



# Coral reef pinnacles act as ecological magnets for the abundance, diversity and biomass of predatory fishes

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**ABSTRACT:** Predation is a key ecological process regulating the structure and diversity of biological communities, yet predators do not exist homogeneously in nature. Coral reefs possess diverse assemblages of predatory fishes, the distribution and abundance of which is well documented for coastal and emergent reefs. However, for remote, isolated and submerged reefs, such as those found on pinnacles and seamounts, our understanding of predatory fish communities is limited. These features are ubiquitous in the world's oceans and frequently targeted by fishers for their presumed fish aggregation properties. Here we describe communities of predatory fishes on a series of pinnacle reefs and contrast these to regional coastal and offshore emergent reefs. Pinnacles supported 2–4× higher abundance, biomass and diversity of predatory fishes compared to emergent reefs. They also supported unique communities, with 32 out of the 63 predator species in our study found only on pinnacle reefs. For species found on all 3 reef types, all were most abundant on pinnacles and the 6 taxa driving differences in community structure were most abundant on pinnacles. Together, our results show that predatory fishes are strongly attracted to pinnacles, although the mechanisms are still unclear. Prioritising the selection of these small ecological magnets in conservation planning would be an effective approach to target the protection of regional reef fish biodiversity.

**KEY WORDS:** Pinnacle reefs · Predatory fishes · Ecological magnets · Biodiversity · Community ecology

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## 1. INTRODUCTION

Predation is one of the most important processes influencing the diversity and structure of ecological communities (Sih et al. 1985, Kerfoot & Sih 1987, Chase et al. 2002, Barbosa & Castellanos 2005). The presence of predators can limit the possibility of single-species monopolies in prey assemblages, promoting species diversity at lower trophic levels (Paine 1966, Menge & Sutherland 1976). On coral reefs, predation plays a major role in limiting prey

population sizes and determining the structure of diverse fish assemblages (Carr et al. 2002, Hixon & Webster 2002, Hixon & Jones 2005; also see reviews by Hixon 1991, 2015). Mechanisms by which this occurs may be directly via mortality or injury, or indirectly, where the presence of predators influences the condition (e.g. fecundity, growth) or behaviour of prey species (Beukers & Jones 1998, Bauman et al. 2019). Decreases in predation pressure typically benefit a small number of prey species, with a consequent reduction in overall diversity (Caley 1993), and

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when removed from coral reefs, the loss of important predator species has been shown to impact ecosystem structure and function (Dulvy et al. 2004, Rosenblatt et al. 2013, Boaden & Kingsford 2015). This is of pressing concern, as human exploitation of the world's oceans has resulted in declines in predatory fish abundance of up to 90% (Myers & Worm 2003).

Notable examples of overexploitation include the overfishing of large groupers throughout the Indo-Pacific region (Sadovy de Mitcheson et al. 2013) and reef-associated sharks globally (Rizzari et al. 2014, MacNeil et al. 2020, Dulvy et al. 2021). Even in isolated offshore reefs (e.g. Pacific Remote Islands Marine National Monument), significant declines in the abundance of predatory fish assemblages have been documented either due to exploitation or large-scale disturbances (Knapp et al. 2011, Carter et al. 2019). In the absence of exploitation, however, predatory fish are an abundant and diverse component of coral reef fish fauna (Sandin et al. 2008, Lester et al. 2009, Friedlander et al. 2010, Rizzari et al. 2014). The abundance and distribution of predatory fish vary across coral reef seascapes and are linked to a number of factors, including habitat type (Espinoza et al. 2014, Hall & Kingsford 2021), depth (Osuka et al. 2022) and topographic complexity (Gratwicke & Speight 2005, Lingo & Szedlmayer 2006, Rogers et al. 2014). Habitat complexity is also important, not only in attracting predators, but in mediating their impact on prey assemblages (Hixon & Beets 1993, Beukers & Jones 1998, Almany 2004). However, our present knowledge of predatory reef fishes and the mechanisms that govern their abundance and distribution are largely based on studies from shallow coastal reefs. Understanding predator assemblages across the spectrum of connected habitats and reef types they occupy is a key step in elucidating the ecology of these organisms and predicting future responses to anthropogenic pressures across whole coral reef seascapes.

One type of understudied coral reef habitat includes submerged features, such as pinnacles and seamounts. These structures are defined as isolated elevations of the sea floor, over which the depth of water is relatively shallow but sufficient for navigation and have shallowest points below 10–20 m (Galbraith et al. 2021). Despite being ubiquitous in the world's oceans, seamounts and pinnacles are poorly described within coral reef seascapes and yet may provide substantial quantities of physical habitat for coral-associated organisms (Harris et al. 2013, Moore et al. 2017). Coral reef habitat on pinnacles and seamounts differs in form and structure from commonly accepted models of coral reefs, with these reefs lack-

ing traditionally described geomorphological zones such as a reef flat or lagoon (Goreau 1959, Done 1982, Roberts et al. 2015, Galbraith et al. 2021). Instead, coral reef habitat on these structures is exposed to the pelagic environment on all sides, essentially composed entirely of reef crest and slope. Estimates of global numbers of seamount-type features range from 100 000 to 25 million (Wessel et al. 2010) and coral reefs can form networks of habitat patches on the summits of pinnacles and seamounts in tropical oceans. Examples of such networks include the seamounts of the Coral Sea between Australia and New Caledonia (Ceccarelli et al. 2013), the Vitória-Trindade chain off the coast of Brazil (Guabiroba et al. 2022) and seamounts of the Hawaiian Archipelago (Sinniger et al. 2013). Yet, despite this habitat potential, relatively few studies have been conducted on seamount and pinnacle reefs globally. A literature search found that of the 36 789 papers on coral reefs published since 1965, only 204 included the term 'seamount', and 81 included the term 'pinnacle' (Web of Science core collection search conducted on 12 April 2022. Search terms: 'Coral reef' only; 'Coral reef' AND 'Seamount'; 'Coral reef' AND 'Pinnacle'. Date range: 1965–2022).

