L., Srinivasan, M., & Eagle, J. V. (2004). Coral decline threatens fish biodiversity in marine reserves. *Proceedings of the National Academy of Sciences, 101*(21), 8251-8253. doi:10.1073/pnas.0401277101

Kerry, J. T., & Bellwood, D. R. (2012). The effect of coral morphology on shelter selection by coral reef fishes. *Coral Reefs, 31*(2), 415-424. doi:10.1007/s00338-011-0859-7

Kingsford, M. (1998). Reef fishes. In M. Kingsford & C. Battershill (Eds.), *Studying temperate marine environments: A handbook for ecologists.* Christchurch, New Zealand: University of Canterbury Press.

Kingsford, M., & Carlson, I. (2010). Patterns of distribution and movement of fishes;*Ophthalmolepis lineolatus* and *Hypoplectrodes maccullochi*, on temperate rocky reefs of south eastern Australia. *Environmental Biology of Fishes, 88*(2), 105-118.

Kingsford, M. J. (2009). Contrasting patterns of reef utilization and recruitment of coral trout (*Plectropomus leopardus*) and snapper *(Lutjanus carponotatus)* at One Tree Island, southern Great Barrier Reef. *Coral Reefs, 28*, 251-264. doi:10.1007/s00338-008-0421-4

Komyakova, V., Munday, P., & Jones, G. (2013). Relative importance of coral cover, habitat complexity and diversity in determining the structure of reef fish communities. *PLoS ONE, 8*, e83178. doi:10.1371/journal.pone.0083178

Kulbicki, M., Bozec, Y. M., Labrosse, P., Letourneur, Y., Mou-Tham, G., & Wantiez, L. (2005). Diet composition of carnivorous fishes from coral reef lagoons of New Caledonia. *Aquatic Living Resources, 18*(3), 231-250. doi:10.1051/alr:2005029

Lefcheck, J. S., Hughes, B. B., Johnson, A. J., Pfirrmann, B. W., Rasher, D. B., Smyth, A. R., Williams, B. L., Beck, M. W., & Orth, R. J. (2019). Are coastal habitats important nurseries? A meta-analysis. *Conservation Letters, 12*(4), e12645. doi:https://doi.org/10.1111/conl.12645

Nagelkerken, I., van der Velde, G., Gorissen, M. W., Meijer, G. J., van't Hof, T., & den Hartog, C. (2000). Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique. *Estuarine Coastal and Shelf Science, 51*(1), 31-44. doi:10.1006/ecss.2000.0617

Nakamura, Y., Horinouchi, M., Nakai, T., & Sano, M. (2003). Food habits of fishes in a seagrass bed on a fringing coral reef at Iriomote Island, southern Japan. *Ichthyological Research, 50*(1), 0015-0022. doi:10.1007/s102280300002

Nash, K. L., Graham, N. A. J., Wilson, S. K., & Bellwood, D. R. (2013). Cross-scale habitat structure drives fish body size distributions on coral reefs. *Ecosystems, 16*(3), 478-490. doi:10.1007/s10021-012-9625-0

Olds, A., Connolly, R., Pitt, K., & Maxwell, P. S. (2012). Primacy of seascape connectivity effects in structuring coral reef fish assemblages. *Marine Ecology Progress Series, 462*, 191-203.

Pratchett, M. S. (2005). Dietary overlap among coral-feeding butterflyfishes (Chaetodontidae) at Lizard Island, northern Great Barrier Reef. *Marine Biology, 148*(2), 373-382. doi:10.1007/s00227-005-0084-4

Pratchett, M. S., & Berumen, M. L. (2008). Interspecific variation in distributions and diets of coral reef butterflyfishes (Teleostei: Chaetodontidae). *Journal of Fish Biology, 73*(7), 1730-1747. doi:10.1111/j.1095-8649.2008.02062.x

Pratchett, M. S., Coker, D. J., Jones, G. P., & Munday, P. L. (2012). Specialization in habitat use by coral reef damselfishes and their susceptibility to habitat loss. *Ecology and Evolution, 2*(9), 2168-2180. doi:10.1002/ece3.321

Quimpo, T. J. R., Cabaitan, P. C., Olavides, R. D. D., Dumalagan Jr., E. E., Munar, J., & Siringan, F. P. (2019). Spatial variability in reef-fish assemblages in shallow and upper mesophotic coral ecosystems in the Philippines. *Journal of Fish Biology, 94*(1), 17-28. doi:https://doi.org/10.1111/jfb.13848

Randall, J. E., Allen, G. R., & Steene, R. G. (1997). *Fishes of the Great Barrier Reef and Coral Sea*. Bathurst, NSW: Crawford House Publishing.

Russ, G. R., Rizzari, J. R., Abesamis, R. A., & Alcala, A. C. (2021). Coral cover a stronger driver of reef fish trophic biomass than fishing. *Ecological Applications*, 22. doi:10.1002/eap.2224

Sambrook, K., Hoey, A. S., Andrefouet, S., Cumming, G. S., Duce, S., & Bonin, M. C. (2019). Beyond the reef: The widespread use of non-reef habitats by coral reef fishes. *Fish and Fisheries, 20*(5), 903-920. doi:10.1111/faf.12383

Sheaves, M. (2009). Consequences of ecological connectivity: the coastal ecosystem mosaic. *Marine Ecology Progress Series, 391*, 107-115.

Sievers, K. T., McClure, E. C., Abesamis, R. A., & Russ, G. R. (2020). Non-reef habitats in a tropical seascape affect density and biomass of fishes on coral reefs. *Ecology and Evolution, 10*(24), 13673-13686. doi:10.1002/ece3.6940

Stowar, M., De'ath, G., Doherty, P., Johansson, C., Speare, P., & Venebles, B. (2008). *Influence of zoning on midshelf shoals of the southern Great Barrier Reef. Report to the Marine and Tropical Sciences Research Facility*. Reef and Rainforest Research Centre Limited, Cairns.

Tano, S. A., Eggertsen, M., Wikstrom, S. A., Berkstrom, C., Buriyo, A. S., & Halling, C. (2017). Tropical seaweed beds as important habitats for juvenile fish. *Marine and Freshwater Research, 68*(10), 1921-1934. doi:10.1071/mf16153

Team, R. C. (2018). R: A language and environment for statistical computing. . Retrieved from URL https://www.R-project.org/.

