Natural variation in coral reef trophic structure across environmental gradients

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Policies designed to address current challenges to the sustainability of fisheries generally use an ecosystem-based approach – one that incorporates interactions between fishes, fishers, and the environment. Fishing alters the trophic structure among coral reef fish but properly assessing those impacts requires an understanding of how and why that structure varies naturally across scales. Using a combination of small- and large-scale surveys, we generated biomass pyramids for 20 uninhabited Pacific islands, and found that (1) the distribution of reef fish biomass across trophic levels is highly scale dependent: trophic structures that appear top-heavy at small scales can take a variety of different states when data are integrated across the broader seascape; (2) reefs can have the greatest biomass at intermediate consumer levels, which we describe as "middle-driven" systems; and (3) in unfished coral reef systems, trophic structure is strongly predicted by energy into the base and middle of the food web, as well as by the interacting effect of water temperature.

Approximately 20% of the world's 7 billion people live in the coastal tropics, and much of this population depends on small-scale fisheries for nutrition (Bell *et al.* 2009; Sale *et al.* 2014). Tropical coral reef ecosystems support such fisheries, but these ecosystems are under threat from stressors including climate change, habitat degradation, and fishing (Bell *et al.* 2013; Hughes *et al.* 2017; Cinner *et al.* 2018) that are predicted to intensify (Cheung *et al.* 2010). Adaptations to maintain the food security of coastal communities might include the transfer of fishing effort to more productive species (Robinson *et al.* 2019) while limiting the harvest of species that perform critical ecosystem functions like herbivory (Bell *et al.* 2013). However, environmental gradients also drive substantial variation in reef ecosystem configurations (Williams *et al.* 2015; Heenan *et al.* 2016). Management, such as catch limits or fisheries baselines, must therefore account for these natural bounds set by the environmental context of reef systems.

Although few marine ecosystems are completely unaffected by humans, minimally affected ecosystems offer insight into natural ecological limits. Examples include remote Indo-Pacific coral reefs located several hundreds of kilometers from the nearest human population centers. Studies from these near-pristine ecosystems can inform fisheries management targets, help evaluate ecosystem status, and have shown, for example, that the fisheries potential of subtropical reefs is lower than that of tropical ones (McClanahan *et al.* 2019). From microbes to top predators, natural gradients in wave energy, water temperature, and primary production are key determinants of coral reef structure and function (Williams *et al.* 2019). The standing biomass of reef fishes can double along gradients of increasing oceanic productivity, and

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accounting for this is essential when isolating the effects of fishery depletion (Williams *et al.* 2015). Similarly, differences in water temperature along a subtropical-to-tropical gradient have substantial effects on the functional composition of herbivorous fish assemblages (Heenan *et al.* 2016). Collectively, incorporating environmental and habitat drivers greatly improves our ability to estimate local carrying capacity and thus the potential scope for recovery (Gorospe *et al.* 2018). More generally, studies of remote reefs have reported highly variable trophic structure; examples include bottom-heavy systems in the Indian Ocean (Graham *et al.* 2017) and extremely upper-trophic level (TL)-dominated "inverted pyramids" on some Pacific reefs (Friedlander and DeMartini 2002; DeMartini *et al.* 2008; Sandin *et al.* 2008). However, it is not clear how much and in what ways variability in the trophic structure of coral reef fish assemblages is driven by environmental factors. This warrants attention if we are to provide the basis for robust small-scale fisheries management that accounts for environmental context.