Like seamounts, pinnacles typically possess small summits with sheer sides descending to substantial depths through the mesophotic and into the aphotic zone (Galbraith et al. 2021). This abrupt topography exposes much of the benthos to open ocean currents, resulting in strong and variable local hydrodynamics, characterised by powerful upwelling and complex eddies (Lavelle & Mohn 2010, Rowden et al. 2010, Galbraith et al. 2022). Such conditions may provide an ideal setting for seasonal aggregations of predators around seamounts and pinnacles (Klimley et al. 2005). Recent work has shown that coral reef predator fishes on both pinnacle and atoll reefs may be overwhelmingly sustained by food webs with pathways originating in offshore pelagic sources, resulting in high abundance and biomass of predators where this occurs (Morato et al. 2010, Fontes et al. 2014, Leitner et al. 2021, Skinner et al. 2021). Pinnacle reefs also support highly diverse communities, despite the relatively small surface area available for coral reef organisms on their summits (Galbraith et al. 2021). These assemblages typically contain taxa also found in coastal reefs as well as unique species, not normally encountered on nearshore or emergent reef systems; thus, pinnacles may be important in both sustaining unique biodiversity as well as providing refuges for a variety of coral reef taxa. However, to date, there have been no studies that focus on the

abundance, diversity, biomass and structure of communities of predatory fishes on coral reef pinnacles.

The present study describes communities of predatory fishes on a series of submerged pinnacle reefs in a low-latitude coral reef system, Kimbe Bay, Papua New Guinea. Recent work from this region examined whole fish communities on these reefs and found them to support abundant and diverse fish assemblages (Galbraith et al. 2021). However, these patterns have not been explored specifically for predatory fishes, which were the conspicuous species driving overall community differences. The principal aim of the current study was therefore to describe predatory fish communities on the pinnacle reefs and to compare and contrast these with 2 shallow-water reef types common in the region: isolated offshore reefs and nearshore fringing reefs. We asked the following questions:

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

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

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

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

## 2. MATERIALS AND METHODS

### 2.1. Study site and survey design

This study was conducted in Kimbe Bay, West New Britain Province, Papua New Guinea. This large tropical embayment is located in the Southern Bismarck Sea in the south-east of the Coral Triangle (5° 30' S, 150° 05' E, Fig. 1a) and possesses a range of coral reef habitat types, including the 3 selected for this study: tracts of emergent nearshore reefs, emergent offshore reefs and submerged pinnacle reefs. We surveyed 4 reefs per habitat type (12 reefs in total) over 2 survey periods (in October 2018 and again in March 2019) (Fig. 1b).

Nearshore reef sites were all located within 5 km of the mainland on a network of fringing reef structures, which have shallow (~0–10 m) tops and extend along the length of the bay's shoreline. Offshore sites were also located on reefs with shallow tops; however, these were all in remote locations (between 9 and 25 km from the nearest landmass). These reefs rise from a deep geologic structure that encircles the outer portion of the bay (ca. 300 m deep, GEBCO Compilation Group 2019). The centre of this structure drops to ~600 m in the middle of the bay (Fig. 1c), and on the northern seaward side, it drops >1000 m to the South Bismarck Plate shelf. The pinnacle reefs in this study also rise from this structure but have summits at depths of 15–30 m. In order to standardise our survey depth, all transects were therefore conducted on reef slopes between 20 and 30 m and similar gradient slopes were selected on all reef types to account for reef slope aspect, which is known to affect coral reef fish assemblages (Jankowski et al. 2015, Moore et al. 2017, Oakley-Cogan et al. 2020). Fishing pressure is also known to reduce numbers of predator fishes on coral reefs (Jackson et al. 2001) and nearshore reefs in Kimbe Bay may experience substantial fishing pressure from nearby human populations. To account for this potential confounding effect, all 4 nearshore survey sites in this study were situated on reefs included in a locally managed marine area scheme, which prohibits fishing and gleaning (*sensu* Chapman 1987) on these reefs. Similarly, we used remote offshore reefs in order to incorporate sites which experience similar levels of isolation as the pinnacles (and thus distance from coastal fishing pressure), but with structural characteristics more similar to nearshore, fringing reef systems.

### 2.2. Data collection

High-definition stereo-video surveys were conducted along 30 × 5 m (150 m<sup>2</sup>) belt transects within the 20–30 m depth band. Pinnacle reefs are exposed to the pelagic environment on all sides, so on nearshore and offshore reefs, surveys were conducted only on exposed, windward slopes, in order to control for reef exposure. For each reef, 5 transects were conducted during each survey period (i.e. 10 per reef, 120 transects total). A diver-operated stereo-video system (SVS, SeaGIS, <https://www.seagis.com.au/>; see Fig. S1 in the Supplement at [www.int-res.com/articles/suppl/m717p143\\_supp.pdf](http://www.int-res.com/articles/suppl/m717p143_supp.pdf)) with 2 GoPro Hero-4 cameras was used to record

