Received: 14 August 2024 | Revised: 9 January 2025 | Accepted: 5 February 2025

DOI: 10.1002/ecy.70065

ARTICLE

ECOLOGY
ECOLOGICAL SOCIETY OF AMERICA

A seascape dichotomy in the role of small consumers for coral reef energy fluxes

Simon J. Brandl[1] | **Helen F. Yan**[2] | **Jordan M. Casey**[1] |
Nina M. D. Schiettekatte[3] | **Julianna J. Renzi**[4] | **Alexandre Mercière**[5] |
Fabien Morat[5] | **Isabelle M. Côté**[6] | **Valeriano Parravicini**[5]

[1]Department of Marine Science, The University of Texas at Austin, Marine Science Institute, Port Aransas, Texas, USA

[2]College of Science and Engineering, James Cook University, Townsville, Queensland, Australia

[3]Hawai'i Institute of Marine Biology, University of Hawai'i at Mānoa, Kāne'ohe, Hawaii, USA

[4]Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, Santa Barbara, California, USA

[5]PSL Université Paris: EPHE-UPVD-CNRS, UAR 3278 CRIOBE, Université de Perpignan, Perpignan, Pyrénées-Orientales, France

[6]Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia, Canada

Correspondence
Simon J. Brandl
Email: simon.brandl@austin.utexas.edu

Funding information
BNP Paribas Foundation, Reef Services; Institut des Récifs Coralliens du Pacifique (IRCP); Agence Nationale pour la Recherche, REEFLUX, Grant/Award Number: ANR-17-CE32-0006; Natural Sciences and Engineering Research Council of Canada (NSERC), Grant/Award Number: RGPIN/03933-2017; Natural Sciences and Engineering Research Council of Canada, Vanier-Banting Fellowship; National Science Foundation, Grant/Award Number: DGE-1650114; Australian Research Council, Laureate Fellowship; Make Our Planet Great Again Postdoctoral Fellowship, Grant/Award Number: mopga-pdf-0000000144; Natural Sciences and Engineering Research Council of Canada, Postgraduate Doctoral Fellowship

Handling Editor: Adriano Caliman

Abstract

Biogeochemical fluxes through ecological communities underpin the functioning of ecosystems worldwide. These fluxes are often heavily influenced by small-bodied consumers, such as insects, worms, mollusks, or small vertebrates, which transfer energy and nutrients from autotrophic sources to larger animals. Although coral reefs are one of the most productive ecosystems in the world, we know relatively little about how small consumers make energy available to larger predators and how their roles may vary across reefs. Here, we use community-scale collections of small, bottom-dwelling ("cryptobenthic") reef fishes along with size spectrum analyses, stable isotopes, and demographic modeling to examine their role in harnessing and transferring carbon in two distinct coral reef habitats. Using a comprehensive dataset from Mo'orea (French Polynesia), we demonstrate that, despite only being separated by a narrow reef crest, forereef and backreef habitats harbor distinct communities of cryptobenthic fishes that play vastly divergent roles in carbon transfer. Forereef communities in Mo'orea are depauperate, largely consisting of predatory and planktivorous species that have comparatively high standing biomass (both individually and collectively). In these communities, the combination of size spectra and isotope values suggests important contributions of pelagic subsidies, but the rate of biomass production and turnover (i.e., the rate at which biomass is replenished) is relatively low. In contrast, cryptobenthic fish communities in the backreef are characterized by high abundances of the smallest bodied species, forming a traditional bottom-heavy trophic pyramid that is fueled by benthic autotrophs. In these communities, benthic productivity fuels rapid production and turnover

---

of fish biomass, while pelagic energy channels are notably less productive. Our integrative approach demonstrates the utility of combining multiple methods (e.g., isotopically informed demographic models) to trace energy fluxes through small consumer communities in complex ecosystems. Furthermore, our results highlight that coral reef productivity dynamics are highly habitat-dependent and the role of the smallest coral reef consumers may be most pronounced in shallow systems with limited connectivity to the open ocean.

