

# Strong hydrodynamic drivers of coral reef fish biodiversity on submerged pinnacle coral reefs

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## Abstract

Hydrodynamic processes are important in all marine environments and on coral reefs drive patterns of habitat zonation, community structure, and biodiversity. Abrupt geomorphological features like pinnacles and seamounts often possess distinct localized currents and these habitats are also often characterized by high abundance and biomass of fishes. However, differences in fish community structure between pinnacles and emergent reefs, and their key drivers are poorly understood. In this study, we compared fish communities among emergent fringing and offshore coral reefs, and submerged pinnacle reefs in Papua New Guinea. Submerged pinnacles possessed higher fish biomass, abundance, and species richness than both fringing and offshore emergent reefs. We collected in-situ current speed and temperature data over a full year at each reef and used random forest analysis to investigate the relative influence of hydrodynamics compared to other well-established drivers of reef fish biodiversity, including habitat and biogeographic factors. Environmental variables explained 70%, 52%, and 5% of variability in models for species richness, abundance and biomass respectively. In all models, average current speed, current speed variability, and reef area were consistently among the most influential variables. Models examining relationships between fish biodiversity metrics and current speed did not yield conclusive results but did highlight the association of distinct hydrodynamic regimes on pinnacles with high fish richness, abundance, and biomass. Our study highlights the strong influence of reef-scale hydrodynamics on fish biodiversity and demonstrates the ecological value of small, submerged coral reefs, which are globally numerous yet remain understudied in coral reef ecology.

Hydrodynamic processes are a fundamental component of the environmental conditions on coral reefs, with movement of water closely linked to the physico-chemical gradients that drive the structure of reefs and their associated ecological communities (Monismith 2007; Lowe and Falter 2015). The

hydrodynamic mechanisms that influence coral reef communities include wave energy gradients (Williams et al. 2013), upwelling (Radice et al. 2019), internal waves (Wyatt et al. 2020), lagoonal flushing (Green et al. 2018), and thermoregulatory currents (Storlazzi et al. 2020). The nature, magnitude and effect of these processes varies considerably within and between reef habitats. For example, classical patterns of coral reef zonation are primarily driven by a gradient of surface wave energy that dissipates from the windward reef crest into the sheltered lagoon (Done 1983) and shelf position generates gradients in exposure between inshore and offshore locations (McClure et al. 2019; Robitzch and Berumen 2020). For coral reef fishes, hydrodynamics have been shown to affect community structure (Jouffray et al. 2019; Samoilyls et al. 2019), larval dispersal, and recruitment patterns (Sponaugle et al. 2002; Bode et al. 2019) and physiological and behavioral adaptations (Liao 2007; Binning and Roche 2015).

Depth, in conjunction with differences in reef geomorphology can also generate distinct hydrodynamic conditions (White et al. 2007; Leitner et al. 2021). However, as for the

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majority of ecological studies on coral reefs, most hydrodynamic studies are conducted on shallow, emergent (crest depth < 10 m), contiguous reefs and, predominantly focus on surface driven processes. Yet globally, there are significant areas of coral reef habitat on submerged bathymetric features (crest depth > 10–20 m; Bridge et al. 2012; Harris et al. 2013). This includes large banks, shoals and distinct detached patch habitats like seamounts and smaller but similar structures; pinnacles, “bommies” and knolls (Abbey and Webster 2011). Many of these submerged reef habitats are sites of enhanced productivity, generated by strong currents interacting with abrupt isolated topographies (Dower et al. 1992; Mohn et al. 2021). In turn, these habitats are often associated with abundant and diverse ecological communities, including coral reef fishes (Moore et al. 2017; Richert et al. 2017).

Numerous habitat and spatial variables are known to be important determinants of reef fish community composition, especially when investigating ecological drivers on different reef morphologies (Bennett et al. 2018; Samoilytė et al. 2019). In evaluating the role of hydrodynamics, it is therefore important to account for other well-established drivers of reef fish biodiversity. Hard coral cover, habitat structural complexity, and habitat area are explicitly positively linked to reef fish diversity (Bell and Galzin 1984; Gratwicke and Speight 2005), and declines in these habitat variables generate concurrent declines in the abundance of reef fishes (Jones et al. 2004; Wilson et al. 2006; Munday et al. 2008). However, the effects of habitat and reef structure on reef fish communities can vary among reef types, with remote and deeper reefs like pinnacles and seamounts often suggested to act as refuges from the effects of habitat loss and other disturbance (Lindfield et al. 2016; Letessier et al. 2019). Even if there is habitat loss on seamounts for example, high biomass and diversity of fishes may be sustained by enhanced biological productivity driven by strong biophysical-coupling in these habitats (Genin 2004; White et al. 2007).

Aspects of biogeography theory are also particularly pertinent to community structure on small, isolated patch habitats like pinnacles, with isolation often associated with lower diversity and/or more distinct community structures (Hobbs et al. 2012; Hachich et al. 2015; Pinheiro et al. 2017). However, although less isolated coastal fringing reefs represent well-connected contiguous habitats, they are also closer to terrestrial disturbances (e.g., pollution and fishing pressure; DeMartini et al. 2008; Brewer et al. 2012). Proximity to mainland therefore is also a factor that needs to be considered when assessing the drivers of reef fish community structure on pinnacles (Mora et al. 2003; Sandin et al. 2008; Williams et al. 2011). While hydrodynamics can remediate some of the effects of isolation from larvae supply at offshore reefs (Paris and Cowen 2004; Simpson et al. 2014) and the negative impacts of land-based run-off on inshore reefs (Fabricius 2011), these effects again vary depending on reef location and morphology (Jones 1997; Brodie et al. 2011). Given the potentially contrasting effects, it is important to

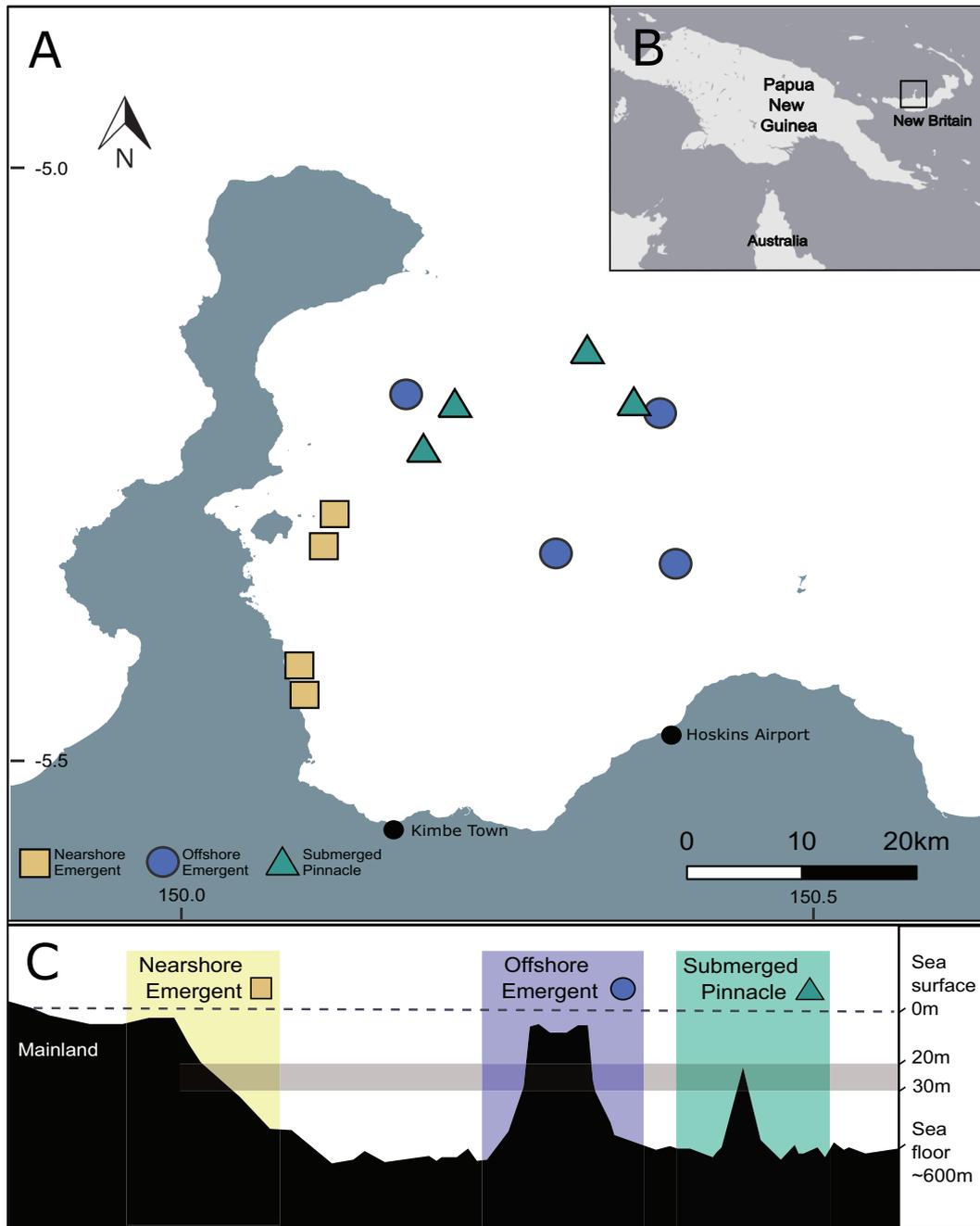
partition out the relative effects of hydrodynamics, habitat structure, and biogeographic factors in shaping communities on different reef formations.