We tested whether the trophic structure of coral reef fish assemblages is related to water temperature, as has been shown for temperate marine systems (Frank *et al.* 2007), and to external inputs of energy (ie oceanic production and irradiance). Primary production in the coastal ocean is limited in part by sunlight, which decreases with depth and latitude (Campbell and Aarup 1989). Light influences benthic primary producers on coral reefs (Gattuso *et al.* 2006) and high irradiance is linked to increased fish biomass (McClanahan *et al.* 2019). How this affects consumers – and ultimately trophic structure – remains unknown. Inputs of energy from outside the defined ecosystem appear to facilitate increased biomass in upper TLs (McCauley *et al.* 2018), as coral reef planktivore and piscivore biomass is positively related to nearshore oceanic production (Williams *et al.* 2015). A recent multi-method study emphasized the importance of both pelagic and cryptobenthic energy

pathways in supporting coral reef fish assemblage productivity (Morais and Bellwood 2019). It has also become clear that small-bodied cryptic fishes, such as blennies and gobies, are key energetic resources sustaining overall reef fish production (Brandl *et al.* 2019). Because of their low detectability in visual surveys (Kulbicki *et al.* 2010), these small fishes tend to be grossly underestimated in survey programs. As such, there is not only high natural variability in reef fish trophic structure, but also potential for method choice to influence conclusions about the status and role of different ecosystem components in driving overall production.

We integrated data from two methods: one a conventional survey in which divers recorded all fishes within small areas, and the other a broader-scale survey that targeted larger-bodied, roving, and generally rare or patchily distributed species not well sampled by smaller-scale methods. These two types of surveys were conducted on the reefs of 20 remote islands and atolls (hereafter "islands") that are largely isolated from direct local human impacts. We combined these data, gathered from methods that survey fish at different measurement scales, to (1) document the degree of variation in trophic structure among different reef ecosystems and (2) quantify the environmental drivers of this variation. Understanding the

sources of uncertainty introduced by method choice, along with the natural constraints set by coral reefs' energetic settings, will improve our ability to identify sustainable levels of fisheries exploitation and recovery potential.

◼ Methods

Reef fish surveys – integrating multiscale data for a community perspective

We used fish survey data collected via two methods by the National Oceanic and Atmospheric Administration (NOAA) Pacific Reef Assessment and Monitoring Program (RAMP) – stationary point count (SPC) and towed-diver method ("tow") – around 20 uninhabited islands in the western central Pacific (Panel 1; WebPanel 1; Figures 1 and 2). From 1034 SPC surveys and 985 towed transects, we calculated individual species biomass using their observed size and abundance as well as published length–weight relationships. TLs were then assigned using FishBase (www.fishbase.org). We made several assumptions in order to integrate the survey data: that (1) learned diver avoidance behavior was minimal, as these were extremely remote systems where fishes had few previous

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Panel 1. The artifacts of measurement scale in community assessments

It has long been recognized that a study's scale of observation contributes to the ecological patterns and processes that are detected (Wiens 1989), yet few studies provide biological justification for their measurement scale (Jackson and Fahrig 2015). Ecologists frequently generalize their findings beyond the scale of observations, which contributes to the underappreciation of scale-related ecological issues (Estes *et al.* 2018). When studying a single species, the size of individual observation units (eg a quadrat or transect) can be matched to the scale of inference (Wiens 1989); however, this is unfeasible for ecosystem-wide assessments. From blennies to barracuda, the resource patch size of species within an ecosystem varies considerably. Furthermore, traits like home range, school size, swimming speed, mobility, curiosity, coloration, and patterning all contribute to detectability and introduce sampling bias (Kulbicki *et al.* 2010). When observations are collected at a scale that does not match the variety of species within an ecosystem, results can be confounded by artifacts of measurement scale. Therefore, there is no single "best" method for ecosystem-wide surveys.

One approach is to use multiple survey methods differing in scale. Here, we used two in-situ methods to survey fish communities (Figure 1; WebPanel 1): the stationary point count (SPC) surveys all species observed within a small area (352 m^2 per survey), and the towed-diver survey targets large-bodied and roving species within a larger area (2200 m^2 per survey).