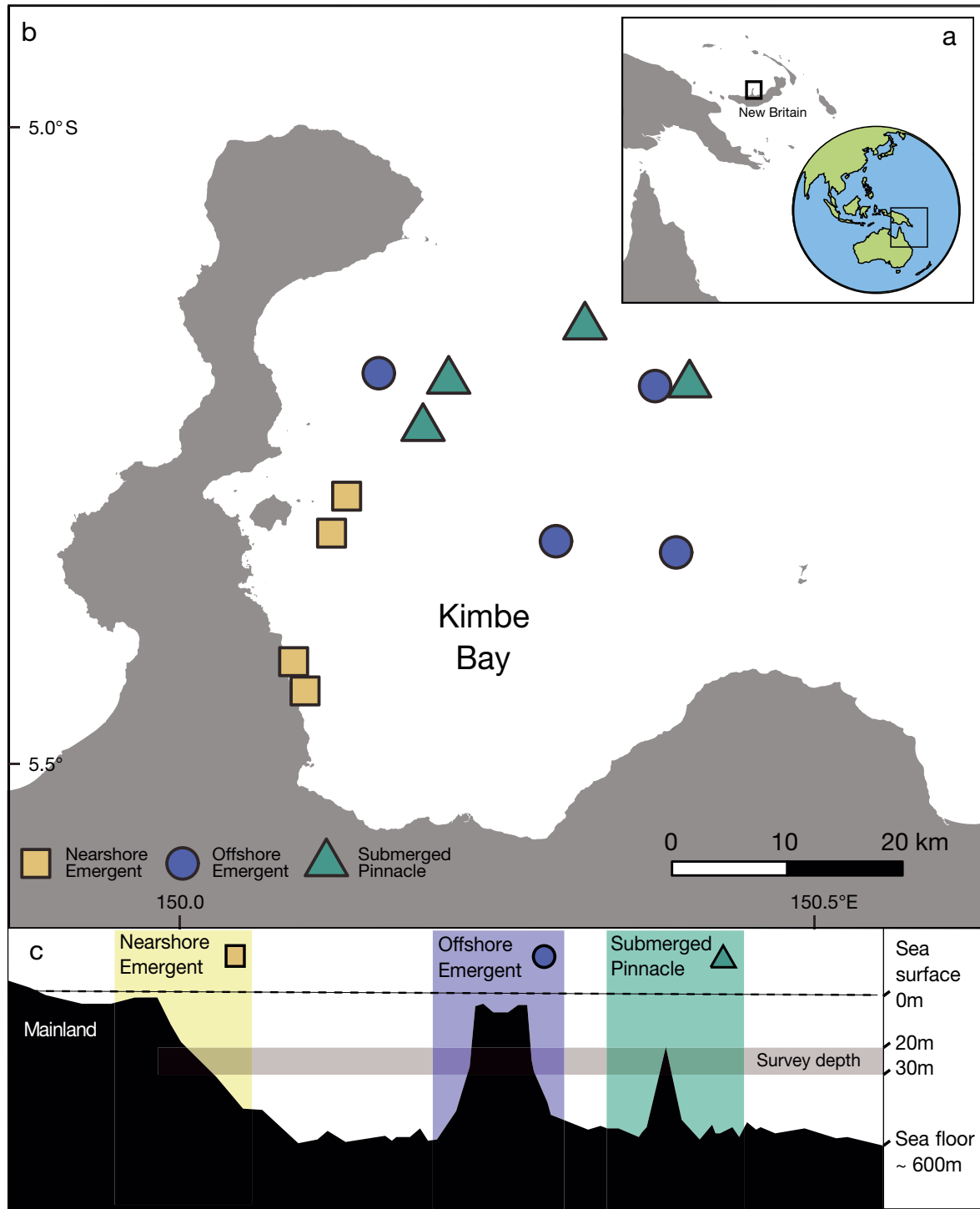


Fig. 1. Study area locations and visual representation of the seascape. (a) Kimbe Bay, situated in the Bismarck Sea on the north coast of the province of West New Britain, Papua New Guinea. (b) Focal sites include 4 nearshore emergent reefs, 4 offshore emergent reefs and 4 submerged pinnacles situated throughout Kimbe Bay. (c) Visual representation of the sea floor showing the 3 reef types and depth zone (20–30 m) surveyed

each survey (Goetze et al. 2019), with the diver maintaining an elevation of 0.5 m above the reef. A second diver followed with a transect tape and in-

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

### 2.3. Transect video processing

Fish transect videos were analysed using the software EventMeasure Stereo (SeaGIS), which uses camera geometric calibration to provide a known field of view (2.5 m either side of the transect, 5 m total) and allows accurate length measurements to be made. Every individual fish that entered the lower two-thirds of the screen was identified to species based on Allen et al. (2003), counted and a fork-length measurement made. Only individuals that were readily observable within these parameters were recorded. From all recorded fish observations, occurrences of predators were extracted.

### 2.4. Selection of predator taxa

Individual observations of fishes were considered predators on the following bases. Firstly, we included all species belonging to any of the following 9 families of known predatory fishes: Serranidae (groupers, Subfamily Epinephelinae only), Carangidae (jacks and trevallies), Carcharhinidae (requiem sharks), Scombridae (tunas and mackerels), Lutjanidae (snappers), Lethrinidae (emperors), Cirrhitidae (hawkfishes), Haemulidae (grunts/sweetlips) and Sphyrnidae (barracudas). In addition, other species were also selected that met the following 3 criteria extracted from FishBase (Froese & Pauly 2023): feeding guild = piscivore, trophic level  $\geq 3.7$  and max length (for species)  $\geq 30$  cm. This resulted in the inclusion of a further 6 species in the analysis: sling-jaw wrasse *Epibulus insidiator* (piscivore, trophic level 4.01, max length 54 cm), blacktip soldierfish *Myripristis botche* (piscivore, trophic level 4, max length 30 cm), cheeklined wrasse *Oxychelinus digramma* (piscivore, trophic level 3.7, max length 40 cm), teira batfish *Platax teira* (piscivore, trophic level 3.95, max length 70 cm), lunar tailed bigeye *Priacanthus hamrur* (piscivore, trophic level 3.82, 45 cm) and sabre squirrelfish *Sargocentron spiniferum* (piscivore, trophic level 3.80, 51 cm). Finally, 1 generalist carnivore with a high trophic level and very large maximum length was also included in the study: humphead wrasse *Cheilinus undulatus* (trophic level 3.99, 229 cm max length). In total, 63 taxa from 13 families from the wider Kimbe Bay fish community were included as predators in all subsequent analyses. A number of predator taxa that are known to exist in the region were not included (e.g. *Gymnothorax* spp.), as these were not recorded on any transect in our study.