Trebilco, R., Dulvy, N., Stewart, H., & Salomon, A. (2015). The role of habitat complexity in shaping the size-structure of a temperate reef fish community. *Marine Ecology Progress Series, 532*. doi:10.3354/meps11330

Unsworth, R. K. F., Bell, J. J., & Smith, D. J. (2007). Tidal fish connectivity of reef and sea grass habitats in the Indo-Pacific. *Journal of the Marine Biological Association of the United Kingdom, 87*(5), 1287-1296. doi:10.1017/S002531540705638X

Webley, J., McInnes, K., Tiexeira, D., Lawson, A., & Quinn, R. (2015). *Statewide Recreational Fishing Survey 2013–14*: Department of Agriculture and Fisheries.

Wen, C. K. C., Pratchett, M. S., Almany, G. R., & Jones, G. P. (2013). Patterns of recruitment and microhabitat associations for three predatory coral reef fishes on the southern Great Barrier Reef, Australia. *Coral Reefs, 32*(2), 389-398. doi:10.1007/s00338-012-0985-x

Wenger, A. S., Rawson, C. A., Wilson, S., Newman, S. J., Travers, M. J., Atkinson, S., Browne, N., Clarke, D., Depczynski, M., Erftemeijer, P. L. A., Evans, R. D., Hobbs, J.-P. A., McIlwain, J. L., McLean, D. L., Saunders, B. J., & Harvey, E. (2018). Management strategies to minimize the dredging impacts of coastal development on fish and fisheries.*Conservation Letters, 11*(5), e12572. doi:https://doi.org/10.1111/conl.12572

Williamson, D. H., Ceccarelli, D. M., Jones, G. P., & Russ, G. R. (2019). *Assessing the Ecological Effects of Management Zoning on Inshore Reefs of the Great Barrier Reef Marine Park.* Townsville, Australia: Great Barrier Reef Marine Park Authority.

Wilson, S. K., Burgess, S. C., Cheal, A. J., Emslie, M., Fisher, R., Miller, I., Polunin, N. V. C., & Sweatman, H. P. A. (2008). Habitat utilization by coral reef fish: implications for specialists vs generalists in a changing environment. *Journal of Animal Ecology, 77*, 220-228.

Wilson, S. K., Depczynski, M., Fisher, R., Holmes, T. H., O'Leary, R. A., & Tinkler, P. (2010). Habitat Associations of Juvenile Fish at Ningaloo Reef, Western Australia: The Importance of Coral and Algae. *PLoS ONE, 5*(12), e15185. doi:10.1371/journal.pone.0015185

Wilson, S. K., Fisher, R., Pratchett, M. S., Graham, N. A. J., Dulvy, N. K., Turner, R. A., Cakacaka, A., Polunin, N. V. C., & Rushton, S. P. (2008). Exploitation and habitat degradation as agents of change within coral reef fish communities. *Global Change Biology, 14*(12), 2796-2809.

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 ± SEM**	**Definition**
Depth (m)	Continuous	Measured in field	2-17	6.25 ± 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 ± 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	Low: essentially a flat surface, with little or no structural features Medium: moderate complexity structural features such as coral and/or bedrock present High: 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	Coral reef: reefs with coral as the underlying substrate- has a range of % live coral and other benthic substrates Rocky reef: reefs with bedrock (granite boulder) as the underlying substrate- often with scattered coral (mostly soft coral), sponges, and hyroids Macroalgae beds: dominated by macroalgae (mostly *Sargassum* spp.) growing on sandy substrates Sand/ rubble bed: 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 ± 1.91	Combined percentage of live hard and live soft corals
% algae			0-100	24.91 ± 2.41	Percentage cover of all visible algae, including turf, coralline, and macroalgae
% bare			0-100	35.11 ± 2.63	Percentage cover of bare sand or rubble, with no substrate biota
% bedrock			0-90	15.88 ± 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		2nd ranked predictor		3rd 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 ± 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