Approximately 10% of the recorded fish species were observed using both methods (WebTable 1). These species included large-bodied low-TL species (parrotfish and surgeonfish), mega mid-trophic planktivorous species (manta rays [*Mobula* spp]), and predators (barracuda, groupers, jacks, and sharks). Some semi-cryptic fishes (eg sabre squirrelfish [*Sargocentron*

spiniferum]) were rarely recorded by either method, and possibly neither method provides reliable detection. For most of those species, encounter rates were lower but densities higher on SPC as compared to tow (WebTable 1). The lower encounter rates on the SPC, particularly of rare species, reflect differences between the two methods in the total area surveyed (SPC ~37 ha, tow ~2130 ha), and these differences indicate high uncertainty in the density estimates of both methods. For example, 120 manta rays were observed on tow, as compared to 25 for a similar number of SPC surveys. Conversely, for species like the camouflage grouper (*Epinephelus polyphekadion*) and yellowlip emperor (*Lethrinus xanthochilus*), encounter rates and density estimates were higher on the small-scale surveys (WebTable 1). This is likely due to those species being easier to detect by SPC divers, who carefully search small areas, than by constantly moving tow divers that travel approximately 1 m above the bottom.

Some species of sharks, jacks, and snappers had similar or lower encounter rates on the SPC as compared to tow (ie similar or fewer numbers were seen in smaller areas), but density estimates on the small-scale surveys were far greater (WebPanel 1; WebTable 2). High estimates on SPC are likely driven by the attraction of some species to divers (Parrish and Boland 2004), potentially leading to systematic overestimates in density, particularly for small-area surveys involving stationary divers (Colvocoresses and Acosta 2007). Generally, tow surveys generate lower estimates of shark and jack density than smaller transects. Rather than ignoring or removing species poorly estimated by SPC (the typical approach to these artifacts of scale and method bias [MacNeil *et al.* 2015; Williams *et al.* 2015]), here we merged the SPC and tow survey data. By doing so, we selectively used both datasets to address known biases of each method.

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interactions with people (Januchowski-Hartley *et al.* 2011); (2) attraction to divers was lower for the tow method, as divers were kept in constant motion at a rate of ~3 km hr^{-1} while surveying the area ahead; and (3) species that were rarely encountered on the SPC are generally poorly estimated by that method. We assumed that small-scale SPC density estimates are most accurate for small and common fishes, whereas the tow method is generally more suitable for surveying large-bodied and rare fishes.

Based on these assumptions and a sensitivity analysis performed on a range of encounter and density ratios (WebPanel 1; WebTable 2), the criteria for integrating species observations from those methods when the species were detected both on tow and by SPC were: (1) to default to using SPC data but (2) for fishes > 50 cm, we used the tow dataset when we were confident that we had overcounted a species with SPC (species density estimate with SPC > 5 times the density calculated with tow), and for species that were very rarely encountered by SPC (the encounter rate by SPC is less than one-fifth that of the tow survey). To assess the difference between biomass estimates per TL from SPC alone as compared to the integrated data, we visually inspected island-level plots of proportional and absolute biomass per TL generated from the SPC (alone) as well as from the SPC and tow data (merged).

Variation in trophic structure

To understand how the amount of biomass in each TL bin varied with absolute total fish biomass, we fitted generalized linear mixed effects models of proportional biomass per TL as a function of total fish biomass (expressed in g m^{-2}). The random effect was marine province (based on the Marine Ecoregions of the World: Hawaii, Central Polynesia, Tropical Northwest Pacific).