### 2.5. Quantifying the effect of reef type

All analyses were performed in R version 4.0.3 (R Core Team 2020). All data exploration and graphic production were conducted using base R, the 'tidyverse' family of R packages (Wickham et al. 2019) and 'arsenal' (Heinzen et al. 2021). Generalised linear mixed effects models (GLMMs) were constructed using the package 'glmmTMB' (Brooks et al. 2017a) to measure the effect of reef type on the abundance, biomass and diversity of predatory reef fishes. GLMM diagnostics were performed using the 'DHARMA' package (Hartig 2022) to assess the assumptions of the model including homogeneity of variance, dispersion and outliers, and additional checks for zero inflation. Model selection was informed from Akaike's information criterion (AIC) using the 'AIC' function in base R. Tukey post hoc pairwise contrasts and 95% confidence intervals in estimated marginal means were calculated using the package 'emmeans' (Lenth 2021) and are reported as either a contrast size (in the measurement units) or as a ratio between reef types.

### 2.6. Abundance and biomass

Animal abundance (or, strictly speaking, density when measured as numbers per unit of area) was extracted from the video as numbers of individual predator fishes observed per transect ( $n = 150 \text{ m}^{-2}$ ). From the recorded fork lengths, biomass for each individual fish observation was calculated using the length-weight equation:

$$W = aL^b \quad (1)$$

where  $L$  represents fish fork length (cm),  $W$  is weight (g), and  $a$  and  $b$  are species-specific constants obtained from FishBase (Froese & Pauly 2023) using the R package 'rfishbase' (Boettiger et al. 2012). Transect biomass totals were then calculated as  $\text{kg } 150 \text{ m}^{-2}$ .

Variation in predator fish abundance and biomass across reef types was assessed using GLMMs, with reef type as the fixed effect and individual reef in each survey period as the random effect to account for temporal and site-specific variation in the presence of predators. Prior work in our study system has reported large variation in whole-fish assemblages across the seascape, with some reefs supporting very small numbers of fishes (Galbraith et al. 2021). In order to model predator abundance and biomass as a proportion of this, abundance and biomass of

whole fish assemblages were included in both models as a log offset term (Zuur et al. 2008, Brooks et al. preprint <https://doi.org/10.1101/132753>). For abundance, a negative binomial residual distribution was selected for the final model, and for biomass, a Tweedie distribution was selected, both with log-link functions.

## 2.7. Diversity

The Shannon-Wiener index was used to quantify diversity ( $H$  150 m<sup>-2</sup>) since it accounts for both the number and evenness of species present while being sensitive to the presence of rare taxa (33 species in our study had total bay-wide observations of 4 or fewer). Species richness was considered as a diversity metric but was not included, as it does not account for evenness of distribution. Simpson's index was also considered but not included for the related reason that it penalises rarity and attributes any survey with 0 observations a score of 1 (21 of the 120 transects across our study had 0 observations of predatory fishes). Differences in diversity were assessed using GLMMs with the same fixed and random effect as above. A Tweedie distribution was selected for the final model.

## 2.8. Assemblage composition

In total, 21 transects from offshore and nearshore reefs contained no observations of predators, so an analytical approach that is robust to large numbers of zero observations was required. The package 'mvabund' (Wang et al. 2022) was therefore used to assess multivariate differences in predator assemblage composition between reef types. The 'manyglm' function of this package was used to fit a multivariate generalised linear model (GLM). As the underlying data were count data, both Poisson and negative binomial distributions were tested for fit. Model diagnostics were conducted using the functions 'plot.manyglm' (to produce residual vs. fit- and QQ-plots) and 'meanvar.plot' (to check mean-variance relationships). Model fits were also compared with AIC using the 'AIC' function in base R. The negative binomial model was selected for pairwise multivariate comparisons, which was conducted using the 'anova.manyglm' function.

It is not possible to include random effects in 'manyglm'; however, reef site was accounted for as a random factor in the model by using probability inte-

gral transform (PIT) residual bootstrapping (aka PIT-trap resampling, Warton et al. 2017) in the package 'permute' (Simpson 2022). Multivariate models from 'mvabund' produce likelihood ratio test (LRT) statistics and corresponding permutation p-values, both for multivariate pairwise comparisons (i.e. between reef types) and for univariate scoring of species' contributions to overall differences. The latter were drawn from the model by including the term  $p.uni = 'adjusted'$ , which corrects p-values to control the family-wise error rate across species, using a resampling-based multiple testing procedure (Westfall et al. 1993).

Differences in assemblage composition across reef types were visualised using non-metric multidimensional scaling (NMDS) in the package 'vegan' (Oksanen et al. 2022). A constant fraction (0.001) was added to all species observations, to allow the inclusion of transects with zero predator observations. Species scores were overlaid for taxa identified as significantly driving differences in the multivariate model and alpha and beta diversity were visualised using the package 'ggvenn' (Yan 2023). Differences in abundance for taxa significantly driving assemblage composition were visualised in point and line plots using 'ggplot2' (Wickham et al. 2019).

## 3. RESULTS

In total, 2560 predatory fishes representing 63 different taxa from 13 families were observed over 120 transects on 12 reefs in Kimbe Bay. From these data, we explored the effect of reef type (submerged pinnacle reefs, offshore emergent reefs and nearshore emergent reefs) on the abundance, biomass and diversity of predatory reef fishes, and investigated patterns of community composition across these habitats.

### 3.1. Abundance, biomass and diversity

The GLMMs provided evidence that pinnacle reefs supported a greater abundance, biomass and diversity of predatory fishes, although the strength of the effect of reef type depended on the indicator.