The aim of this study was to establish the relative importance of hydrodynamics in shaping fish communities on morphologically distinct coral reef types, including nearshore and offshore emergent reefs and offshore submerged pinnacles. The study took place in Kimbe Bay, Papua New Guinea (5°30'S, 150°05'E), where these are the typical reef types and can be found in relatively close proximity (Fig. 1). In a recent study, we found that these pinnacles support distinct communities of fishes, with a significantly greater abundance and species richness compared to emergent reefs in both nearshore and offshore locations (Galbraith et al. 2021). In that study, both emergent and submerged reef morphologies were surveyed at the same depth (20–30 m) and we found that established habitat-based drivers of reef fish species richness, abundance, diversity and biomass (e.g., hard coral cover and benthic diversity) did not explain much of the variation in fish communities. This suggests that at the depths surveyed, other environmental factors are more influential in driving fish community structure. Following on from that work, this study investigated aspects of hydrodynamics as key drivers of fish biodiversity on emergent and submerged reefs below 20 m. We hypothesized that the distinct hydrodynamics found on submerged pinnacle coral reefs in Kimbe Bay support higher biodiversity than would be expected at small, isolated patch reefs. The specific objectives were: (1) To build on previous surveys of the same reefs to quantify fish biodiversity (species richness, abundance and biomass) and compare these metrics between the three distinct reef types. (2) Establish the relative influence of a combination of habitat, hydrodynamic and biogeographical variables on reef fish communities below 20 m. (3) Examine the nature of the relationship between fish communities and hydrodynamic variables and test for differences in these relationships between reef types. Current speeds and associated temperature regimes differ between emergent reefs and submerged pinnacle reefs in Kimbe Bay (Galbraith et al. 2022). We therefore expect that changes in magnitude of important hydrodynamic variables may result in different associations with fish species richness, abundance, diversity, and biomass.

## Methods

### Study area and sampling design

Kimbe Bay is a large tropical bay on the island of New Britain in the Bismarck Sea (5°30'S, 150°05'E, Fig. 1). The bay possesses a rich seascape including nearshore emergent fringing coral reefs, offshore emergent atolls and guyots as well as numerous submerged coral pinnacles (Green et al. 2007). Twelve reef sites were chosen for this study: four nearshore emergent reefs, four offshore emergent reefs, and four offshore submerged pinnacles. All emergent reefs had crests at depths above 10 m whereas submerged pinnacle crests were all deeper



**Fig. 1.** (A) Kimbe Bay and survey reefs; four offshore submerged pinnacles (green), four offshore emergent reefs (blue), and four nearshore emergent reefs (yellow). (B) Location of study site (outlined by black box) relative to mainland Papua New Guinea and Australia. (C) Schematic illustrating differences in morphology and crest depth between the three reef types.

than 15 m. All nearshore reefs were within 5 km from mainland coastline and all offshore reefs between 9 and 25 m from the nearest main landmass (Supporting Information Table S1).

## Data collection

### Fish and benthic surveys

To establish measures of fish and benthic community diversity at each reef, surveys were conducted on SCUBA in

October–November 2018 and April–May 2019. At each site, five replicate 30 m (length) by 5 m (width) belt transects were conducted along the horizontal contour of the reef within a depth band of 20–30 m. Fish communities were surveyed using diver-operated stereo-video (DOV) based on protocols described in Goetze et al. 2019. Briefly, the first diver swam a stereo-video system (SeaGIS Pty, Australia) housing two GoPro Hero 4 cameras pointing forwards at 0.5 m above the reef at a

steady speed (approx. 20 m/min). A second diver followed behind with a tape and signaled to the first diver when to end the transect. Both divers then returned along the transect, using another GoPro Hero 4 camera to conduct a video benthic point-intercept transect (Supplementary Fig. S1). The tape was marked with two random points every meter and the benthos directly under the tape filmed. Surveys were not conducted on steep slopes or walls. Near-horizontal ridges and low gradient slopes were selected at each reef to account for the effects of reef slope aspect which is a known driver of coral reef community differences (Jankowski et al. 2015).

### Video analysis

Fish survey videos were analyzed in the software EventMeasure Stereo (SeaGIS). Cameras used to conduct stereo-video surveys were calibrated before and after the surveys using a 3D calibration cube and CAL software (SeaGIS Pty, Australia). This allows for lengths of fish to be estimated within a known field-of-view (2.5 m either side of transect). For each transect every individual that entered the lower two-thirds of the screen was identified to species. Length estimates were made in EventMeasure using fork-length. If an individual could not be measured (e.g., too close to one camera) an average length for that species was applied. Visual surveys tend to underestimate counts of small, benthic-dwelling, or cryptic fish (Galland et al. 2017); therefore, these groups are not well represented in this present study.

Benthic video point intercept transects were played back at a slow frame rate and the benthic substrate directly beneath each point identified. The substrate was classified as one of 47 types based on taxonomic group and morphology (Supplementary Table S2). From this data, we then calculated benthic diversity (Simpson's  $D$ ), total hard coral cover (percentage), complex hard coral cover (percentage), and richness (number of substrate types) for each transect.

### Hydrodynamic data

To characterize current flow and thermal regimes at each site, Marotte HS Drag Tilt Current Meters (Marine Geophysics Laboratory, Australia) were installed at a fixed depth between 20 and 30 m depth during May–July 2018 (Supplementary Table S1). Current meters were installed on northerly sides of each reef at horizontal areas of reef where there were no surrounding obstacles to prevent free movement of the instrument. The current meters recorded temperature ( $^{\circ}\text{C}$ ), current direction (degree from north) and current speed ( $\text{cm s}^{-1}$ ) every 10 s during deployments. Current meters were recovered in September–October 2019, data downloaded and processed using the software MarotteHSConfig (<http://www.marinegeophysics.com.au/software/>). One current meter deployed at an offshore emergent site (Kimbe Island) was not successfully recovered during the study and consequently this site was removed from all further analysis.

### Selection of environmental variables

To compare the relative influence of hydrodynamic variables with other important environmental drivers of reef fish assemblage structure, we calculated 6 hydrodynamic variables using the data collected from current meters for the full study period (1 year). These were an annual daily mean, standard deviation, and maximum for both temperature and current speed at each site (Supplementary Table S3). We also derived seven other environmental variables relevant to reef fish ecology and the scale of our study; two biogeographical and five habitat-related. Distance to nearest neighboring reef (km) and distance to nearest mainland (km) were selected as biogeographical variables, measured in the GIS software QGIS (QGIS Development Team 2022, QGIS Geographic Information System, Open Source Geospatial Foundation Project; <http://qgis.osgeo.org/>). Average benthic diversity, benthic richness, total hard coral cover (%), and complex hard coral cover (%) were chosen as habitat variables and derived from the benthic video surveys at each site. The final habitat variable, reef area ( $\text{km}^2$ ), was calculated by conducting in-situ measurements of the submerged pinnacles and GIS spatial analysis QGIS for emergent reef area calculations. Further descriptions of all environmental variables and references pertaining to rationale for variable selection are presented in Table 1.

### Data analysis

All data analysis was conducted in R Studio (R Core Development Team 2023).

### Fish community structure metrics

Using counts and length measurements obtained from stereo-video analysis we calculated three metrics of fish community diversity for each transect: fish species richness ( $S\ 150\ \text{m}^{-2}$ ), abundance (total individuals  $150\ \text{m}^{-2}$ ), and biomass ( $\text{kg}\ 150\ \text{m}^{-2}$ ). Biomass was calculated using the length-weight equation:

$$W = aL^b$$

where  $L$  represents fish fork length (cm),  $W$  is weight in grams and  $a$  and  $b$  are species specific constants obtained from FishBase (Froese et al. 2013) using the R package “rfishbase” (Boettiger et al. 2012).

We compared mean fish community structure metrics between reef types with Generalized Linear Mixed Effects Models (GLMMs) using the package “glmmTMB” (Brooks et al. 2017) with data pooled from both survey years. Models for fish species richness and abundance were fitted with a negative binomial error distribution and log link and models for fish diversity and (log10) biomass were fitted with Gaussian error distribution and identity link. For all models, site was fitted as a random effect. Standard model diagnostics were performed for normality, homogeneity of variance and linearity

**Table 1.** Thirteen environmental variables used in random forest analysis, data source, range, units, and literature supporting selection rationale.