KEYWORDS
allochthonous resources, bioenergetics, coral reef trophodynamics, cryptic fish, ecosystem function, food web, size structure, spatial subsidies, stable isotope analysis, trophic dynamics

INTRODUCTION

How do energy and nutrients move through ecosystems? This has been a central question in ecology since the early 1900s, and answering it relies on detailed knowledge of an ecosystem's structure (i.e., biological community composition and environmental conditions) and function (i.e., rates of energy and nutrient transfer) (Odum, 1968). However, identifying the dominant species and processes that underpin ecosystem functioning is difficult and frequently relies on the extrapolation of organismal properties (e.g., length–mass conversion to calculate standing biomass), chemical tracers (e.g., stable isotopes), or simulation approaches (e.g., demographic modeling) to approximate how vital elements move through ecosystems (Brown et al., 2004; DeAngelis, 1980; Odum, 1962). Over the past decades, these methods, alongside a deepening understanding of the complex topography of natural food webs, have dramatically increased our understanding of system-wide energy and nutrient fluxes (Allen & Wesner, 2016; Atkinson et al., 2017; Polis & Strong, 1996). Yet, studies that integrate multiple techniques are still rare (but see [Nobre et al., 2019; Norris et al., 2007]), despite their potential to yield insights into the elemental cycles of Earth's ecosystems.

To understand system-wide energy fluxes, it is critical to identify both the autotrophic organisms or groups that account for the bulk of energy provision in a system, from microscopic phytoplankton to gigantic redwood trees, and the consumers that pass energy to higher trophic levels. However, most ecosystems are not closed entities, which permit either directional or reciprocal exchange of energetic subsidies across ecotones (Nakano & Murakami, 2001; Polis et al., 1997; Spiller et al., 2010). Stable isotopes can be used to determine whether energy sources are autochthonous (i.e., produced locally) or allochthonous (i.e., originating outside the system), while also providing insights into the length of food chains by quantifying isotopic enrichment across trophic levels. For example, the carbon isotope ratio ($\delta^{13}C$) has been used to characterize the importance of benthic versus pelagic primary production for freshwater fishes (Vander Zanden & Vadeboncoeur, 2002), the consumption of marine subsidies by wolf populations (Adams et al., 2010), and the relative use of inshore versus offshore foraging grounds in seabirds (Hobson et al., 1994). In turn, the nitrogen isotope ratio ($\delta^{15}N$) has revealed determinants of food chain lengths and trophic structuring in a range of aquatic and terrestrial ecosystems (Post et al., 2000; Potapov, Brose, et al., 2019; Takimoto et al., 2008; Vander Zanden et al., 1999). As such, stable isotope analyses of carbon and nitrogen using both bulk tissues and compound-specific approaches (Whiteman et al., 2019) are important tools for understanding energy fluxes within and across ecosystems.

While linking large, emblematic consumers like wolves or sharks to various carbon sources is useful, it omits critical information on how carbon is sequestered and transferred by the countless small-bodied consumers that dominate many ecosystems (Manca et al., 2022). These organisms often occur in great numbers, have the capacity to exploit microscopic food sources, and exhibit rapid growth and turnover, giving them an important role in connecting various compartments of food webs (Barnes et al., 2016; Baxter et al., 2005; Potapov, 2022). Yet, due to their small size, they are often difficult to monitor and, concerningly, small consumers may be particularly vulnerable to anthropogenic impacts (Brandl et al., 2024; Koltz, Burkle, et al., 2018; Pollierer et al., 2023; Ripple et al., 2017; Wagner et al., 2021). Understanding the pathways, pace, and efficiency with which these organisms make essential elements available to larger consumers requires not only a detailed inventory of the small consumer species that are present but also a holistic understanding of their internal food web structure, their size structure, and the life history and physiology of the dominant species (Blanchard et al., 2017; Trebilco et al., 2013; White et al., 2007). A range of approaches has been developed to quantify and generalize these dynamics, including size spectrum analyses and a variety of modeling approaches that rely on organismal traits, stoichiometry, and bioenergetics (Christensen & Walters, 2004; Elser et al., 2000; Hanson et al., 1997; Trebilco et al., 2013). Combining one or more of these approaches with stable isotope analyses in small consumer communities has recently yielded insights into food web compartmentalization, energy channels, and human-mediated changes, ranging from arctic invertebrate food webs (Koltz, Asmus, et al., 2018) to temperate soil invertebrates (Potapov et al., 2021) and tropical rainforests (Pollierer et al., 2023). Such multi-method approaches are particularly useful in systems where even small consumers can obtain carbon from resources across boundary layers, such as the interface between below-and aboveground invertebrates (Potapov, 2022).