Many islands lacked species in the 2.5–3 and 3.5–4 trophic bins, so we grouped TLs as 2–2.99 (TL2), 3–3.99 (TL3), and > 4 (TL4). There was a clear increase in absolute biomass of planktivorous species (TL3) around islands with high total fish biomass (Figure 2; WebPanel 2a). A metric multidimensional scaling (MDS) of the proportional contribution of individual species to TL3 biomass per island was used to identify key species in that TL. The MDS was based on a Euclidean distance matrix. We calculated to what
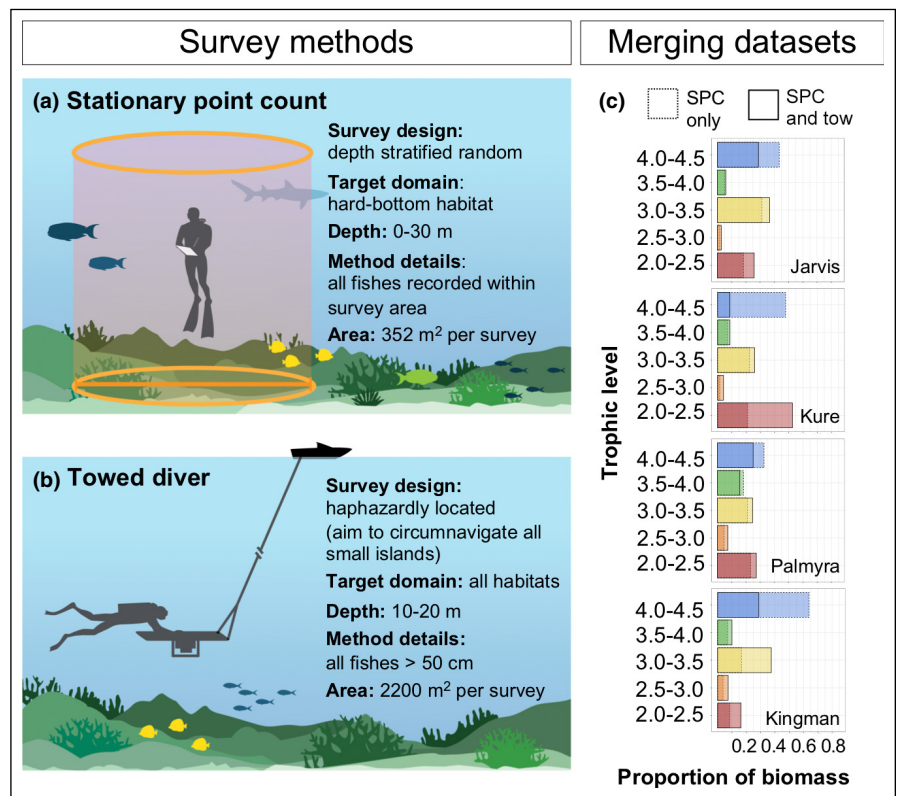
Figure 1. Survey method influences estimated trophic structure of coral reef fish assemblages. Two sampling methods were used to survey fishes: the (a) stationary point count (SPC) and (b) the towed-diver method (tow). The SPC is a generalist survey method optimized to capture all fishes within a small area (352 m^2 per survey). The tow survey method samples large (> 50 cm total length) fish over a large area (2200 m^2 per survey). (c) Inverted pyramids around Kure and Palmyra atolls, and around Jarvis and Kingman islands, were apparent with the SPC dataset, but not when the SPC and tow datasets were combined (see WebFigure 1 for all islands).
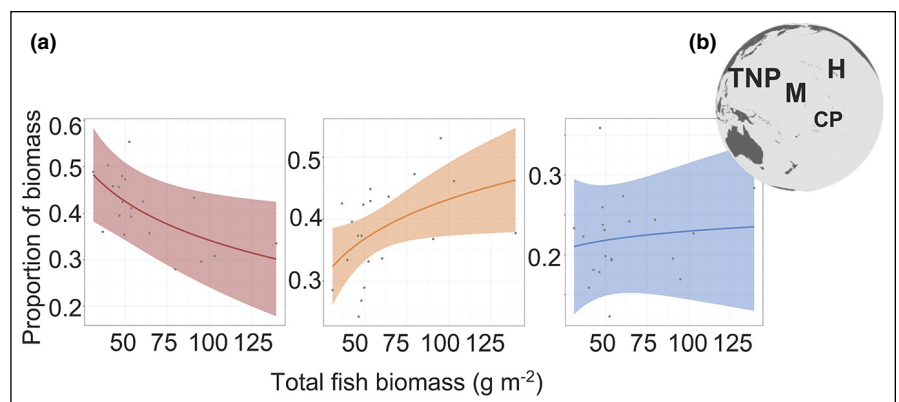
Figure 2. The relationship between proportion of biomass per trophic level and total fish biomass. (a) Proportion of biomass per trophic level (TL; red = 2–3, orange = 3–4, blue = greater than 4) across all study locations, modeled as a function of total fish biomass (g m^{-2}) with transparent bands showing the 95% confidence limit. (b) Locations of surveyed island regions. H = Hawaii, CP = Central Polynesia, M = Marshall Islands, TNP = Tropical Northwest Pacific.

degree different TL3 species drove the patterns seen within the MDS plot by calculating the Pearson's correlation (*r*) of each species with each MDS axis. Those species with *r* ≥ 0.7 were overlaid

as a biplot, with the length of the vector proportional to the correlation strength (WebPanel 2b).