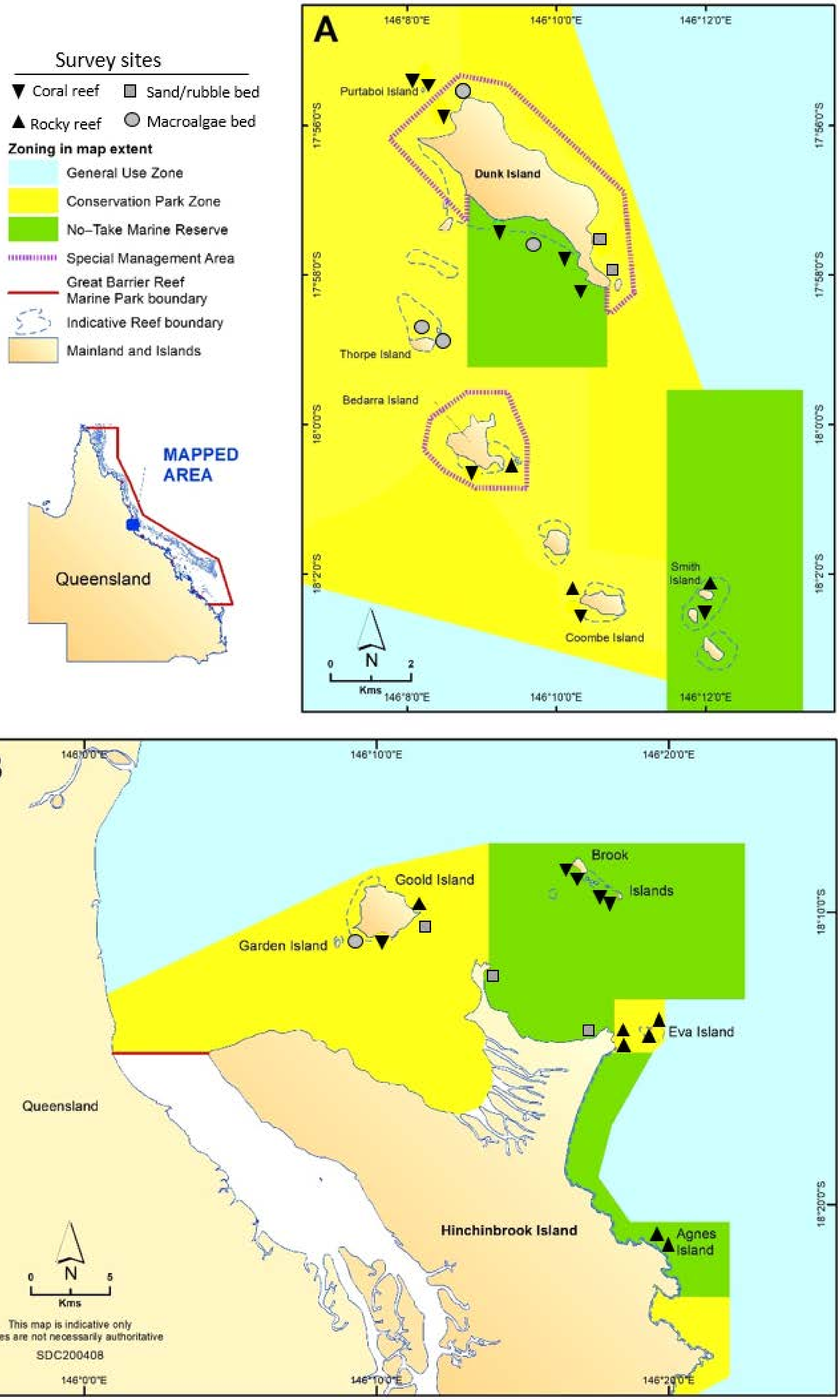
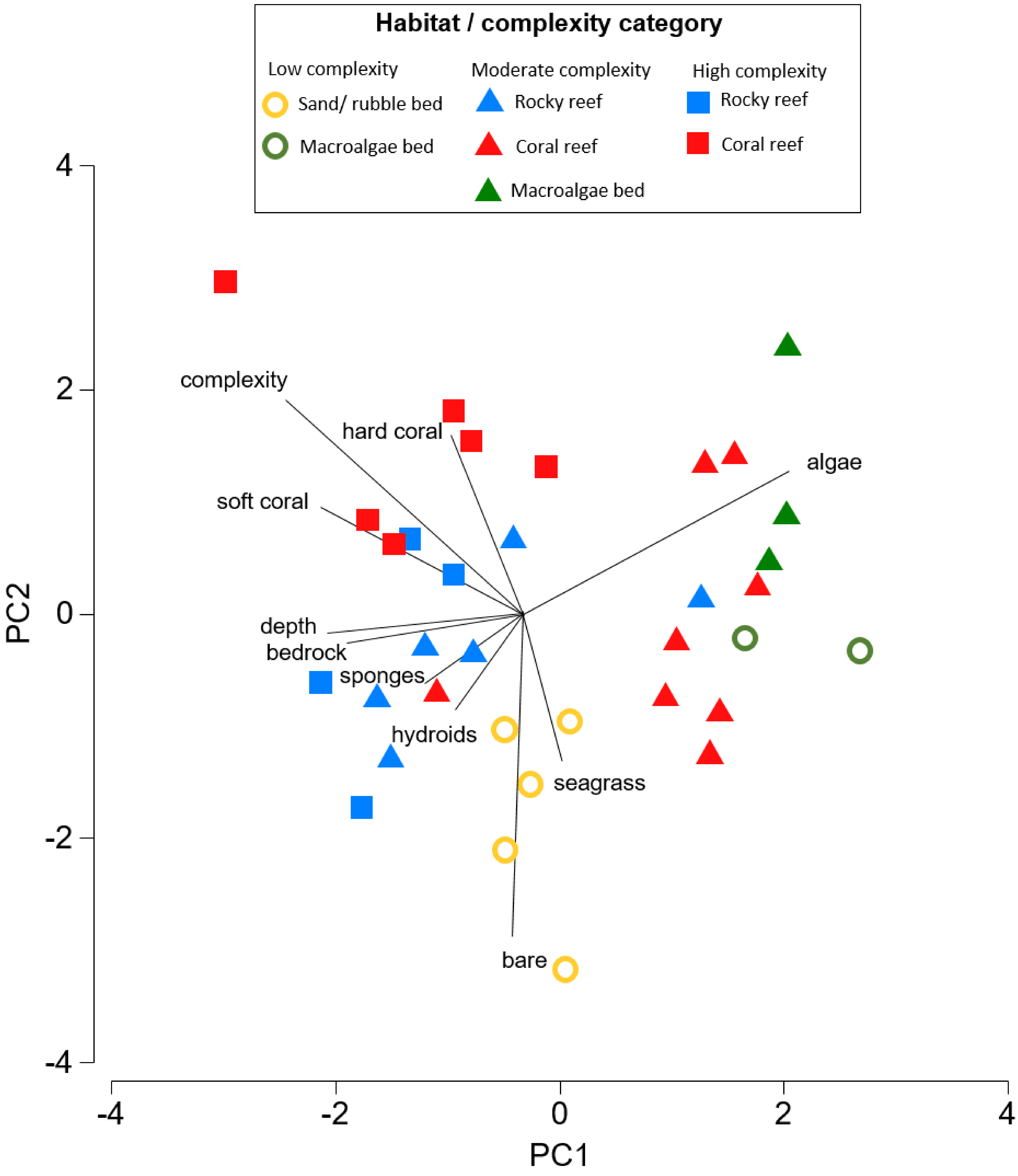

Survey sites
▼ Coral reef
▲ Rocky reef
■ Sand/rubble bed
● Macroalgae bed
Zoning in map extent
General Use Zone
Conservation Park Zone
No-Take Marine Reserve
Special Management Area
Great Barrier Reef Marine Park boundary
Indicative Reef boundary
Mainland and Islands
MAPPED AREA
Queensland
A
146°8'0"E
146°10'0"E
146°12'0"E
17°56'0"S
17°58'0"S
18°0'0"S
18°2'0"S
Purtaboi Island
Dunk Island
Thorpe Island
Bedarra Island
Smith Island
Coombe Island
N
0
2
Kms
B
146°0'0"E
146°10'0"E
146°20'0"E
18°10'0"S
18°20'0"S
Brook Islands
Goold Island
Garden Island
Eva Island
Queensland
Hinchinbrook Island
Agnes Island
N
0
5
Kms
This map is indicative only
Names are not necessarily authoritative
SDC200408