Mean predator numbers were significantly higher on pinnacles than on both nearshore and offshore reefs, while there was no observable difference in predator abundance between offshore and nearshore reefs (Fig. 2a,d; Table S1). On average, pinnacles supported 16.6 predators 150 m<sup>-2</sup> (95% CI [7.9–25.3]), compared to 5.4 (95% CI [2.4–8.4]) for offshore reefs and 5 (95% CI [1.9–8.1]) for nearshore reefs.



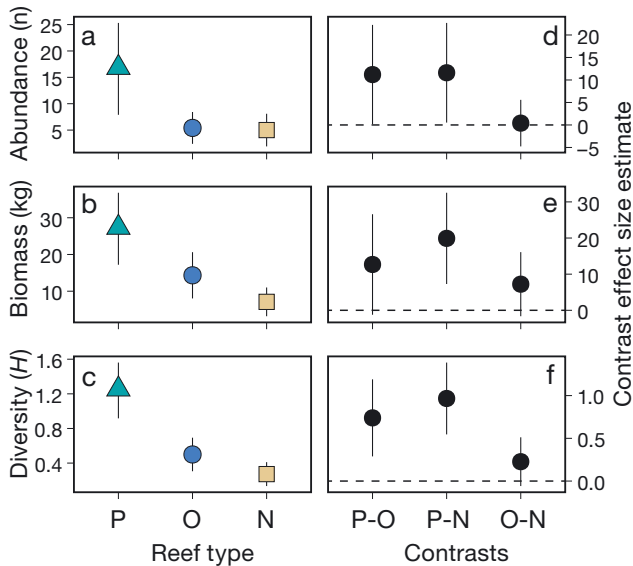


Fig. 2. Estimated marginal means ( $\pm 95\%$  CI) for (a) abundance ( $n\ 150\ m^{-2}$ ), (b) biomass ( $kg\ 150\ m^{-2}$ ) and (c) diversity (Shannon-Wiener  $H\ 150\ m^{-2}$ ). (d–f) Pairwise contrasts ( $\pm 95\%$  CI). CIs that cross the zero level are considered non-significant. P: Pinnacle reef; O: offshore reef; N: nearshore reef. Post hoc pairwise contrasts are P–O: pinnacle–offshore; P–N: pinnacle–nearshore; O–N: offshore–nearshore

Mean predator biomass also differed between reef types, with pinnacle reefs supporting  $27\ kg\ 150\ m^{-2}$  (95% CI [17.2–36.8]) compared to  $7.1$  on nearshore reef types (95% CI [3.2–11]) and  $19.9$  on offshore reef types (95% CI [7.3–32.5]). The greater biomass on pinnacle reefs compared to nearshore reefs was significant (biomass contrast ratio 3.8:1 (95% CI [1.73–8.37])), although the differences in biomass between pinnacles and offshore, or offshore and nearshore were not statistically significant (Fig. 2b,e; Table S2).

Similar patterns were found in the diversity of predatory reef fishes (Fig. 2c,f; Table S3), where mean Shannon diversity ( $H$ ) ranged from 0.27 to 1.24 per  $150\ m^2$  among reef types. Pinnacles supported a greater diversity of predatory fishes than offshore reefs ( $H$  contrast ratio: 2.48:1, 95% CI [1.42–4.34]) and nearshore reefs (4.54:1, 95% CI [2.30–8.98], Fig. 2c,f). Offshore reefs also had higher average diversity levels than nearshore reefs, although the magnitude of this effect was less than for pinnacle to other reefs ( $H$  contrast ratio: 1.83:1, 95% CI [0.85–3.93]).

### 3.2. Assemblage composition

Of the 63 predator fish taxa observed during this study, 53 (84%) were observed on pinnacle reefs and just 6 species were shared by all 3 reef types (Fig. 3b): *Carangoides bajad*, *Cephalopholis microprion*, *Lutjanus biguttatus*, *L. gibbus*, *Macolor macularis* and *Plectropomus oligacanthus* and all were most abundant on pinnacle reefs (Table 1). Pinnacles also had the largest number of unique species (32), while nearshore and offshore reefs had 4 and 2 unique species, respectively (Fig. 3b; Table S4). Ten taxa were not observed on pinnacles and the multivariate GLM identified significant differences in community composition between reef types (total multivariate LRT = 507,  $df = 119$ ,  $p = 0.02$ ), with the biggest pairwise difference being between pinnacle and nearshore reefs (LRT = 339,  $p = 0.001$ , Table 2).

The multivariate GLM also identified 6 species significantly driving these differences in community composition: *Sphyraena qenie* (LRT 31.07,  $p = 0.02$ ), *Caranx sexfasciatus* (LRT 32.01,  $p = 0.02$ ), *M. macularis* (LRT 58.08,  $p = 0.02$ ), *Caranx melampygus* (LRT 35.33,  $p = 0.02$ ), *L. gibbus* (LRT 23.61,  $p = 0.045$ ) and *Cephalopholis cyanostigma* (LRT 22.14,  $p = 0.045$ ). These taxa were all most abundant on pinnacle reefs, with the 2 *Caranx* species and *S. qenie* entirely absent from any survey on nearshore or offshore emergent reefs. The 2 lutjanid taxa were present across all reef types, although *M. macularis* was ca.