Biophysical drivers of coral reef fish trophic structure

We fitted generalized linear models to investigate the influence that external energy inputs (sunlight and oceanic productivity) and water temperature had on biomass in each TL. Specifically, we modeled biomass as a function of irradiance (Einsteins m^{-2} d^{-1}), sea-surface temperature (°C), and chlorophyll *a* (mg m^{-3}, a proxy for phytoplankton biomass and therefore oceanic primary production). These biophysical drivers were island-level satellite-derived climatologies (long-term means; Gove *et al.* 2013). All models were fitted in R (www.r-project.org).
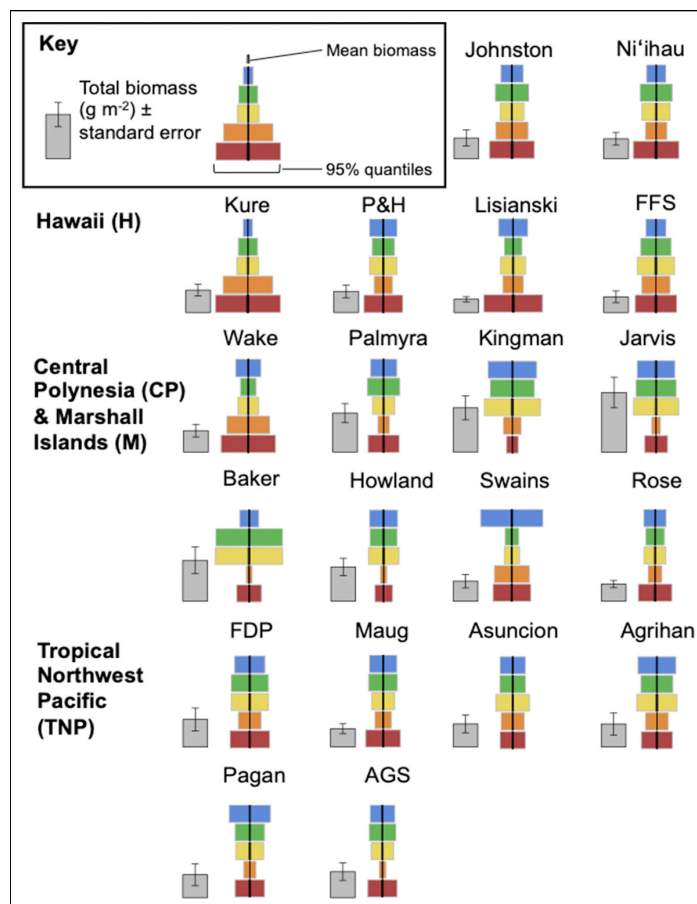
Figure 3. Trophic structure of fish assemblages at coral reef islands. Gray bars represent total reef fish biomass (± standard error) around each island, ranging from 31 g m^{-2} (Lisianksi Island) to 140 g m^{-2} (Jarvis Island). Transparent colored plots represent trophic pyramids for each island, with biomass per TL (proportion of total) (red = 2–2.5, orange = 2.5–3, yellow = 3–3.5, green = 3.5–4, blue = 4–4.5). Means (dark center bars in pyramids) and 95% quantiles (colored bars) were generated from a Monte Carlo simulation. Individual species biomasses were drawn from distributions based on mean and standard error from the in-situ survey data, and species TL designations from the FishBase website (fixed standard error 0.1; www.fishbase.org). FDP = Farallon de Pajaros; FFS = French Frigate Shoals; P&H = Pearl and Hermes; AGS = Alamagan, Guguan, Sarigan.