Figure 2



Habitat / complexity category
Low complexity
Sand/ rubble bed
Macroalgae bed
Moderate complexity
Rocky reef
Coral reef
Macroalgae bed
High complexity
Rocky reef
Coral reef
complexity
hard coral
soft coral
algae
depth
bedrock
sponges
hydroids
seagrass
bare
4
2
0
-2
-4
PC2
-4
-2
0
2
4
PC1

Figure 3

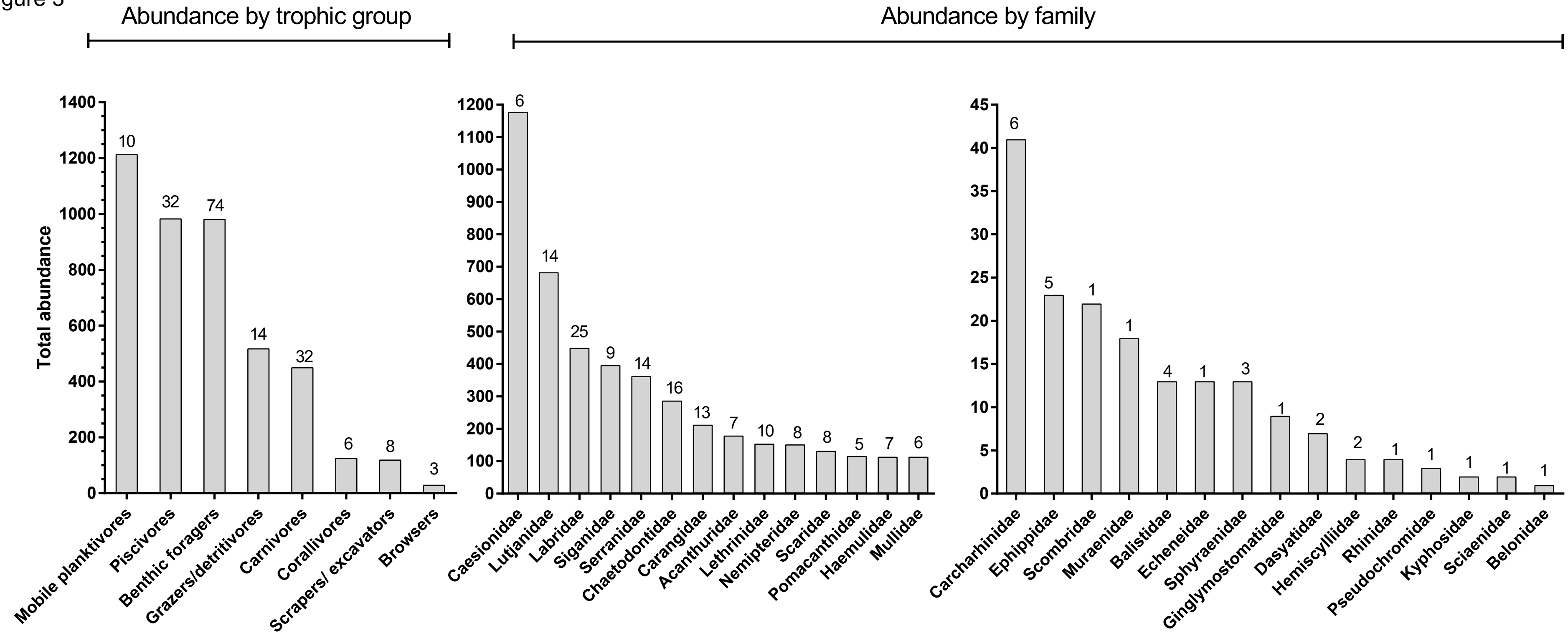

Abundance by trophic group
Abundance by family
Total abundance
0
200
400
600
800
1000
1200
1400
Mobile planktivores 10
Piscivores 32
Benthic foragers 74
Grazers/detritivores 14
Carnivores 32
Corallivores 6
Scrapers/ excavators 8
Browsers 3
0
100
200
300
400
500
600
700
800
900
1000
1100
1200
Caesionidae 6
Lutjanidae 14
Labridae 25
Siganidae 9
Serranidae 14
Chaetodontidae 16
Carangidae 13
Acanthuridae 7
Lethrinidae 10
Nemipteridae 8
Scaridae 8
Pomacanthidae 5
Haemulidae 7
Mullidae 6
0
5
10
15
20
25
30
35
40
45
Carcharhinidae 6
Ephippidae 5
Scombridae 1
Muraenidae 1
Balistidae 4
Echeneidae 1
Sphyraenidae 3
Ginglymostomatidae 1
Dasyatidae 2
Hemiscylliidae 2
Rhinidae 1
Pseudochromidae 1
Kyphosidae 1
Sciaenidae 1
Belonidae 1