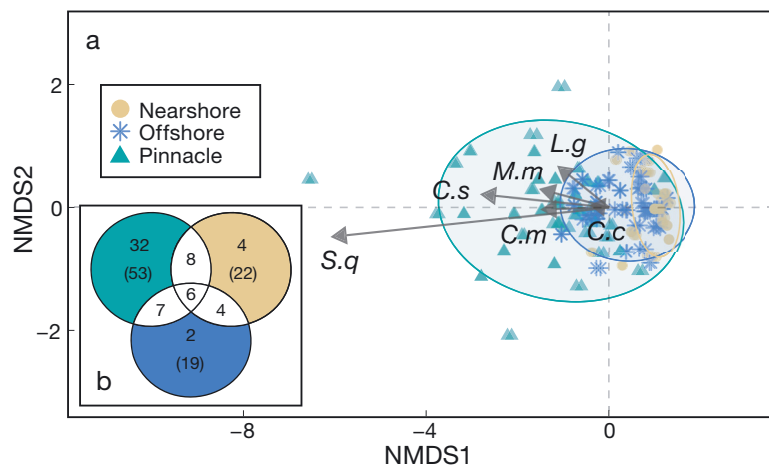


Fig. 3. Differences in assemblage composition across reef types. (a) Non-metric multidimensional scaling with 95% CI ellipses presented. Species loadings plotted for the 6 significant taxa identified in the multivariate generalised linear model: *Macolor macularis* (*M.m*), *Caranx melampygus* (*C.m*), *Sphyraena qenie* (*S.q*), *Caranx sexfasciatus* (*C.s*), *Lutjanus gibbus* (*L.g*) and *Cephalopholis cyanostigma* (*C.c*). Stress = 0.15. (b) Alpha and beta diversity (shared and unique taxa) across reef types. Numbers in parentheses are total numbers of species observed at each reef type

Table 1. Average predator fish abundance (numbers per 150 m<sup>2</sup>, ±SE) of the 20 most abundant species in this study. Taxa are sorted based on likelihood ratio test (LRT) scores and p-values from the multivariate generalised linear model. \*taxa significantly contributing to differences in assemblage composition; † taxa encountered across all reef types; †† taxa designated as planktivores, although literature suggests this is likely combined with piscivory for these species (Allen 1985)

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

4–100 times more abundant on pinnacle reefs than the other 2 reef types, while *L. gibbus* was 5–10 times more abundant. The serranid *C. cyanostigma* was not observed at all on nearshore reefs, and, while relatively rare on both other reef types, was nearly 50% more abundant on pinnacles than on offshore reefs (Table 2, Fig. 4). This broad pattern was also followed at the family level, with the pinnacle reefs supporting 6 predator families with representatives not found on the other 2 reef types. This included the only observations of reef sharks *Carcharhinus amblyrhynchos*, of which just 6 were observed on 2 of the pinnacles (Table S4). Members of the nocturnal families Holocentridae and Priacanthidae were also only observed on 1 pinnacle, Bradford Shoals. Neither nearshore nor offshore reefs had families not observed on pinnacle reefs. The multivariate visualisation identified the same pattern, with substantial separation of communities across reef types and species scores for the 6 significant taxa strongly aligning with the first NMDS axis (Fig. 3a).

#### 4. DISCUSSION

Our results highlight a strong effect of reef type on the abundance, biomass and diversity of predatory fishes in Kimbe Bay, Papua New Guinea and suggest that pinnacle reefs are particularly important in driving these patterns. Pinnacle reefs support significantly (2–4×) more abundant and diverse assemblages with higher biomass densities than nearby coastal and offshore emergent reef types. Predator assemblages were also distinct on pinnacles compared to those of emergent reef habitats, with over 50% of the taxa recorded across our study being observed only on pinnacle reefs. Similar accumulations of diversity and biomass have been reported for broader fish assemblages on the pinnacles used in this study (Galbraith et al. 2021) and for predator taxa on pinnacles and seamounts across the wider Indo-Pacific (Letessier et al. 2019). Overall, this suggests that offshore pinnacle reefs are biodiversity 'hotspots' for a range of spe-



Table 2. Pairwise contrasts in assemblage composition across all reef types. LRT: likelihood ratio test

Pairwise contrast	LRT	Adjusted p
Pinnacle vs. Nearshore	338.6074	0.001
Pinnacle vs. Offshore	268.4959	0.001
Offshore vs. Nearshore	87.0182	0.001

cies, including predatory fishes that are either resident on, or are attracted to and aggregate around these unique structures. Given the multiple lines of evidence emerging for these effects, we propose that pinnacle reefs may function as ‘ecological magnets’, concentrating both biota and associated ecological interactions across multiple trophic levels into small focal points, with the capacity to sustain large numbers of predators. The obvious conservation value of these habitats, in combination with small individual area and high potential for exploitation, highlights the need to incorporate pinnacle reefs into future management plans, with reducing fishing pressure and other human impacts a high priority.

While patterns in abundance, biomass and diversity among reef types were similar, the drivers of these may be different. The significant contrast in overall abundance (on average over 3× greater on pinnacle reefs) was in part due to substantial schools of barracuda (*Sphyraena* spp.) and trevally (*Caranx* spp.), neither of which were observed at nearshore or offshore emergent reefs. This was particularly noticeable at one pinnacle site (Bradford Shoals; Fig. S2), where schools of several hundred *S. qenie* markedly influenced overall abundance and biomass

patterns. For these and other similar species, pinnacles may be acting as sites of daily aggregations, with pelagic foraging potentially occurring elsewhere at night, although anecdotal evidence suggests that these 2 taxa may also be nocturnally active in the immediate vicinity of the pinnacles (B. J. Cresswell, G. F. Galbraith, H. B. Harrison & G. P. Jones pers. obs.). Other species of predatory fishes on pinnacles may be less likely to make substantial movements away from these structures, which are isolated from other coral reef habitat by many kilometres of distance and hundreds of metres of water depth. Despite this isolation, patterns of distribution and abundance were consistent across the whole predator assemblage: 19 out of the 20 most commonly observed species in our study were more abundant on pinnacles than on the other 2 reef types. Most of these were lutjanids and serranids, likely to have stronger habitat associations and smaller home ranges compared to the carangids and sphyraenids in this study, particularly when found on pinnacle reef summits (Afonso et al. 2016). Inclusion or exclusion of nocturnal species may also influence overall patterns in a study like this; however, overall numbers of such taxa were in single digits and unlikely to alter the patterns we observed.