Model fitting and selection, as well as assessments of model performance, are detailed in WebPanels 3 and 4.

■ Results

Influence of reef fish survey sampling scale on trophic biomass estimates

The tendency for the SPC data to overestimate higher-TL piscivores was evident when biomass pyramids generated from the SPC data were compared with the integrated SPC and tow data (summarized in Figure 1; all islands in WebFigure 1). Top-heavy fish communities (more biomass in TL4 and above; less biomass below TL4) were evident around 11 islands for SPC data alone (WebFigure 1). When the data were integrated, only one island, Swains, exhibited trophic inversion (Figure 2; WebFigure 1). This result was robust to a wide range of decision criteria used to merge the two datasets (WebTable 2), with the pooled dataset used for all subsequent analyses.

Variation in trophic structure

Considerable natural variation exists in fish assemblage trophic structure on coral reefs (Figure 3). The mean proportion of biomass in TL2 and TL3 was 0.39, ranging from ~0.20 (around Howland, Baker, Jarvis, and Kingman islands in Central Polynesia) to 0.6 around Kure Atoll in the Northwestern Hawaiian Islands, the most northerly location surveyed (Figure 3). Swains Island had the lowest proportion of biomass in the mid-TLs (0.32; all-island mean proportion of biomass in those TLs was 0.38), whereas Baker Island had over half of the total biomass in the mid-TLs. Across all islands, the mean proportion of biomass in TL4 and above was 0.22 (range: 0.06 around Kure to 0.43 around Swains). Estimates of total fish biomass (± standard error) varied greatly among islands, from 31 ± 6 g m^{-2} around Lisianksi Island to 140 ± 36 g m^{-2} around Jarvis Island (Figure 3). The proportion of biomass in low TLs (TL2) was lower at sites with greater total fish biomass (t = –2.39, P = 0.03) (WebPanel 2), while the proportion of mid-TL biomass (ie TL3) was higher at sites with greater total fish biomass (t = 2.11, P = 0.05) (Figure 2). Locations with the highest total biomass (Kingman, Jarvis, Baker, Howland, and Farallon de Pajaros [FDP]) had high proportions of biomass in TL3 species. This included planktivorous rays (*Mobula* spp), anthias (*Luzonichthys whitleyi* and *Pseudanthias olivaceus*), small wrasses (*Anampses meleagrides* and *Labroides dimidiatus*), sweepers (*Pempheris oualensis*), and fusilier (*Caesio teres*) (WebPanel 2). The proportion of biomass in TL4 and above did not vary predictably with total fish biomass (t = 0.37, P = 0.71) (Figure 2).