Figure 4

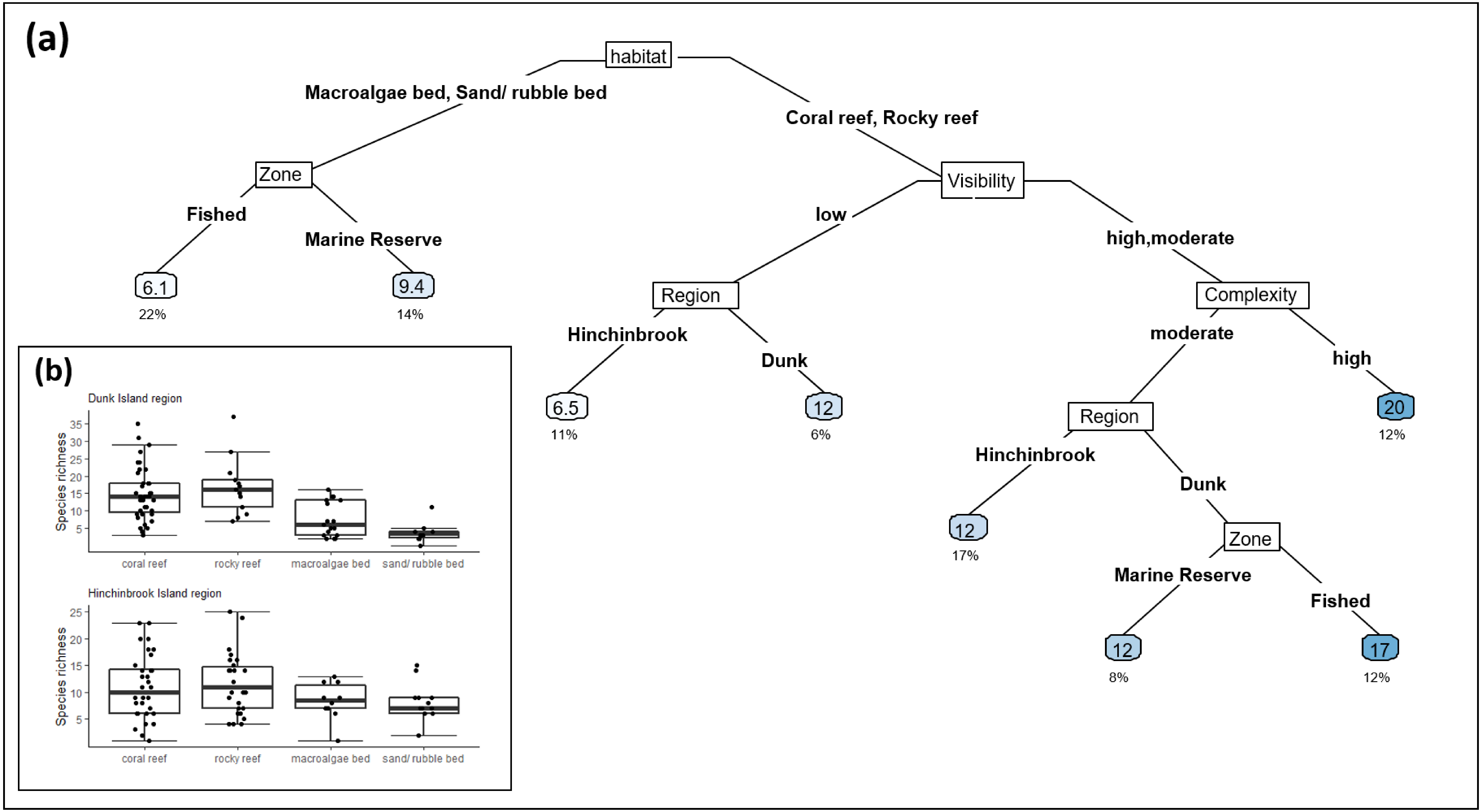

(a)
habitat
Macroalgae bed, Sand/ rubble bed
Coral reef, Rocky reef
Zone
Fished
Marine Reserve
6.1
22%
9.4
14%
Visibility
low
high,moderate
Region
Hinchinbrook
Dunk
6.5
11%
12
6%
Complexity
moderate
high
20
12%
Region
Hinchinbrook
Dunk
12
17%
Zone
Marine Reserve
Fished
12
8%
17
12%
(b)
Dunk Island region
Species richness
5
10
15
20
25
30
35
coral reef
rocky reef
macroalgae bed
sand/ rubble bed
Hinchinbrook Island region
Species richness
5
10
15
20
25
coral reef
rocky reef
macroalgae bed
sand/ rubble bed