Differences in predator biomass were similar to abundance. However, while pinnacles had the most overall biomass, there was also a 2-fold difference between offshore and nearshore reef types. The fact that the differences in biomass between pinnacles and offshore reefs were less striking than differences in abundance might be attributed to the high levels of diversity on the pinnacles, where we observed

numerous smaller-bodied lutjanid and serranid species that were either absent or less abundant on offshore reefs (e.g. *Pinjalo* spp. and *Cephalopholis* spp.). Such species may have been truly absent on offshore reefs or may have been more cryptic in these habitats compared to pinnacles and thus less likely to be detected during our surveys. As species are accumulated in survey counts, there is an increasing chance that this will be because of the inclusion of smaller, rarer and more cryptic taxa, rather than common or large-bodied species. As a consequence for the predator assemblages in our study, high abundance combined with high diversity may actually translate to relatively

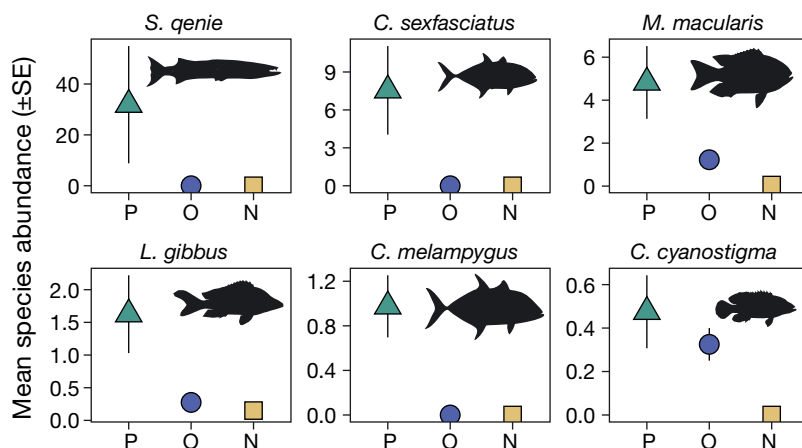


Fig. 4. Abundance (n 150 m<sup>-2</sup> [±95% CI]) of the 6 major taxa driving significant differences in predator assemblage composition between reef types. P: pinnacle reef; O: offshore reef; N: nearshore reef. Full species names are given in Fig. 3

lower observed biomass. A complementary explanation is that large-bodied predators, more commonly found on the pinnacles, may skew biomass estimates on these structures, although numbers of sharks observed across the entire study were low.

Diversity patterns across reef types were again similar, with the pinnacles supporting ca. 2–5× more predator fish diversity than offshore or nearshore reefs, respectively. Strong species–habitat linkages behind this trend are likely due to the presence of a range of unique or enhanced beneficial resources available on pinnacles. These may take the form of food, shelter, navigation or mating opportunities, each operating at different strengths across taxa and for specific life-history events or phases. The actual structure of pinnacles may also promote 2 other ecological phenomena that could enhance biodiversity. Firstly, pinnacle summits are small, which means their occupants must live in close proximity. Such proximity may increase competition, in turn promoting strong resource partitioning and high levels of assemblage diversity, or alternatively may promote positive species interactions between predator species that enhance prey detection and capture (Auster et al. 2013, 2019, Campanella et al. 2019). Secondly, the ‘conical’ shape of pinnacle summits means that a large amount of reef surface area is in contact with, and influenced by, surrounding ocean water, increasing the potential for edge effects on these habitats. Edge effects can promote diversity (Bellaver et al. 2023), particularly for small, isolated habitat patches (Ting & Shaolin 2008). Potential implications of high predator diversity on wider communities on pinnacles seem obvious: prey species must avoid a larger variety of predator taxa (‘diffuse predation’ sensu Hixon 1991). That whole fish assemblages on pinnacles are also the most diverse within Kimbe Bay (Galbraith et al. 2021) supports the concept of predation together with competition as interacting regulators of diversity at lower trophic levels, at least in our study system.

Differences in diversity were also reflected in the important differences in community composition between reef types. While this can be mainly attributed to variability in abundance of just 6 species identified by the multivariate GLM, only 6 other taxa were shared by all 3 reef types and, despite being relatively small, pinnacles possessed 32 unique species. However, the pinnacles also supported all but 10 out of the 63 taxa observed in this study. This number is reduced to 4 when offshore reefs are included, suggesting that the isolation and depth of both offshore and pinnacle reefs collectively provide a valuable

potential source of biodiversity refugia and, if used as spawning locations, an important larval resupply source for other reefs in the area. This may be particularly important for predatory fish populations and communities on shallow, nearshore reefs, which may be particularly impacted by localised anthropogenic disturbances such as overfishing, pollution and coastal development. Spatial differences in assemblage structure also have implications for overall seascape connectivity and diversity: organisms with restricted distributions (less than 10% of taxa were recorded on all 3 reef types) are less able to use the spectrum of otherwise available habitats in the course of their existence. Any local threat to such a taxon would directly translate to a seascape effect. Further, while gamma diversity may be high across our study system, correspondingly high levels of beta diversity may actually decrease functional redundancy among predators at a local scale and therefore in predation as an ecosystem process, a pattern observed in other trophic guilds of coral reef fishes (Bellwood et al. 2003).

Differences in benthic habitat, quality and complexity, as well as frequency and intensity of disturbances, are known drivers of diversity and abundance on coral reefs. However, recent work on the same reefs used in this study found no effect of variation in benthic composition on broad fish community structure (Galbraith et al. 2021). Rugosity, the number and size of holes, crevices and overhangs and reef aspect are additional benthic structural complexity measures which have been linked to reef-scale variability in fish communities, including predators (Hixon 2015, Agudo-Adriani et al. 2019). Alternatively, more detailed measures of habitat complexity and quality may therefore be needed to elucidate the relationships between fish communities and the types of reef habitat in our study system. Furthermore, site quality, prey availability and the presence of conspecifics are potential covariates and may confound the perceived effect of relatively simple habitat metrics such as total coral cover. Direct links between predatory fishes and benthic systems are likely more ambiguous over time and space (e.g. diurnal foraging behaviour (Papastamatiou et al. 2015, Williams et al. 2018)). Clearly, further study is warranted on dietary pathways and predation pressure to better understand links between predator fishes and benthic trophodynamics in these systems.