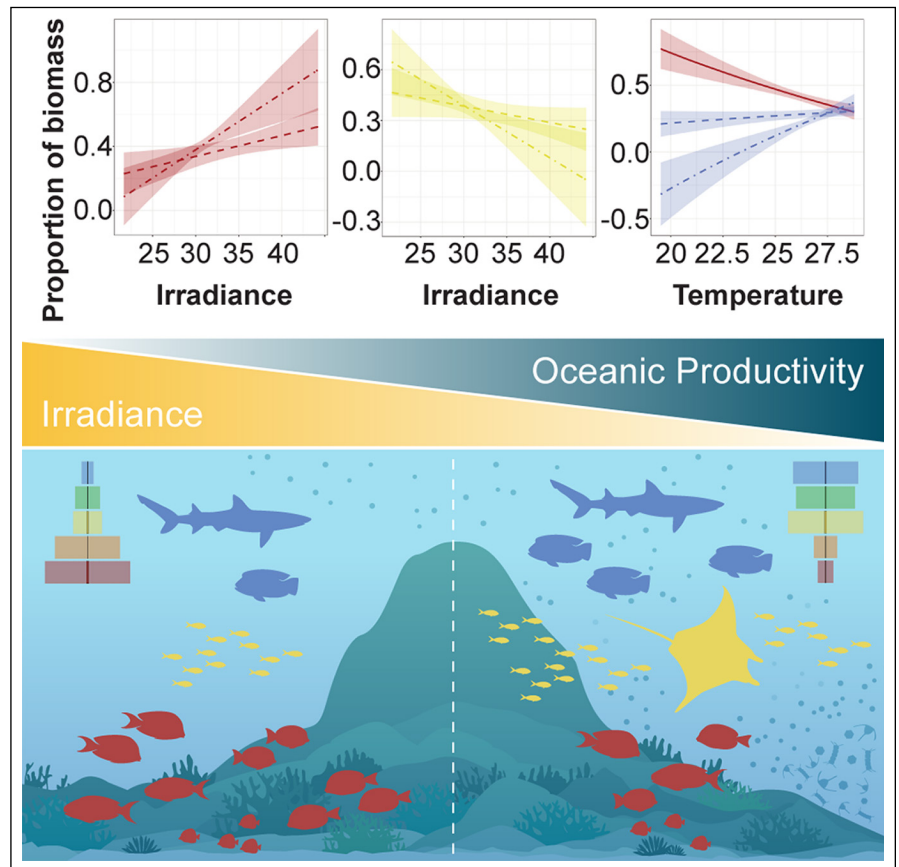### Biophysical drivers of coral reef fish trophic structure

The biophysical parameters of a reef – temperature, irradiance, and oceanic primary production – were important predictors of its fish assemblage trophic structure (WebPanel

4). However, the direction of effect for these parameters differed among TLs. With the exception of TL2 biomass, there were clear best performing models in the model sets (WebPanel 4). The explanatory power of the models of TL2 biomass was relatively poor ($F_{1,15}$ = 279.90, P < 0.001, adjusted R^2 = 0.23), suggesting the importance of drivers not considered in this analysis (WebPanel 4). Overall, a substantial amount of variation in lower and upper TL biomass was associated with gradients in temperature, irradiance, and oceanic primary production (proportional models adjusted R^2 > 0.70). The proportion of biomass in TL2 increased with irradiance and decreased with temperature, with an interacting effect between irradiance and oceanic primary production ($F_{4,15}$ = 16.39, P < 0.001, adjusted R^2 = 0.76) (WebPanel 4; Figure 4). In contrast, the degree to which reefs were top-heavy (ie more biomass in TL4 and above) increased with temperature. This was true in absolute and proportional terms for TL4 (WebPanel 4; Figure 4). Fish communities were more top-heavy on coral reefs with warmer water and higher oceanic primary production, but this effect of temperature was diminished in the most productive locations (WebPanel 4). Absolute mid-TL biomass was closely and positively associated with oceanic primary production (Akaike weight 0.6, marginal R^2 = 0.84) (WebPanel 4). Similar to TL4, the proportion of biomass in mid-TLs increased with temperature and decreased with irradiance but this was also conditional on oceanic primary production; the effect of irradiance was lower in more productive locations.

Figure 4. The relationship between irradiance, oceanic primary production, and water temperature on the trophic structure of coral reef fish assemblages. (a) Predicted proportion of biomass and 95% confidence intervals for TLs 2–3 (red), 3–4 (yellow), and > 4 (blue) by irradiance (Einsteins m^{-2} d^{-1}), temperature (°C), and the interacting effect of oceanic primary production (mg m^{-3}) (dashes: high-chlorophyll a, dot-dashes: low-chlorophyll a). (b) Conceptual diagram of a bottom-heavy and middle-driven fish assemblage, with fish color representing TLs (red = 2–3, yellow = 3–4, blue = greater than 4) and inset pyramids from Kure Atoll (left) and Kingman Island (right).

Discussion

Using a multi-method approach to synthesize data from 20 remote Pacific islands, we show that reef fish trophic structure varies considerably and that carrying capacity fluctuates in relation to environmental context. The trophic structure of fish assemblages on remote coral reefs can therefore assume a diversity of forms, including recently described "concave" shapes indicative of bottom-driven systems (Graham *et al*. 2017) and "convex" systems in which biomass is greatest at intermediate consumer levels. The evidence we present of such "middle-driven" systems for coral reefs is, to the best of our knowledge, the first of its kind.