Figure 5

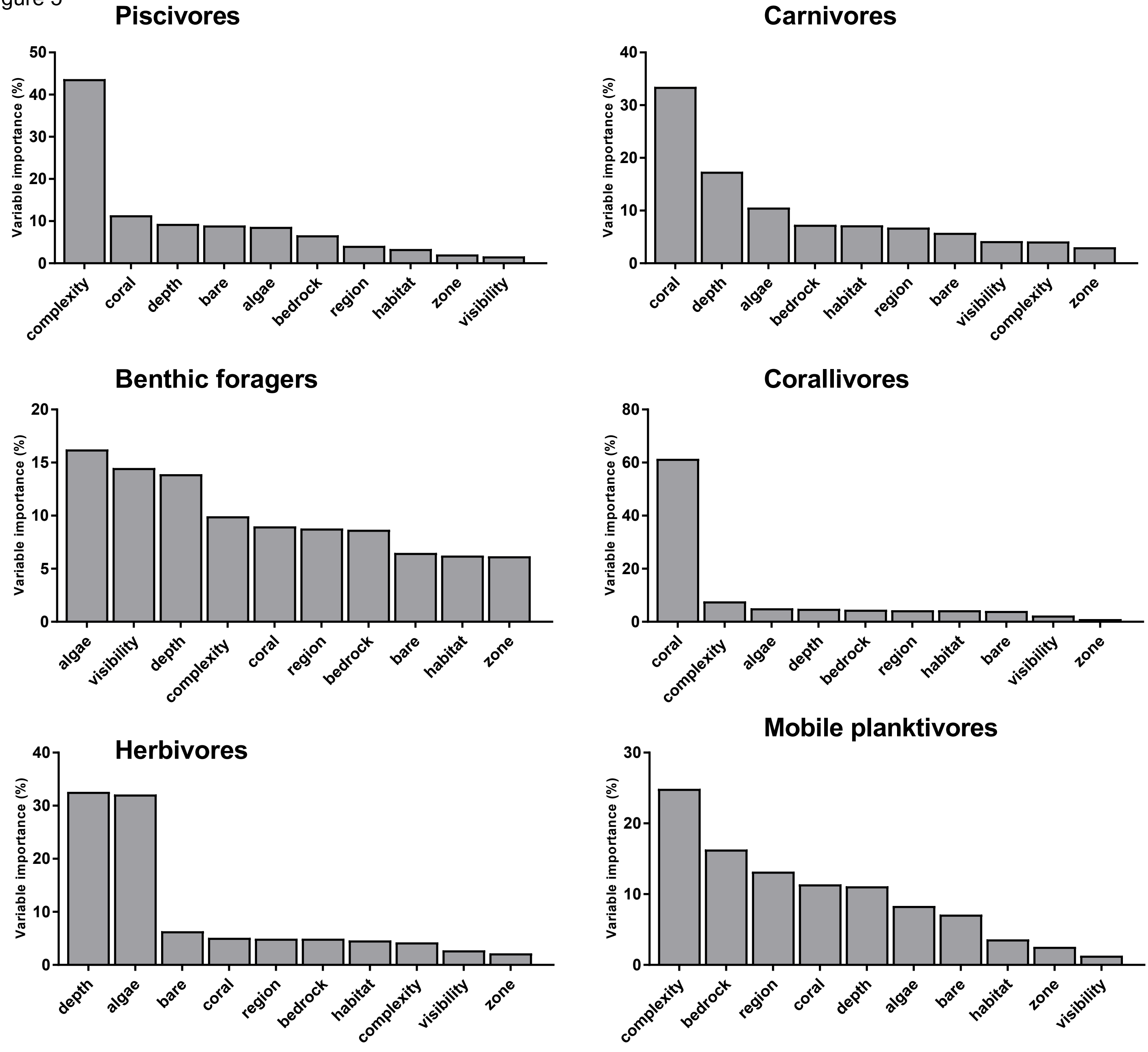
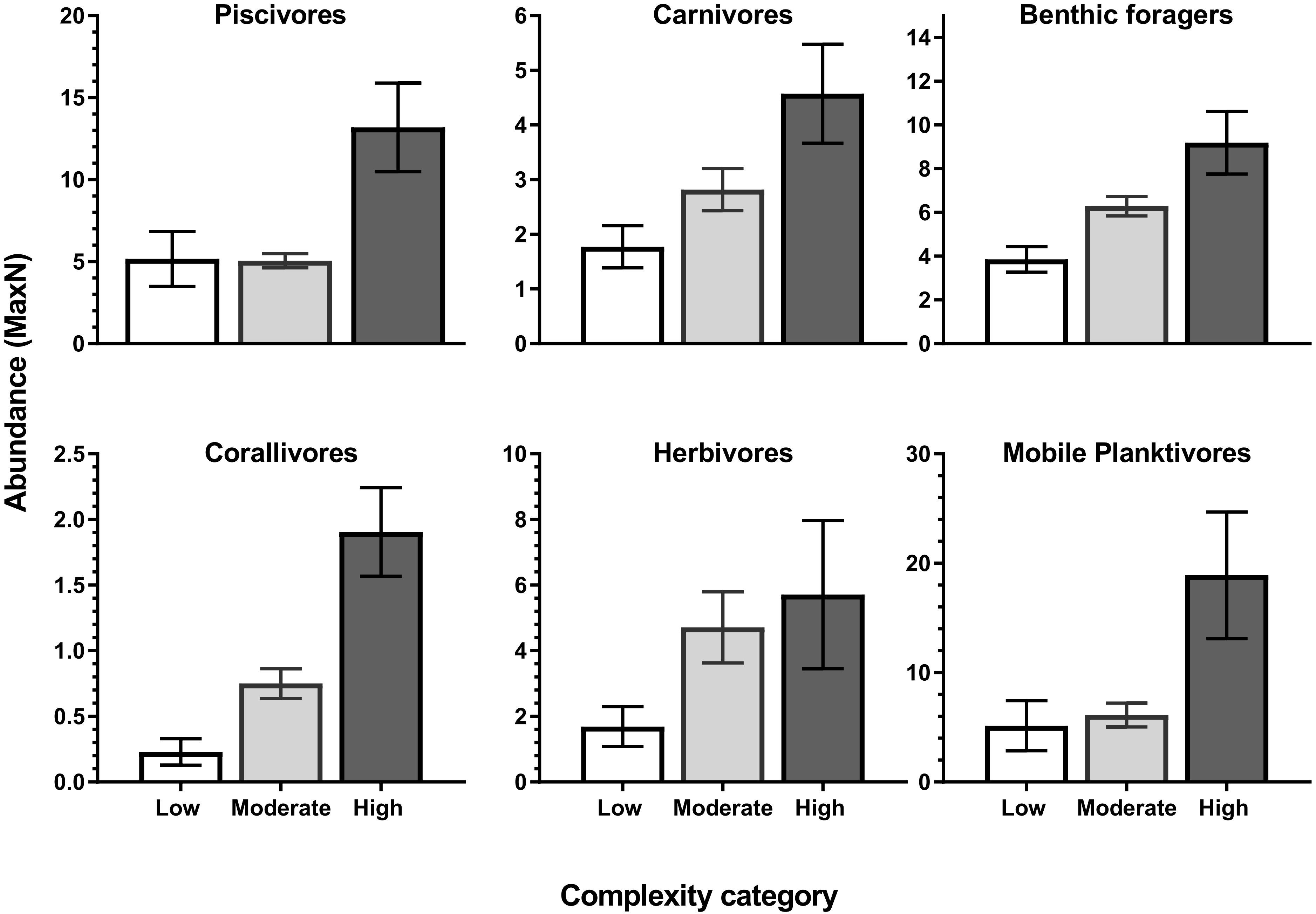
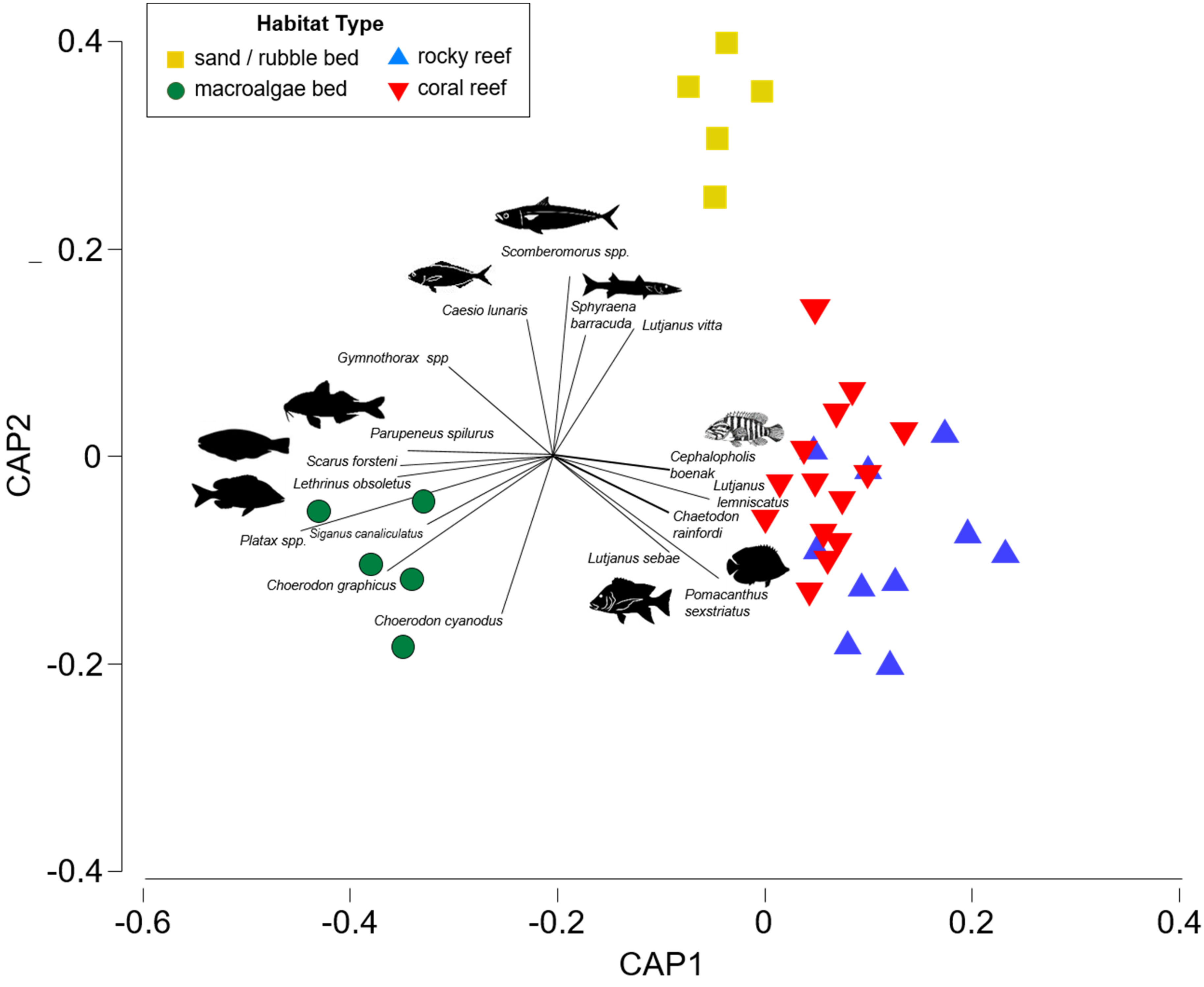