Movement of water at all scales is also a known driver of community ecology in coastal systems (Young et al. 2021) and seamounts or pinnacles (Klimley et al. 2005, Campanella et al. 2021, Bridges

et al. 2022). Recent work in our study system has demonstrated the importance of hydrodynamic forces in shaping wider biological communities (Galbraith et al. 2022) where pinnacles are characterised by strong ocean currents leading to localised upwelling and complex eddies. These same hydrodynamics may be particularly important for predator species: fishers and divers have long utilised local knowledge of currents, eddies and other water movement to inform where and when to seek out aggregations of charismatic predator species (Richert et al. 2017). Precisely what benefit such currents may provide to predatory fishes is yet to be described (but see Fisher et al. 2018); however, a growing body of work suggests that reef food webs that are exposed to allochthonous pelagic nutrient inputs may receive a substantial benefit from these. A recent study in the Maldives demonstrated that, for a number of coral reef predator taxa, trophic pathways with offshore pelagic origins are far more important in diets than local, reef-based sources (Skinner et al. 2021). These pathways may sustain wider fish productivity, even on degraded reefs (Morais & Bellwood 2019). Given that mobile predators themselves may act as vectors of nutrients from the wider pelagic environment onto coral reefs (Williams et al. 2018), where reefs host large numbers of these predator taxa, such nutrient inputs may be particularly important. Despite this, these inputs to coral reefs are often referred to as 'pelagic subsidies' or 'contributions' to 'nutrient cycling' (Papastamatiou et al. 2015, Morais & Bellwood 2019), but if these paradigms hold across a wide biogeographic area, the term 'pelagic-dominated sources' may be more appropriate.

Predator assemblages on coastal reefs of the region may be affected by extensive local agricultural activity and associated terrestrial runoff, which is known to promote high algal cover and smothering of the benthos with sediment (Beger & Possingham 2008). Both of these processes are characteristic of reef degradation and are potential drivers of altered fish communities (Fabricius 2005). Habitat degradation by coral bleaching events has also affected the reefs of Kimbe Bay over the past 2 decades (Jones et al. 2004) and recovery of reef communities from these bleaching events has varied, with reefs farther offshore showing greater ability to recover compared to those closer to terrestrial stressors (e.g. sedimentation from runoff) (Munday 2004). Relationships between benthic habitat dynamics and fish community structure can vary as a product of seascape position and temporal stochastic environmental change (Tsai et al. 2022).

Another explanation for low levels of abundance, diversity and biomass observed on nearshore reefs is the possibility of direct anthropogenic disturbance. The most obvious example of such disturbance is that of increased fishing pressure closer to shore. If present, the expected effect of this would be decreased numbers of certain fishery target species, but is less likely to account for the absence of over two-thirds of the taxa across our study (41 of 63 species) on coastal reefs. Additionally, we took steps to control for fishing pressure by using only nearshore reefs that are protected under the locally managed marine area scheme, established in 2007. This programme is widely regarded to be effective and the local communities are effectively engaged in enforcing protection on these reefs (Green et al. 2009). Conversely, both the pinnacles and offshore reefs may experience some degree of residual protection thanks to their remote and isolated settings. Offshore reefs with emergent crests may be easier to locate for the limited numbers of local fishers with the means of accessing these reefs such as power boats, while the pinnacles can only be located with GPS equipment. Given that both powered vessels and GPS technology are typically unavailable to subsistence and artisanal fishers of the region, fishing pressure alone is unlikely to explain differences in predator fish communities between these 2 reef types. The second form of direct anthropogenic disturbance that may be operating is altered fish behaviour (and thus presence or absence in our surveys) as a result of the presence of divers in the water (Dearden et al. 2010). Such an effect may have occurred during our surveys; however, it seems likely that this effect would have been similar across reef types, rather than differing between them, and likely affected cryptic taxa (Goetze et al. 2019), rather than the large-bodied predators that were the focus of this study. In addition, we aimed to use best practice methods for in-water surveys, including the use of a second diver to deploy transect tapes (Dickens et al. 2011).

In conclusion, our study reveals distinct patterns in predator fish abundance, diversity and community structure on pinnacle reefs and raises questions about why and how these habitats support unique communities of these organisms. Broadly, our results lend weight to international calls for protecting pinnacle and seamount structures as unique hotspots of biodiversity and commercially valuable predatory species (Pitcher et al. 2010, Richert et al. 2017, Watling & Auster 2017). Further work is required to better understand these unique systems, their biological communities and their broader ecological role in wider coral reef seascapes. From a conservation

perspective, large predatory fishes are clearly under considerable threat from extreme overfishing throughout the world's oceans (Myers & Worm 2003). Pinnacles represent quintessential 'biodiversity hot-spots' (sensu Myers 1988), where a large proportion of the abundance, biomass and diversity of predators is confined to small geographic areas. At an oceanic scale, pinnacles may be mere dots in the wider seascape, but they appear to function as ecological magnets for predatory fishes. While in one sense this makes them vulnerable, it also makes it possible to conserve a large proportion of species assemblages in relatively few and small marine protected areas. Such areas, however, must allow pinnacle reefs to remain unmarked in order to maximise their inherent safeguard against exploitation, namely isolation.

*Data availability.* See <https://github.com/bjccresswell/KimbePreds> for fully reproducible code, data and the results of the literature search.

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