Variable	Description	Source	Range	Unit	Rationale and supporting literature
Biogeographical Nearest mainland	Distance to closest mainland coast	GIS	0.73–24.59	km	Isolation and connectivity-patterns of habitat fragmentation strongly influence reef fish communities both positively and negatively, e.g., increased distance from terrestrial/anthropogenic impacts but also other important marine habitats.
Nearest neighboring reef	Distance to closest area of coral reef	GIS	0.11–12.01	km	Isolation and connectivity-habitats closer to other sources of immigration and recruitment. Patch dynamics, fish movement between habitats.
Hydrodynamic Mean temperature	Daily mean (12-months)	Current meter	29.7–32.03	°C	Longer-term temperature trends critically determine species distributions to sites with values within tolerable thermal ranges. Potential metabolic effects on growth and biomass.
Mean current	Daily mean (12-months)	Current meter	3.89–8.88	cm s <sup>-1</sup>	Longer-term current speed trends may determine species distributions to sites with values within tolerable ranges. Species with physiological or behavioral adaptations to living in high currents.
Temperature variability (SD)	Standard deviation (12-months)	Current meter	0.47–1.16	°C	Energetic variability can influence population dynamics. Variability in sea temperature affects a number of important ecological processes that may affect fish community structure.
Current variability (SD)	Standard deviation (12-months)	Current meter	0.7–4.7	cm s <sup>-1</sup>	Energetic variability can influence population dynamics. High variability in current speed and a stochastic hydrodynamic environment may determine species distributions and enhance biophysical coupling.
Temperature maximum	Average daily maximum (12-months)	Current meter	31.2–35.2	°C	Thermal maxima are known to limit species distributions, metabolic processes and reef energetics. Annual average maximum define habitat suitability for some fishes.
Current maximum	Average daily maximum (12-months)	Current meter	9.13–60.30	cm s <sup>-1</sup>	Strong currents provide energetic costs and opportunities. Longer-term maximum current speeds define habitat suitability for some fishes.

(Continues)

**Table 1.** Continued

Variable	Description	Source	Range	Unit	Rationale and supporting literature
Habitat					
Hard coral cover	Percent cover of hard coral	Benthic video transects	6.67–71.67	% cover	Hard coral cover affects abundance of coral-associated species and increases habitat complexity. (Bell and Galzin 1984; Jones et al. 2004; Gratwicke and Speight 2005; Wilson et al. 2006; Messmer et al. 2011; Fahrig 2013)
Complex hard coral cover	Percent cover of complex hard coral	Benthic video transects	0–33.34	% cover	Higher complex coral cover and subsequently reef fish diversity, richness and abundance.
Benthic diversity	Simpson's D	Benthic video transects	0.62–0.89	D	Increased diversity of benthic habitat increases habitat complexity and subsequently reef fish diversity, richness, and abundance.
Benthic richness	Variety of different benthic groups	Benthic video transects	7–14	n	Increased variety of benthic habitat increases habitat complexity and subsequently reef fish diversity, richness, and abundance.
Reef area	Total area of reef habitat above 30 m depth contour	GIS emergent reef. In-situ measurements submerged pinnacles	0.00013–0.62	km <sup>2</sup>	Species-area and biogeography—larger areas of habitat support higher numbers of species, and individuals.

Hydrodynamic variables for current speed and temperature are means, standard deviations and maxima for the annual period (September 2018–September 2019).

using the “DHARMA” package (Hartig 2020). For each model, coefficient estimates and 95% confidence intervals (CI) were extracted and plotted including pairwise comparisons between estimates made using “emmeans” (Lenth 2020). Standardized partial effects are presented as ratio estimates where there is evidence to suggest a significant effect if the CI does not contain one.

### Relative influence of environmental variables on fish communities

Random forest (RF) models were used to assess the relative influence of 13 environmental variables on three univariate fish community metrics: species richness, abundance, and biomass. RF is a machine learning technique well suited to inherent issues of non-linearity and multicorrelation characteristic of ecological data (Breiman 2001). Additionally, RF is an effective approach when the numbers of observations are comparatively low compared to the number of predictors (Svetnik et al. 2003). Briefly, RF constructs an ensemble of multiple decision trees using bootstrapped random samples of the original data. The results are aggregated and the relative importance of each predictor on the response is scored based on its effect on mean squared error (MSE) i.e., factors with the greatest effect on MSE have the largest influence on the response (Breiman 2001). RF models were implemented in R using “RandomForestSRC” (Ishwaran and Kogalur 2022) with the default setting of 2/3 available data used to grow each tree and 1/3 data used for internal model validation (Liaw and Wiener 2002). RF model parameters *ntree* (the number of trees to grow) and *mtry* (the number of variables to consider at a given split) and node size were optimized for each model using the function “tune” within RandomForestSRC. An overall  $R^2$  value for each model generated and variable importance plots were generated based on percentage increased MSE. For each RF model, partial dependency plots for the effect on the response when all other variables are held constant were produced for the top four environmental predictors in each model.

### Relationships between fish community structure metrics and important hydrodynamic variables

Although partial plots from RF models are excellent visualizations of the general trends assessed in the model, they do not allow for detailed exploration of these relationships, particularly when trying to examine differences in a response between different groups.

We therefore used GLMMs to examine the relationships between the most important hydrodynamic variables identified by the RF analysis and fish community structure metrics. In each RF model, mean current speed was the most influential hydrodynamic variable. For each fish metric (richness, abundance and biomass) we constructed GLMMs using the package *glmmTMB* (Brooks et al. 2017). Each model contained an interaction effect between continuous fixed effects and the

categorical fixed effect “reef type” (three levels: “nearshore,” “offshore,” and “pinnacle”). “Site” was included in all models to account for potential differences between individual reef sites. The GLMMs for fish richness and abundance were fitted with a negative binomial error family and a log link. The GLMM for fish biomass fitted log<sub>10</sub> biomass with a gaussian error family and identity link. The range of mean current speed recorded differed substantially between the three reef types, therefore for all GLMMs current speed was centered individually for each reef type to fit the model and then back transformed for final interpretation. Model fit was assessed using standard diagnostic techniques for normality, homogeneity of variance and linearity using the “performance” (Lüdecke et al. 2020) and “DHARMA” (Hartig, 2020) packages. For each model, coefficient estimates and 95% CIs were extracted and plotted including pairwise comparisons between estimates made using the functions *emmeans* and *emtrends* from the package “emmeans” (Lenth 2020). Slope coefficients are presented as estimates on the response scale where the evidence suggests a significant effect if the CI does not contain zero. *r.squaredGLMM* from the “MuMin” package (Bartoń 2019) was used to calculate a pseudo-R-Square estimate (Nakagawa et al. 2017) which produces a marginal  $R^2$  (m) (an approximation variance explained by fixed effects) and a conditional  $R^2$  (c) (an approximation of variance explained by the entire model including fixed and random effects). All plots for GLMMs were created using “ggplot2” (Wickham 2016). All hydrodynamic and fish abundance, diversity, biomass and richness data are available at <https://doi.org/10.6084/m9.figshare.23972610.v1> (Galbraith 2023).

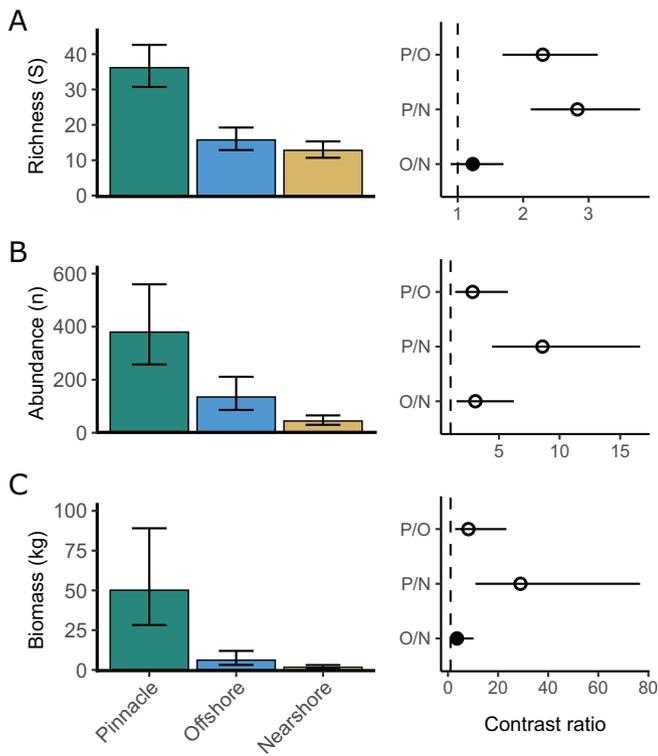
## Results

### Fish biodiversity

A total of 13,122 individuals representing 191 fish species were identified from the combined survey data. Pinnacle reefs had highest mean species richness ( $S = 36.19$ , 95% CI [33.72–42.63]), which was 2.3 times that of offshore reefs (95% CI [1.69–3.14]) and 2.8 times the mean richness of nearshore reefs (95% CI [2.11–3.78]) (Fig. 2A). The pinnacles also had highest total fish abundance of 379.66 individuals per  $150 \text{ m}^{-2}$  (95% CI [257.52–559.72]) (Fig. 2B) and highest total biomass of 50.13 kg  $150 \text{ m}^{-2}$  (95% CI [21.33–78.94]) (Fig. 2C). These results are consistent with a previous study conducted at the same reef sites (Galbraith et al. 2021).