Piscivores
Variable importance (%)
0
10
20
30
40
50
complexity
coral
depth
bare
algae
bedrock
region
habitat
zone
visibility
Carnivores
Variable importance (%)
0
10
20
30
40
coral
depth
algae
bedrock
habitat
region
bare
visibility
complexity
zone
Benthic foragers
Variable importance (%)
0
5
10
15
20
algae
visibility
depth
complexity
coral
region
bedrock
bare
habitat
zone
Corallivores
Variable importance (%)
0
20
40
60
80
coral
complexity
algae
depth
bedrock
region
habitat
bare
visibility
zone
Herbivores
Variable importance (%)
0
10
20
30
40
depth
algae
bare
coral
region
bedrock
habitat
complexity
visibility
zone
Mobile planktivores
Variable importance (%)
0
10
20
30
complexity
bedrock
region
coral
depth
algae
bare
habitat
zone
visibility

Figure 6



Piscivores
Carnivores
Benthic foragers
Corallivores
Herbivores
Mobile Planktivores
Abundance (MaxN)
Complexity category
Low
Moderate
High
0
5
10
15
20
0
1
2
3
4
5
6
0
2
4
6
8
10
12
14
0.0
0.5
1.0
1.5
2.0
2.5
0
2
4
6
8
10
0
10
20
30

Figure 7



Habitat Type
🟨 sand / rubble bed
● macroalgae bed
▲ rocky reef
▼ coral reef
Scomberomorus spp.
Caesio lunaris
Sphyraena barracuda
Lutjanus vitta
Gymnothorax spp
Parupeneus spilurus
Scarus forsteni
Lethrinus obsoletus
Platax spp.
Siganus canaliculatus
Choerodon graphicus
Choerodon cyanodus
Cephalopholis boenak
Lutjanus lemniscatus
Chaetodon rainfordi
Lutjanus sebae
Pomacanthus sexstriatus
0.4
0.2
0
-0.2
-0.4
CAP2
-0.6
-0.4
-0.2
0
0.2
0.4
CAP1