Like all complex multidimensional structures, inferences about the ecosystem properties of coral reefs are sensitive to the choices made about the scale of observation. This is because individual species interact with their environment in ways that vary in space and time, so that there is no single correct scale to observe and describe an ecosystem (Levin 1992). For example, spawning aggregations that attract and concentrate predators can lead to temporarily inverted trophic pyramids that would not exist outside of this specific temporal period (Mourier *et al*. 2016). Such inverted pyramids have been reported from small-scale surveys on remote coral reefs (Friedlander and DeMartini 2002; DeMartini *et al*. 2008; Sandin *et al*. 2008), prompting debate on their theoretical feasibility (Trebilco *et al*. 2016; Woodson *et al*. 2018) and criticism that they arise as an artifact of sampling bias (Bradley *et al*. 2017; McCauley *et al*. 2018). However, few studies have considered the explicit role of sampling scale in how we understand what is natural, or in how such patterns change across the broader seascape.

Given the array of reef fish life histories, which contributes to wide variation in detectability across species (Kulbicki *et al*. 2010; Ruppert *et al*. 2018), it seems unrealistic to quantify the trophic structure of reef fishes at a single scale. We therefore integrated data at two scales (approximately at meters and

kilometers) to demonstrate that estimated reef fish trophic distributions were highly scale dependent, and that trophic structure varies widely among locations due to differences in environmental drivers. Our results highlight the need to consider scale when making community-wide inferences. Integrative multiscale approaches are especially important to provide a full ecosystem perspective for fisheries management.

Recent studies have shown how humans can substantially alter the trophic organization of coral reef fish assemblages (Graham *et al.* 2017; McCauley *et al.* 2018; Ruppert *et al.* 2018). What has been lacking, however, is an understanding of how gradients in natural environmental drivers simultaneously or independently influence spatial variation in reef fish assemblage structure. One finding of our analysis is that bottom-heavy pyramids were associated with higher irradiance. Similar to other benthic primary producers whose distributions are limited by light intensity (Gattuso *et al.* 2006; Muir *et al.* 2015), coral reefs have a greater proportion of reef fish biomass in low TLs in areas with high irradiance. Presumably, primary consumers benefit from the higher rates of benthic primary production, as increased irradiance bolsters the base of the food web. Higher fisheries production in tropical coral reefs than in the subtropics is due in part to higher solar radiation (McClanahan *et al.* 2019). As such, coral reef fisheries that target lower TLs may be more viable where energy into the base of the food web is higher and therefore where fish assemblages are more naturally bottom-heavy.

Our results show that the proportion of biomass in higher TLs is greater in warmer waters and in areas of higher oceanic primary production. Middle-driven systems – in which biomass is greatest at intermediate consumer levels, like those with high biomass of planktivorous species (WebPanel 2) – had the greatest total reef fish biomass and capacity to sustain higher TLs. Coral reef predators, total fish productivity, and therefore associated fisheries are largely sustained by pelagic and cryptobenthic energetic pathways (McCauley *et al.* 2012; Frisch *et al.* 2014; Brandl *et al.* 2019). We demonstrate that reef systems can be bottom-heavy in areas of high irradiance, and middle-driven when external energetic subsidies, delivered by a panoply of biophysical processes, are maximized. Middle-driven systems have the greatest capacity for total reef fish community biomass, and in turn greater fisheries productivity. Ecosystem-based approaches to management would benefit from greater recognition that coral reef trophic structures are naturally constrained to be top- or bottom-heavy, or indeed middle-driven, and that where any given reef lies on this spectrum is influenced by the surrounding energetic environment. When setting management targets and adaptation strategies, it is vital to acknowledge that human impacts are superimposed over natural constraints on the carrying capacity and recovery potential of local fisheries.

Acknowledgements

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