### Relative influence of hydrodynamics and other environmental variables

Environmental variables differed considerably among reef types. Pinnacles are all smaller than other reef sites and were characterized by higher average current speeds, higher variability in current speed and lower temperatures (Supplementary Tables S1, S3). Offshore reefs experienced highest mean temperatures annually and are larger in area



**Fig. 2.** Estimated mean diversity metrics observed at each reef type and contrast ratios for pairwise comparisons. **(A)** Species richness ( $S$   $150\text{ m}^{-2}$ ); **(B)** Total abundance (individuals  $150\text{ m}^{-2}$ ); and **(C)** Total biomass ( $\text{kg}$   $150\text{ m}^{-2}$ ). Point ranges represent 95% CI where non-shaded points in contrast plots indicate significant pairwise differences.

than other reef types. Nearshore reefs were closest to other neighboring reefs, mainland, and had the lowest range in current speed, but the highest range in temperature. The other habitat-related variables did not differ substantially between reef sites or morphologies, but complex coral cover was generally higher at pinnacle reefs (8.2%, SEM = 2.9%) compared to offshore (1.2%, SEM = 0.5%) and nearshore (3.6%, SEM = 1.3%) sites (Supplementary Table S5).

The RF model for fish species richness ranked reef area, mean current speed, and current speed variability as the most influential factors (Fig. 3A,  $R^2 = 0.70$ ). Surprisingly, all other habitat related variables were among the least influential. Partial plots of the four most influential variables show that richness was lowest on reefs with larger areas (Fig. 3A.i) and higher on reefs with greater average current speeds (Fig. 3A.ii). There was an increasing trend in fish richness with annual current variability (Fig. 3A.iii) and increasing distance from nearest mainland (Fig. 3A.iv).

The RF model for fish abundance ranked mean current speed, current variability, reef area and distance to nearest mainland as the top four most important variables (Fig. 3D,  $R^2 = 0.53$ ). Increasing mean annual current speed (Fig. 3D.i) and mean annual current variability (Fig. 3D.ii) resulted in

increasing fish abundance whereas reef area demonstrated the same relationship as the richness RF model; smaller reefs had more fish (Fig. 3D.iii). Between 5 and 10 km from nearest mainland, abundance of fish increased sharply and peaked at around 15 km (Fig. 3D.iv).

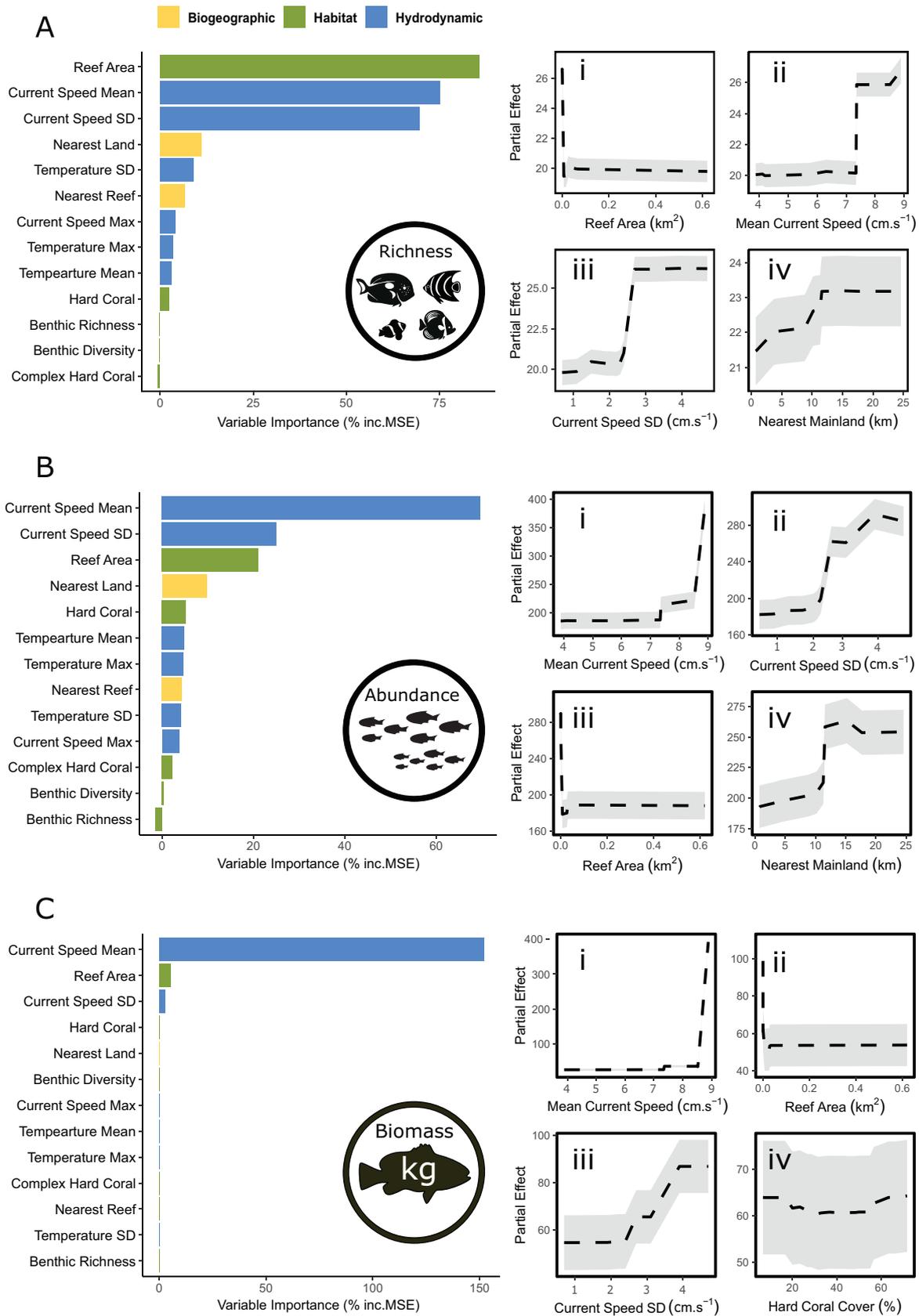
Hydrodynamic and habitat variables were most important in the final RF model for fish biomass (Fig. 3B) but the model explained relatively little variability in the data ( $R^2 = 0.05$ ). As for richness and abundance, mean current speed was the most influential variable, which showed a sudden increase in biomass at current speeds over  $8\text{ cm s}^{-1}$  and peak response at a flow of around  $8.5\text{ cm s}^{-1}$  (Fig. 3A.ii,B.i). Reef area was the second most influential variable, showing the same trend as richness and diversity; smaller reefs had greater fish biomass (Fig. 3C.iii). Current variability was the third most influential variable for biomass which showed a similar response to species richness; increasing annual current variability led to increased biomass (Fig. 3C.ii). Distance to nearest neighboring reef was the fourth most influential variable which showed a peak response in biomass at around 10 km which remained generally high with increasing distance (Fig. 3C.i). Model summaries and results from all RF models are presented in Supplementary Table S6.

### Effect of current speed on fish community structure metrics

The GLMM for fish species richness found no significant evidence of a significant effect of increasing current speed on pinnacles (slope estimate = 2.64, 95% CI [-7.50-12.78]) or offshore reefs (slope estimate = -1.84, 95% CI [-4.09-0.38]), but nearshore reefs showed a small positive trend (slope estimate = 3.09, 95% CI [0.70-0.55]). The overall model had an  $R^2_m = 0.73$  and  $R^2_c = 0.76$  (Fig. 4A, Supplementary Table S7). Pairwise tests of slopes confirmed that only nearshore and offshore reefs differed in the nature of response in fish richness to increasing current speed variability (offshore-nearshore slope contrast = -4.94, 95% CI [-8.22 - -1.67], Fig. 4A).

Mean annual current speed explained 63% of variability in the abundance GLMM ( $R^2_m = 0.63$ ,  $R^2_c = 0.78$ , Fig. 4B, Supplementary Table S7). At mean annual current speed at each reef type, pinnacles had 2.87 times the number of fish compared to offshore reefs (95% CI [1.11-7.17]) and 8.42 times the number of fish compared to nearshore reefs (95% CI [3.59-19.75]). However, we found no evidence to suggest that increasing mean annual current speed increased fish abundance on any of the three reef types.

The final model for fish biomass explained 59% of variability in biomass data ( $R^2_m = 0.59$ ,  $R^2_c = 0.74$ , Fig. 4C, Supplementary Table S7). At an average level of annual current speed variability, pinnacle reefs had 28.94 times the estimated biomass of fish compared to nearshore reefs (95% CI [7.05-118.84]) and 8.14 times that on offshore reefs (95% CI [1.77-37.42]). Offshore reefs also had 3.56 times estimated biomass than nearshore reefs (95% CI [0.77-16.35]). We



(Figure legend continues on next page.)

found no evidence for contrasting slopes between any of the three reef types (Fig. 4). Full model summaries and pairwise comparisons for all GLMMs of fish responses and current speed are reported in Supplementary Table S7.

## Discussion

Our study strongly suggests that the higher richness, abundance, and biomass of fishes on submerged pinnacles is largely driven by hydrodynamic processes. We found that mean current speed and the variability in these speeds explained a large amount of variation in fish diversity and biomass between the three different reef habitat types. Reef area was the only habitat variable to consistently rank highly in RF models and the nature of the relationship with fish metrics was always negative, i.e., the smallest reefs supported greatest fish biodiversity. Although hard coral was among the top five most influential variables for fish abundance and biomass, all other benthic habitat variables were constantly ranked as the least important in RF models. Of the biogeographic variables, distance to nearest mainland was in the top five most influential variables in all RF models, but did not represent a large proportion of the overall variable importance in any model (0.08% – 14.39% MSE). Distance to next neighboring reef did not rank highly in any model. There was no significant relationship between fish abundance and biomass with current speed, but there were contrasting responses between reef types for fish species richness. Overall, this suggests that the habitat-specific environmental conditions driving diversity patterns are themselves generated by the different reef morphologies at the depths studied.