Supporting information Table S1

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	*Acanthurus*	*blochii*	Herbivore (grazer / detritivore)	x	x	x	x	103
Acanthuridae	*Acanthurus*	*dussumieri*	Herbivore (grazer / detritivore)	x				1
Acanthuridae	*Acanthurus*	*grammoptilus*	Herbivore (grazer / detritivore)	x			x	4
Acanthuridae	*Acanthurus*	*spp.*	Herbivore (grazer / detritivore)	x	x		x	29
Acanthuridae	*Ctenochaetus*	*spp.*	Herbivore (grazer / detritivore)	x	x			5
Acanthuridae	*Naso*	*spp.*	Herbivore (browser)	x	x	x	x	25
Acanthuridae	*Naso*	*unicornis*	Herbivore (browser)	x	x			3
Balistidae	*Abalistes*	*spp.*	Benthic forager	x	x	x	x	8
Balistidae	*Pseudobalistes*	*flavimarginatus*	Benthic forager	x			x	2
Balistidae	*Pseudobalistes*	*spp.*	Benthic forager			x		1
Balistidae	*Sufflamen*	*spp.*	Benthic forager		x			1
Belonidae	*Tylosurus*	*spp.*	Piscivore			x		1
Caesionidae	*Caesio*	*caerulaurea*	Mobile planktivore	x	x			96
Caesionidae	*Caesio*	*cuning*	Mobile planktivore	x	x	x	x	819
Caesionidae	*Caesio*	*lunaris*	Mobile planktivore			x		40
Caesionidae	*Caesio*	*spp.*	Mobile planktivore	x	x	x	x	113
Caesionidae	*Pterocaesio*	*marri*	Mobile planktivore	x				1
Caesionidae	*Pterocaesio*	*spp.*	Mobile planktivore				x	45
Carangidae	*Atule*	*mate*	Mobile planktivore	x	x	x		57
Carangidae	*Carangoides*	*ferdau*	Benthic forager	x	x		x	8
Carangidae	*Carangoides*	*fulvoguttatus*	Piscivore				x	1
Carangidae	*Carangoides*	*gymnostethus*	Carnivore		x	x		42
Carangidae	*Carangoides*	*oblongus*	Carnivore		x			1
Carangidae	*Carangoides*	*plagiotaenia*	Carnivore	x				1
Carangidae	*Carangoides*	*spp.*	Carnivore	x	x	x	x	6
Carangidae	*Caranx*	*ignobilis*	Piscivore			x	x	4
Carangidae	*Caranx*	*lugubris*	Piscivore		x		x	2
Carangidae	*Caranx*	*melampygus*	Piscivore	x	x	x	x	47
Carangidae	*Caranx*	*papuensis*	Piscivore			x	x	14
Carangidae	*Caranx*	*spp.*	Piscivore	x	x			4
Carangidae	*Pseudocaranx*	*dentex*	Benthic forager			x	x	3
Carcharhinidae	*Carcharhinus*	*amblyrhynchos*	Piscivore	x			x	2
Carcharhinidae	*Carcharhinus*	*leucas*	Piscivore		x			1
Carcharhinidae	*Carcharhinus*	*limbatus*	Piscivore		x			1
Carcharhinidae	*Carcharhinus*	*melanopterus*	Piscivore	x	x	x	x	27

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

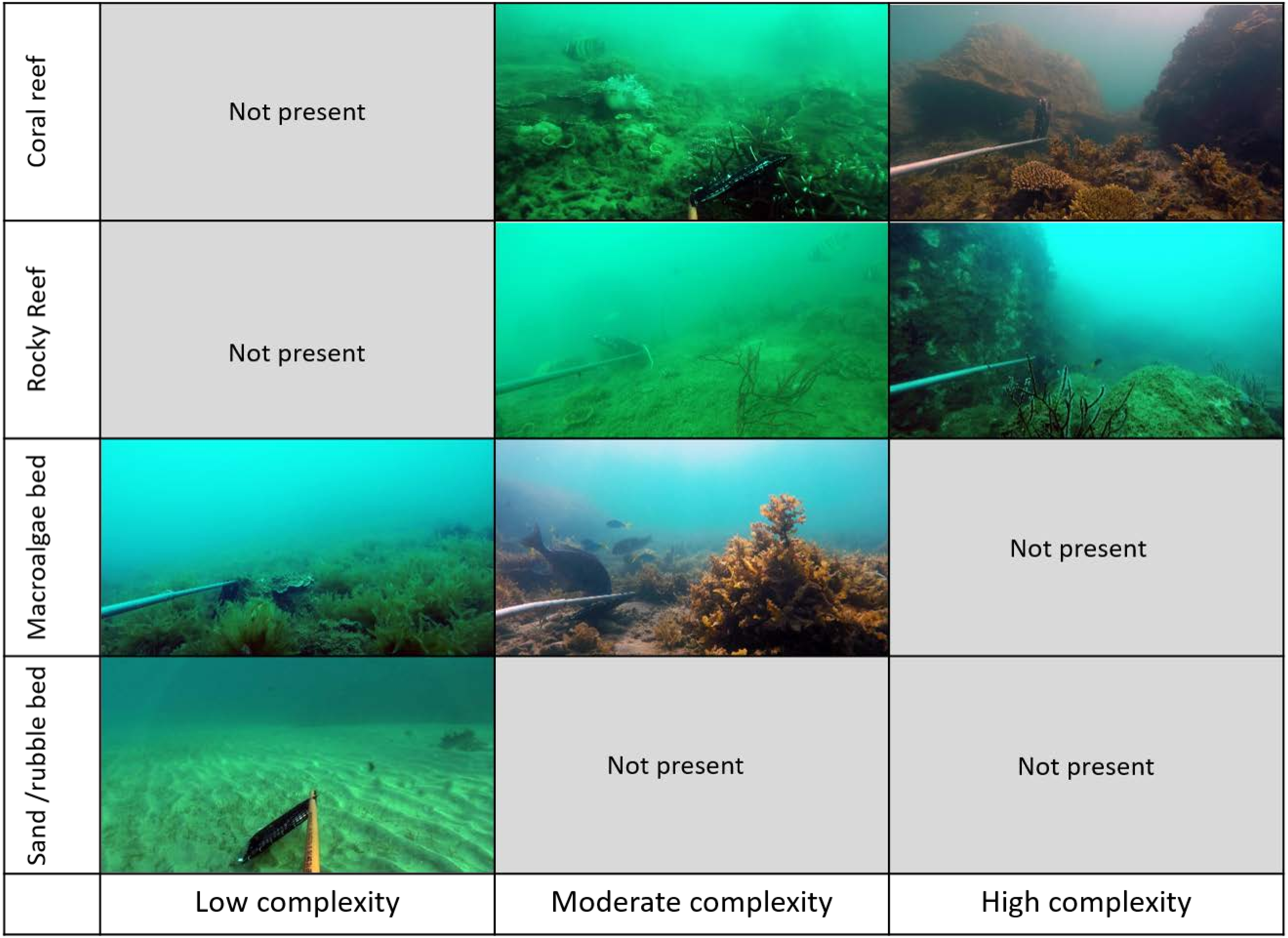
Family	Genus	Species	Trophic group	Occurrence by habitat type				Total Max N
				R	C	S	M	
Labridae	*Cheilinus*	*fasciatus*	Benthic forager	x	x		x	7
Labridae	*Cheilinus*	*trilobatus*	Benthic forager		x			2
Labridae	*Cheilio*	*inermis*	Benthic forager				x	1
Labridae	*Choerodon*	*anchorago*	Benthic forager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

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

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

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

Supporting information Figure S1



Supporting information Figure S2