These results contribute to growing evidence that pinnacles in tropical seas act as patches of ecologically important coral reef habitat, capable of supporting high species richness, abundance, biomass despite being smaller in size compared to larger, shallow coral reefs (Moore et al. 2017; Wagner et al. 2020; Leitner et al. 2021). This inverse relationship between all fish metrics and reef area is surprising, as ecological theory predicts that the smallest and most isolated reefs in our study (the pinnacles) should support the fewest species and individuals due to lower colonization rates. However, the direct effects of habitat area, isolation and spatial arrangement on species richness and abundance are difficult to disentangle as they usually co-vary and as such, the nature of these relationships can vary considerably (Ewers and Didham 2006; Bonin et al. 2011).

One potential explanation for the link between the hydrodynamic drivers and fish metrics in our study, is that site-specific hydrodynamic conditions increase resource availability within a small habitat area. The effect of this is

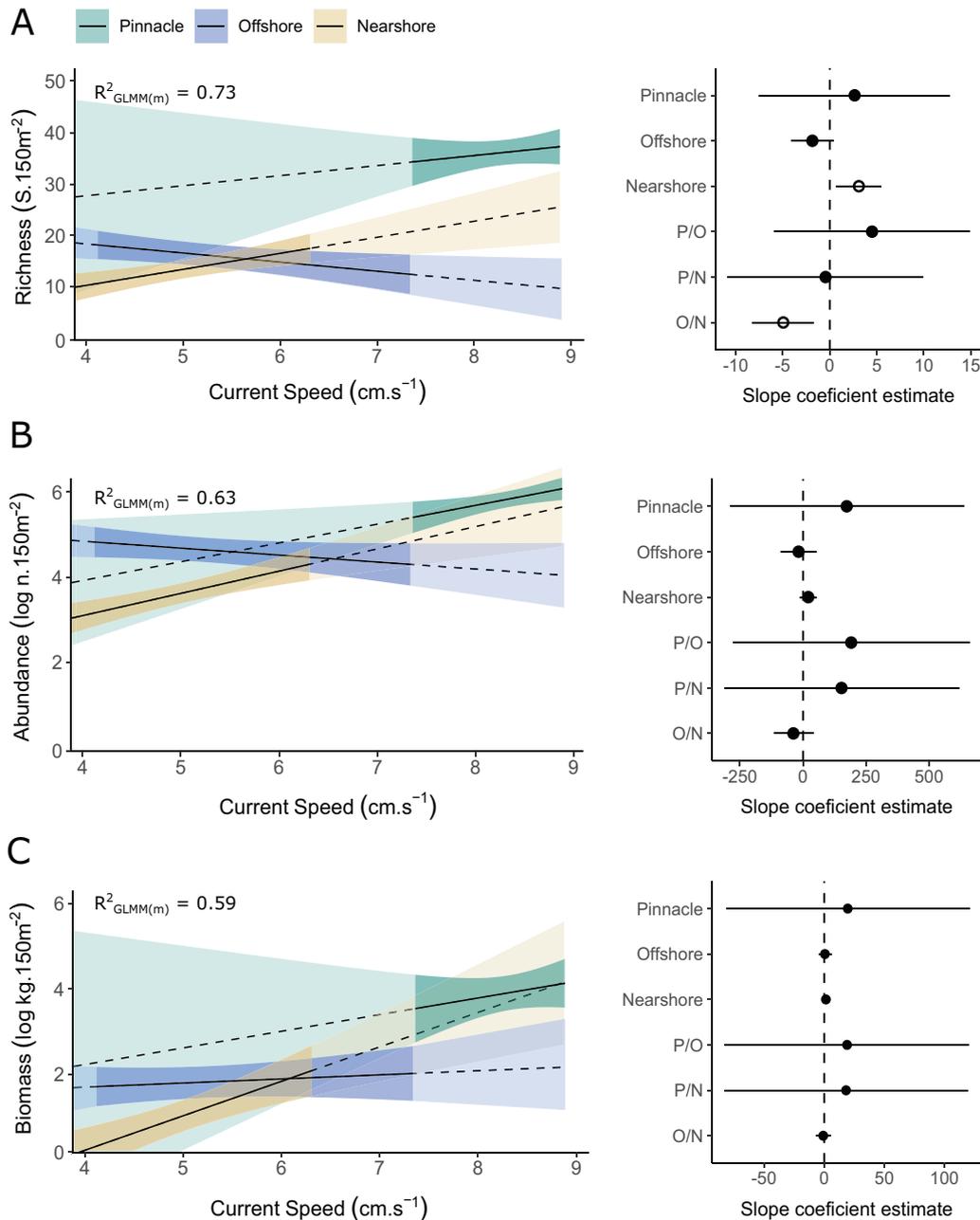
increased species richness and abundance through the provision of energy (Wright 1983; Carrara and Vázquez 2010). We suggest that these mechanisms are like the enhanced biophysical-coupling and energetic focusing found to occur on seamounts (White et al. 2007; Lavelle and Mohn 2010). The pinnacles in our study have been shown to possess distinct hydrodynamic regimes, characterized by markedly higher current speeds compared to the nearshore and offshore emergent reefs (Galbraith et al. 2022). Through localized hydrodynamics generated at submerged and steep-side reef morphologies, we propose that the habitat quality is enhanced for reef fishes on pinnacle coral reefs, despite small overall area, greater depths and relative isolation in offshore positions.

This explanation is reflected by the presence of abundant schools of large-bodied planktivores and predatory fishes driving the high abundance and biomass of fishes at the pinnacles. Planktivores derive direct energetic benefits from increased pelagic inputs and in turn, reefs with higher pelagic subsidies support higher trophic levels (Skinner et al. 2021). The pinnacle sites in this study also support highly abundant and species rich predator fish communities compared to the emergent reef types in Kimbe Bay, which are composed of both site-attached meso-predators (e.g., *Cephalopholis* spp, *Epinephelus* spp.) and larger, mobile species (e.g., *Sphyrna* spp, *Caranx* spp) (Cresswell et al. 2023). Predation is an important structuring mechanism in reef fish communities (Hixon and Jones 2005) and smaller, site-attached predators on the pinnacles undoubtedly must directly capture prey from the surrounding habitat, influencing patterns in local abundance of prey species (Stewart and Jones 2001; Stier et al. 2017). However, in the case of highly mobile predators, the resources derived from the pinnacles may be less direct and again, may be related to the distinct hydrodynamic conditions. High flow environments may provide opportunities for resting (Barreiros et al. 2002), the formation of breeding or spawning aggregations (Fisher et al. 2018) and thermoregulation (Watanabe et al. 2021). Further, if transient predators are moving to feed in pelagic, or other reef environments, their presence on the pinnacles may further enhance energetic subsidies through feces deposited on the reef and consumed by other species (Robertson 1982; Rempel et al. 2022). Elucidating the role of predation in shaping fish communities on isolated submerged reefs is challenging outside of experimental and mathematical studies but presents a stimulating avenue for further investigation in our study system.

While average daily current speed was overwhelmingly the most important environmental variable in the RF model for

(Figure legend continued from previous page.)

**Fig. 3.** Relative importance of biogeographic, habitat and hydrodynamic variables in (A) fish richness, (B) total fish abundance, and (C) total fish biomass RF models for fish communities in Kimbe Bay. Factors with highest values of percent increase in mean square error indicate more important variables in the RF model. Partial plots for the top four most influential variables are denoted by numerals i–iv for each model.



**Fig. 4.** GLMMs of the relationship between (A) fish species richness (S), (B) total fish abundance (n), and (C) fish biomass (kg) and daily average current speed (cm s<sup>-1</sup>) on three different reef types in Kimbe Bay. Solid lines represent the true range of recorded data for current speeds at each reef type with 95% CIs plotted as opaque shaded ribbons. Dashed lines represent GLMM trend outside of the observed range of current speeds at each reef type and corresponding 95% CIs as transparent ribbons. Caterpillar plots for each model present slope coefficient estimates for each reef type and pairwise comparisons between slopes (P = Pinnacle, O = Offshore and N = Nearshore). Non-shaded points in caterpillar plots indicate a significant trend or significantly different pairwise comparison. All model coefficients are reported on the response scale but trends for abundance and biomass are presented on the natural log scale to aid visualization of slopes with markedly different ranges in the response variable.

fish biomass, the model explained very little of the total variability in biomass ( $R^2 = 0.05$ ). This was markedly less than both richness ( $R^2 = 0.70$ ) and abundance ( $R^2 = 0.53$ ) models. Similarly, the GLMMs testing the direct relationship between current speed and fish biomass did not yield conclusive

results. This analysis did, however, highlight the very different range in current speeds experienced by the different reef types over the study period and the association of strong currents on the pinnacles with high fish species richness, abundance and biomass. The likely combined effects of current speed and

habitat variables already discussed, together with the range of ecological benefits strong currents confer to different species, individuals and populations may partly explain the large variability in the models and the lack of clear general trends. More complex modeling approaches may be required to better understand these relationships which could include fish species or family specific responses and co-variance with important habitat metrics.

Despite the low ranking of most habitat variables in our results, the ability of currents to boost fish biodiversity on coral reefs should be considered in conjunction with habitat complexity. While high current flow can provide benefits to fishes on coral reefs it also presents increased energetic costs to individual organisms (Fulton et al. 2013; Nadler et al. 2018). In order to take advantage of high-flow conditions, morphological and behavioral adaptations have developed in some species to enhance swimming performance and reduce energetic costs (Liao 2007). However, many adaptations depend on the availability of sufficient complex habitat which not only provides important refuge from predation but is also used to shelter from strong currents (Johansen et al. 2008; Eggertsen et al. 2016). We observed weak negative trends in species richness and abundance at offshore sites with increasing annual current speed in contrast to nearshore and pinnacles sites. Supplementary analysis in this study and previous work conducted at the same sites found that offshore reefs had the lowest percentage cover (1.2%) of complex hard coral compared to nearshore (3.6%) and pinnacle reefs (8.2%) (Supplementary Table S5). This suggests that while currents may increase niche space and resources for some species, strong flows restrict the distribution of others. Therefore, only when combined with sufficiently high habitat complexity can the greatest number of species access the additional resources provided by high current speed environments.

Distance to nearest mainland was ranked in the top five variables in all RF models. However, this effect was relatively small, and fish diversity and biomass at offshore emergent reefs is similar to nearshore emergent reefs, despite being just as isolated as the pinnacles. Distance to mainland is often used as a proxy for fishing pressure on coral reefs as nearshore habitats are closer and therefore more accessible to human population centers (DeMartini et al. 2008; Williams et al. 2011). We controlled for this covariate by selecting nearshore sites which are part of a well-established locally managed marine area (Green et al. 2009). The submerged nature of the pinnacles could make these reefs harder for fishers to access, although these sites are well known among local communities and are also frequently visited by local dive and game-fishing tourism operators. Isolation from other coral reef habitats is another key determinant of reef fish community structure that did not rank highly in our analyses. The effect of isolation however, varies considerably with scale. Small-scale isolation in patchy habitats can promote abundance and species richness (Belmaker et al. 2005; Jones et al. 2020), but

extreme large-scale isolation is sometimes associated with low species diversity (Sandin et al. 2008; Luiz et al. 2015). The pinnacles in our study and the seascape of Kimbe Bay arguably represent a mesoscale level of isolation from other reefs. At this intermediate level, important ecological processes may operate at optimal levels. For example, mesoscale isolation may result in optimal foraging distances to other larger reefs for mobile predators, while retaining the benefits of residency in the high current environments of the pinnacles. In terms of recruitment, current strength, variability, and relative current direction can increase larval recruitment at isolated reefs (Jones 1997; Simpson et al. 2014) and also generate biophysical retention mechanisms that promote self-recruitment (Paris and Cowen 2004; Beldade et al. 2016). High current speeds could therefore enhance recruitment on small, submerged pinnacle reefs, despite their relative isolation from other larval sources. Overall, we suggest that the additional resources and other ecological benefits derived from high current speeds for individuals and populations likely explain the greatest biodiversity recorded on the pinnacles and the prominence of hydrodynamic variables in our results.

Temperature variables were somewhat important for fish species richness and abundance but were some of the least influential variables for fish biomass. Although average annual temperatures on the pinnacles are slightly cooler than emergent reefs in Kimbe Bay (Galbraith et al. 2022), the magnitude of this difference is small and seasonal patterns are remarkably low here (Srinivasan and Jones 2006). Our previous investigation of hydrodynamic regimes and thermal profiles on the pinnacles in Kimbe Bay hints at potential thermoregulatory processes at these sites but this has not been empirically shown. Direct temperature related effects on coral reef communities initially affect scleractinian corals and responses in fish communities to rising or variable temperature regimes are often not immediately apparent (Graham et al. 2007; Munday et al. 2008). It seems likely that the influence of water temperature on fish communities in our study co-varies with current speed and extending this study over a longer timeframe may reveal stronger temporal relationships. This would be important to determine both the effects of predicted future warming on submerged pinnacles and to test whether site-specific hydrodynamic conditions confer resilience to thermal stress in coral reef communities.

Teasing out the relative importance of well-established environmental variables as drivers of diversity is a source of constant challenge and debate in ecology. We found that site-specific hydrodynamic variables at morphologically distinct reefs and at greater depths, override the importance of established drivers of reef fish community structure including habitat size, complexity, hard coral cover or isolation. Tropical coral reefs on submerged bathymetric features, such as the pinnacles in this study, are ubiquitous across coastal shelves supporting productive ecological communities, yet remain understudied compared to emergent reefs. Established

ecological paradigms for seamounts suggest that biophysical-coupling by strong and distinct hydrodynamics are drivers of biodiversity on these structures and our results provide some evidence that these processes may operate in a similar way on pinnacle coral reefs. We suggest that these mechanisms enhance reef habitat quality and explain how these patch habitats can support higher numbers of species and individuals than might be expected for the small area. Specific investigation of these biophysical mechanisms are therefore warranted to understand the pathways through which physical properties of submerged reef habitats generate ecological responses. For example, trophic studies utilizing isotope chemistry could determine how energetic pathways between pelagic and reef habitats are facilitated by local mixing, advection and/or retention of food sources. Similarly, genetic connectivity studies in conjunction with biophysical modeling may elucidate the extent of larval retention by current in small, submerged reef habitats.

The global coral reef seascape is changing, coral cover and habitat complexity continue to decline globally. Identifying reef-scale environmental conditions like hydrodynamics that enhance or maintain habitat quality will be essential to understand the future of coral reef fishes. These variables should be more regularly incorporated into reef-scale studies to better understand patterns of coral reef biodiversity and ecological responses to disturbance alongside other key drivers. Morphologically distinct, deeper and diverse submerged reefs represent highly productive and potentially resilient coral habitats. These hotspots of diversity warrant further investigation in other seascapes and their ecological value should be more frequently considered in marine management and conservation.

#### Data availability statement

All hydrodynamic and fish abundance, diversity, biomass, and richness data are available at <https://doi.org/10.6084/m9.figshare.23972610.v1>.

#### References

- Abbey, E., and J. M. Webster. 2011. Submerged reefs, p. 1058–1062. *In* D. Hopley [ed.], *Encyclopedia of modern coral reefs*. Springer.
- Barreiros, J., R. Santos, and A. E. de Borba. 2002. Food habits, schooling and predatory behaviour of the yellowmouth barracuda, *Sphyaena viridensis* (Perciformes: Sphyaenidae) in the Azores. *Cybium Int J Ichthyol* **26**: 83–88.
- Bartoń, K. 2019. MuMIn: Multi-model inference (R package version 0.12.2).
- Beldade, R., S. J. Holbrook, R. J. Schmitt, S. Planes, and G. Bernardi. 2016. Spatial patterns of self-recruitment of a coral reef fish in relation to Island-scale retention mechanisms. *Mol. Ecol.* **25**: 5203–5211.
- Bell, J. D., and R. Galzin. 1984. Influence of live coral cover on coral-reef fish communities. *Mar. Ecol. Prog. Ser.* **15**: 265–274.
- Belmaker, J., N. Shashar, and Y. Ziv. 2005. Effects of small-scale isolation and predation on fish diversity on experimental reefs. *Mar. Ecol. Prog. Ser.* **289**: 273–283.
- Bennett, S., A. R. Halford, J. H. Choat, J.-P. A. Hobbs, J. Santana-Garcon, A. M. Ayling, E. S. Harvey, and S. J. Newman. 2018. Geography and Island geomorphology shape fish assemblage structure on isolated coral reef systems. *Ecol. Evol.* **8**: 6242–6252.
- Binning, S. A., and D. G. Roche. 2015. Water flow and fin shape polymorphism in coral reef fishes. *Ecology* **96**: 828–839.
- Bode, M., J. M. Leis, L. B. Mason, D. H. Williamson, H. B. Harrison, S. Choukroun, and G. P. Jones. 2019. Successful validation of a larval dispersal model using genetic parentage data. *PLoS Biol.* **17**: e3000380.
- Boettiger, C., D. T. Lang, and P. C. Wainwright. 2012. Rfishbase: Exploring, manipulating and visualizing FishBase data from R. *J. Fish Biol.* **81**: 2030–2039.
- Bonin, M. C., G. R. Almany, and G. P. Jones. 2011. Contrasting effects of habitat loss and fragmentation on coral-associated reef fishes. *Ecology* **92**: 1503–1512.
- Breiman, L. 2001. Random forests. *Mach Learn* **45**: 5–32.
- Brewer, T. D., J. E. Cinner, R. Fisher, A. Green, and S. K. Wilson. 2012. Market access, population density, and socioeconomic development explain diversity and functional group biomass of coral reef fish assemblages. *Glob. Environ. Chang.* **22**: 399–406.
- Bridge, T., R. Beaman, T. Done, and J. Webster. 2012. Predicting the location and spatial extent of submerged coral reef habitat in the great barrier reef world heritage area, Australia. *PLoS One* **7**: e48203.
- Brodie, J. E., and others. 2011. Terrestrial pollutant runoff to the great barrier reef: An update of issues, priorities and management responses. *Mar Pollut Bull* **65**: 81–100.
- Brooks, M., K. Kristensen, A. Magnusson, C. Berg, N. Nielsen, H. Skaug, M. Maechler, and B. Bolker. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J* **9**: 378–400.
- Carrara, R., and D. P. Vázquez. 2010. The species-energy theory: A role for energy variability. *Ecography (Cop)* **33**: 942–948.
- Cresswell, B., G. Galbraith, H. Harrison, M. McCormick, and G. Jones. 2023. Coral reef pinnacles act as ecological magnets for the abundance, diversity and biomass of predatory fishes. *Mar. Ecol. Prog. Ser.* **717**: 143–156.
- DeMartini, E. E., A. M. Friedlander, S. A., Sandin, and E. Sala. 2008. Differences in fish-assemblage structure between fished and unfished atolls in the northern Line Islands, Central Pacific. *Mar Ecol Prog Ser.* **365**: 199–215. doi:10.3354/meps07501

- Done, T. J. 1983. Coral zonation: Its nature and significance, p. 107–147. *In* D. J. Barnes [ed.], Perspectives on coral reefs. Australian Institute of Marine Science.
- Dower, J., H. Freeland, and K. Juniper. 1992. A strong biological response to oceanic flow past cobb seamount. *Deep Sea Res Part A Oceanogr Res Pap* **39**: 1139–1145.
- Eggersen, L., L. Hammar, and M. Gullström. 2016. Effects of tidal current-induced flow on reef fish behaviour and function on a subtropical rocky reef. *Mar. Ecol. Prog. Ser.* **559**: 175–192.
- Ewers, R. M., and R. K. Didham. 2006. Confounding factors in the detection of species responses to habitat fragmentation. *Biol. Rev.* **81**: 117–142.
- Fabricius, K. E. 2011. Factors determining the resilience of coral reefs to eutrophication: A review and conceptual model. p. 493–505. *In* Z. Dubinsky and N. Stambler [eds.], Coral reefs: An ecosystem in transition. Springer. doi:10.1007/978-94-007-0114-4\_28
- Fahrig, L. 2013. Rethinking patch size and isolation effects: The habitat amount hypothesis. *J. Biogeogr.* **40**: 1649–1663.
- Fisher, E. E., J. H. Choat, M. I. McCormick, and M. Cappo. 2018. Relative influence of environmental factors on the timing and occurrence of multi-species coral reef fish aggregations. *PloS One* **13**: 1–23.
- Froese, R., J. T. Thorson, and R. B. Reyes. 2013. A Bayesian approach for estimating length-weight relationships in fishes. *J Appl Ichthyol* **30**: 78–85.
- Fulton, C. J., J. L. Johansen, and J. F. Steffensen. 2013. Energetic extremes in aquatic locomotion by coral reef fishes. *PloS One* **8**: e54033.
- Galbraith, G. 2023. Data for strong hydrodynamic drivers. *Limnol Oceanogr.* doi:10.6084/m9.figshare.23972610.v1
- Galbraith, G. F., B. J. Cresswell, M. I. McCormick, T. C. Bridge, and G. P. Jones. 2021. High diversity, abundance and distinct fish assemblages on submerged coral reef pinnacles compared to shallow emergent reefs. *Coral Reefs* **40**: 335–354.
- Galbraith, G. F., B. J. Cresswell, M. I. McCormick, T. C. Bridge, and G. P. Jones. 2022. Contrasting hydrodynamic regimes of submerged pinnacle and emergent coral reefs. *PloS One* **17**: e0273092.
- Galland, G., B. Erisman, O. Aburto-Oropeza, and P. Hastings. 2017. Contribution of cryptobenthic fishes to estimating community dynamics of sub-tropical reefs. *Mar Ecol Prog Ser* **584**: 175–184.
- Genin, A. 2004. Bio-physical coupling in the formation of zooplankton and fish aggregations over abrupt topographies. *J. Mar. Syst.* **50**: 3–20.
- Goetze, J. S., and others. 2019. A field and video analysis guide for diver operated stereo-video. *Methods Ecol Evol* **10**: 1083–1090.
- Graham, N. A. J., S. K. Wilson, S. Jennings, N. V. C. Polunin, J. Robinson, J. P. Bijoux, and T. M. Daw. 2007. Lag effects in the impacts of mass coral bleaching on coral reef fish, fisheries, and ecosystems. *Conserv. Biol.* **21**: 1291–1300.
- Gratwicke, B., and M. R. Speight. 2005. The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. *J. Fish Biol.* **66**: 650–667.
- Green, A., P. Lokani, S. Sheppard, J. Almany, S. Keu, J. Aitsi, J. Warku Karvon, R. Hamilton, and G. Lipsett-Moore. 2007. Scientific Design of a Resilient Network of marine protected areas. Kimbe Bay, West New Britain, Papua New Guinea. TNC Pacific Island Countries Report No. 2/07.
- Green, A., and others. 2009. Designing a resilient network of marine protected areas for Kimbe Bay, Papua New Guinea. *Oryx* **43**: 488–498.
- Green, R. H., R. J. Lowe, and M. L. Buckley. 2018. Hydrodynamics of a tidally forced coral reef atoll. *J Geophys Res Ocean* **123**: 7084–7101.
- Hachich, N. F., M. B. Bonsall, E. M. Arraut, D. R. Barneche, T. M. Lewinsohn, and S. R. Floeter. 2015. Island biogeography: Patterns of marine shallow-water organisms in the Atlantic Ocean. *J. Biogeogr.* **42**: 1871–1882.
- Harris, P. T., T. C. L. Bridge, R. J. Beaman, J. M. Webster, S. L. Nichol, and B. P. Brooke. 2013. Submerged banks in the great barrier reef, Australia, greatly increase available coral reef habitat. *ICES J Mar Sci* **70**: 284–293.
- Hartig, F. 2020. DHARMA: Residual diagnostics for hierarchical (multi-level/mixed) regression models. R package.
- Hixon, M. A., and G. P. Jones. 2005. Competition, predation, and density-dependent mortality in demersal marine fishes. *Ecology* **86**: 2847–2859.
- Hobbs, J.-P. A., G. P. Jones, P. L. Munday, S. R. Connolly, and M. Srinivasan. 2012. Biogeography and the structure of coral reef fish communities on isolated islands. *J. Biogeogr.* **39**: 130–139.
- Illing, B., A. T. Downie, M. Beghin, and J. L. Rummer. 2020. Critical thermal maxima of early life stages of three tropical fishes: Effects of rearing temperature and experimental heating rate. *J. Therm. Biol.* **90**: 102582.
- Ishwaran H, Kogalur U (2022) Fast unified random forests for survival, regression, and classification (RF-SRC). randomForestSRC-package.
- Jankowski, M., N. Graham, and G. Jones. 2015. Depth gradients in diversity, distribution and habitat specialisation in coral reef fishes: Implications for the depth-refuge hypothesis. *Mar. Ecol. Prog. Ser.* **540**: 203–215.
- Johansen, J. L., D. R. Bellwood, and C. J. Fulton. 2008. Coral reef fishes exploit flow refuges in high-flow habitats. *Mar. Ecol. Prog. Ser.* **360**: 219–226.
- Jones, G. P. 1997. Relationships between recruitment and postrecruitment processes in lagoonal populations of two coral reef fishes. *J Exp Mar Bio Ecol* **213**: 231–246.
- Jones, G. P., M. I. McCormick, M. Srinivasan, and J. V. Eagle. 2004. Coral decline threatens fish biodiversity in marine reserves. *Proc. Natl. Acad. Sci.* **101**: 8251–8253.

- Jones, G. P., G. Barone, K. Sambrook, and M. C. Bonin. 2020. Isolation promotes abundance and species richness of fishes recruiting to coral reef patches. *Mar. Biol.* **167**: 167.
- Jouffray, J.-B., and others. 2019. Parsing human and biophysical drivers of coral reef regimes. *Proc R Soc B Biol Sci* **286**: 20182544.
- Lavelle, J. W., and C. Mohn. 2010. Motion, commotion, and biophysical connections at Deep Ocean seamounts. *Oceanography* **23**: 90–103.
- Leitner, A., T. Friedrich, C. Kelley, S. Travis, D. Partridge, B. Powell, and J. Drazen. 2021. Biogeophysical influence of large-scale bathymetric habitat types on mesophotic and upper bathyal demersal fish assemblages: A Hawaiian case study. *Mar. Ecol. Prog. Ser.* **659**: 219–236.
- Lenth, R. L. 2020. Emmeans: Estimated marginal means, aka least-squares means. *emmeans*-package.
- Letessier, T. B., and others. 2019. Remote reefs and seamounts are the last refuges for marine predators across the Indo-Pacific. *PLoS Biol.* **17**: e3000366.
- Liao, J. C. 2007. A review of fish swimming mechanics and behaviour in altered flows. *Philos Trans R Soc B Biol Sci* **362**: 1973–1993.
- Liaw, A., and M. Wiener. 2002. Classification and regression by randomForest. *R News* **2**: 18–22.
- Lindfield, S. J., E. S. Harvey, A. R. Halford, and J. L. McIlwain. 2016. Mesophotic depths as refuge areas for fishery-targeted species on coral reefs. *Coral Reefs* **35**: 125–137.
- Lowe, R. J., and J. L. Falter. 2015. Oceanic forcing of coral reefs. *Ann. Rev. Mar. Sci.* **7**: 43–66.
- Lüdecke, D., D. Makowski, P. Waggoner, and I. Patil. 2020. Performance: Assessment of regression models performance. *binned\_residuals*.
- Luiz, O. J., T. C. Mendes, D. R. Barneche, C. G. W. Ferreira, R. Noguchi, R. C. Villça, C. A. Rangel, J. L. Gasparini, and C. E. L. Ferreira. 2015. Community structure of reef fishes on a remote oceanic Island (St Peter and St Paul's archipelago, equatorial Atlantic): The relative influence of abiotic and biotic variables. *Mar. Freshw. Res.* **66**: 739–749.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of Island biogeography*. Princeton University Press.
- McClure, E., L. Richardson, A. Graba-Landry, Z. Loffler, G. Russ, and A. Hoey. 2019. Cross-shelf differences in the response of herbivorous fish assemblages to severe environmental disturbances. *Diversity* **11**: 23.
- Messmer, V., G. P. Jones, P. L. Munday, S. J. Holbrook, R. J. Schmitt, and A. J. Brooks. 2011. Habitat biodiversity as a determinant of fish community structure on coral reefs. *Ecology* **92**: 2285–2298.
- Mohn, C., M. White, A. Denda, S. Erofeeva, B. Springer, R. Turnewitsch, and B. Christiansen. 2021. Dynamics of currents and biological scattering layers around Senghor seamount, a shallow seamount inside a tropical Northeast Atlantic eddy corridor. *Deep Sea Res Part I Oceanogr Res Pap* **171**: 103497.
- Monismith, S. G. 2007. Hydrodynamics of coral reefs. *Annu. Rev. Fluid Mech.* **39**: 37–55.
- Moore, C., M. Cappo, B. Radford, and A. Heyward. 2017. Submerged oceanic shoals of North Western Australia are a major reservoir of marine biodiversity. *Coral Reefs* **36**: 719–734.
- Mora, C., P. M. Chittaro, P. F. Sale, J. P. Kritzer, and S. A. Ludsin. 2003. Patterns and processes in reef fish diversity. *Nature* **421**: 933–936.
- Munday, P. L., G. P. Jones, M. S. Pratchett, and A. J. Williams. 2008. Climate change and the future for coral reef fishes. *Fish Fish.* **9**: 261–285.
- Nadler, L. E., S. S. Killen, P. Domenici, and M. I. McCormick. 2018. Role of water flow regime in the swimming behaviour and escape performance of a schooling fish. *Biol Open* **7**: bio031997. doi:10.1242/bio.031997
- Nakagawa, S., P. C. D. Johnson, and H. Schielzeth. 2017. The coefficient of determination R<sup>2</sup> and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *J. R. Soc. Interface* **14**: 20170213.
- Paris, C. B., and R. K. Cowen. 2004. Direct evidence of a biophysical retention mechanism for coral reef fish larvae. *Limnol. Oceanogr.* **49**: 1964–1979.
- Pinheiro, H. T., G. Bernardi, T. Simon, J.-C. Joyeux, R. M. Macieira, J. L. Gasparini, C. Rocha, and L. A. Rocha. 2017. Island biogeography of marine organisms. *Nature* **549**: 82–85.
- Quimbayo, J. P., and others. 2019. Determinants of reef fish assemblages in tropical oceanic islands. *Ecography (Cop)* **42**: 77–87.
- R Core Development Team. 2023. *R: A language and environment for statistical computing*. R Core Development Team.
- Radice, V. Z., O. Hoegh-Guldberg, B. Fry, M. D. Fox, and S. G. Dove. 2019. Upwelling as the major source of nitrogen for shallow and deep reef-building corals across an oceanic atoll system. *Funct Ecol* **33**: 1120–1134.
- Rempel, H. S., A. K. Siebert, J. C. Van Wert, K. N. Bodwin, and B. I. Ruttenberg. 2022. Feces consumption by nominally herbivorous fishes in the Caribbean: An underappreciated source of nutrients? *Coral Reefs* **41**: 355–367.
- Richert, J., S. J. Jorgensen, J. T. Ketchum, L. Mohajerani, and P. Klimley. 2017. The importance of pinnacles and seamounts to pelagic fishes and fisheries off the southern Baja California peninsula. *Oceanogr Fish* **4**: 555644.
- Robertson, D. R. 1982. Fish feces as fish food on a Pacific coral reef. *Mar. Ecol. Prog. Ser.* **7**: 253–265.
- Robitzch, V., and M. L. Berumen. 2020. Recruitment of coral reef fishes along a cross-shelf gradient in the Red Sea peaks outside the hottest season. *Coral Reefs* **39**: 1565–1579.
- Samoilys, M. A., A. Halford, and K. Osuka. 2019. Disentangling drivers of the abundance of coral reef fishes in the Western Indian Ocean. *Ecol. Evol.* **9**: 4149–4167.

- Sandin, S., M. J. Vermeij, and A. Hurlbert. 2008. Island biogeography of Caribbean coral reef fish. *Glob. Ecol. Biogeogr.* **17**: 770–777.
- Simpson, S. D., H. B. Harrison, M. R. Claereboudt, and S. Planes. 2014. Long-distance dispersal via ocean currents connects Omani clownfish populations throughout entire species range. *PLoS One* **9**: e107610.
- Skinner, C., A. C. Mill, M. D. Fox, S. P. Newman, Y. Zhu, A. Kuhl, and N. V. C. Polunin. 2021. Offshore pelagic subsidies dominate carbon inputs to coral reef predators. *Sci. Adv.* **7**: eabf3792.
- Sponaugle, S., and others. 2002. Predicting self-recruitment in marine populations: Biophysical correlates and mechanisms. *Bull Mar Sci* **70**: 341–375.
- Srinivasan, M., and G. P. Jones. 2006. Extended breeding and recruitment periods of fishes on a low latitude coral reef. *Coral Reefs* **25**: 673–682.
- Stewart, B. D., and G. P. Jones. 2001. Associations between the abundance of piscivorous fishes and their prey coral reefs: Implications for prey-fish mortality. *Mar. Biol.* **138**: 383–397.
- Stier, A. C., C. D. Stallings, J. F. Samhuri, M. A. Albins, and G. R. Almany. 2017. Biodiversity effects of the predation gauntlet. *Coral Reefs* **36**: 601–606.
- Storlazzi, C. D., O. M. Cheriton, R. van Hooijdonk, Z. Zhao, and R. Brainard. 2020. Internal tides can provide thermal refugia that will buffer some coral reefs from future global warming. *Sci. Rep.* **10**: 13435.
- Svetnik, V., A. Liaw, C. Tong, J. Christopher Culbertson, R. P. Sheridan, and B. P. Feuston. 2003. Random Forest: A classification and regression tool for compound classification and QSAR modeling. *J. Chem. Inf. Comput. Sci.* **43**: 1947–1958.
- Wagner, D., A. M. Friedlander, R. L. Pyle, C. M. Brooks, K. M. Gjerde, and T. A. Wilhelm. 2020. Coral reefs of the high seas: Hidden biodiversity hotspots in need of protection. *Front. Mar. Sci.* **7**: 567428. doi:10.3389/fmars.2020.567428
- Watanabe, Y. Y., I. Nakamura, and W. C. Chiang. 2021. Behavioural thermoregulation linked to foraging in blue sharks. *Mar. Biol.* **168**: 1–10.
- White, M., I. Bashmachnikov, J. Arístegui, and A. Martins. 2007. Biophysical coupling on seamounts; physical processes and seamount productivity. *Ecology, Fisheries & Conservation*. Blackwell Publishing Ltd, p. 65–84.
- Wickham, H. 2016. *ggplot2: Elegant graphics for data analysis*. Springer-Verlag. [accessed 2023 January 25]. <https://ggplot2.tidyverse.org>
- Williams, G. J., J. E. Smith, E. J. Conklin, J. M. Gove, E. Sala, and S. A. Sandin. 2013. Benthic communities at two remote Pacific coral reefs: Effects of reef habitat, depth, and wave energy gradients on spatial patterns. *PeerJ* **2013**: e81.
- Williams, I. D., and others. 2011. Differences in reef fish assemblages between populated and remote reefs spanning multiple archipelagos across the central and Western Pacific. *J Mar Biol* **2011**: 1–14.
- Wilson, S. K., N. A. J. Graham, M. S. Pratchett, G. P. Jones, and N. V. C. Polunin. 2006. Multiple disturbances and the global degradation of coral reefs: Are reef fishes at risk or resilient? *Glob. Chang. Biol.* **12**: 2220–2234.
- Wright, D. H. 1983. Species-energy theory: An extension of species-area theory. *Oikos* **41**: 496.
- Wyatt, A. S. J., J. J. Leichter, L. T. Toth, T. Miyajima, R. B. Aronson, and T. Nagata. 2020. Heat accumulation on coral reefs mitigated by internal waves. *Nat. Geosci.* **13**: 28–34.

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#### Conflict of Interest

None declared.

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