Tropical coral reefs are the world's most diverse marine ecosystem, and their high productivity has been a subject of intense investigation. As early as the mid-1900s, researchers have sought to quantify the sources and pathways of energy on coral reefs (Odum & Odum, 1955; Sargent & Austin, 1954), and since then, identifying crucial protagonists in coral reef productivity has remained a popular research topic (Brandl et al., 2019; De Goeij et al., 2013; Hatcher, 1988; Morais & Bellwood, 2019; Rougerie et al., 1992; Skinner et al., 2021; Wild et al., 2004). At the heart of this discourse lies the extent to which coral reef consumers, typically reef fishes, are supported by pelagically derived subsidies (i.e., energy that arrives on reefs via planktonic organisms from the open ocean) or benthically derived autochthonous resources (i.e., benthic autotrophs that only exist on the reef). The relative contributions of these two energy sources depend on a reef's configuration and interface with the pelagic zone, both at the scale of entire reefs (e.g., atolls vs. barrier reefs; Hatcher, 1997) and specific zones within reefs (e.g., forereefs vs. backreefs; Wyatt et al., 2012, 2013). Accordingly, many large, mobile consumers for which energy sources have been evaluated using stable isotope approaches show mixed signatures of benthic versus pelagic energy (Frisch et al., 2016; Hilting et al., 2013), although there is also clear context-dependency based on the nature and location of the reef systems (McMahon et al., 2016; Skinner et al., 2021). However, actual links between planktonic or microalgal resources and larger coral reef predators are largely unresolved, and comparatively little is known about how carbon enters the coral reef fish food web and how it is transferred in early stages. Indeed, we are just now beginning to use complementary approaches to trace energy fluxes through coral reef ecosystems (Robinson et al., 2023).

Cryptobenthic fishes are small consumers that can play a critical role in energetic transfer on coral reefs (Brandl et al., 2019). These fishes, which generally account for approximately half of all reef fish species and individuals on a given reef (Brandl et al., 2018), display some of the most unusual vertebrate life histories, combining rapid growth (Depczynski & Bellwood, 2006), short lifespans (Depczynski & Bellwood, 2005a; Goldsworthy et al., 2022; Hernaman & Munday, 2005), and unique larval dynamics (Brandl et al., 2019) to compensate for extreme mortality rates. Despite their strong associations with the benthos, cryptobenthic fishes display a wide range of trophic strategies, ranging from herbivores and detritivores (e.g., most species in the Blenniidae) to benthic microcarnivores (e.g., gobies in the genus *Eviota*, most members of the Tripterygiidae) to planktivores (e.g., most species in the Apogonidae or gobies in the genus *Trimma*) (Brandl et al., 2018; Depczynski & Bellwood, 2003; Hernaman et al., 2009). Thus, despite their limited mobility (Depczynski & Bellwood, 2004), they collectively have access to a wide range of resources and may obtain either benthic or pelagic carbon. Yet, to date, little is known about how energy is transported through cryptobenthic fish communities and how their unique life-history strategy and role on coral reefs may interact with these two complementary energy channels.

Here, we examine communities of small reef fishes across two habitats in Mo'orea, French Polynesia. Specifically, we sampled cryptobenthic fish communities on the forereef and backreef to assess differences in community structure and composition. We then used size spectrum analyses, stable isotope analyses, and demographic models to determine how habitat characteristics and differences in cryptobenthic fish community structure shape the role of small consumers as conduits of energy on coral reefs.

METHODS

Field collections

The study was performed on reefs surrounding the island of Mo'orea, French Polynesia. Mo'orea is surrounded by a well-developed barrier reef (henceforth the "forereef"), which encloses a shallow lagoon that features both backreefs and fringing reefs, separated by a narrow, navigable channel. The ocean-facing forereef is exposed to oceanic swell year-round, while the lagoonal backreefs are sheltered from oceanic waves.

Between November 2017 and February 2020, we performed 50 whole-community collections of cryptobenthic fishes on the forereef and lagoonal backreef around the entire island (Appendix S1: Table S1). For our collections, we used enclosed anesthetic stations following previously established protocols for the collection of cryptobenthic fishes (Brandl et al., 2017). In brief, we selected a small, elevated reef outcrop (mean surface area: 4.90 $m^2 \pm 0.13$ m^2 SE), noted its depth, and measured its curved surface length using a tape measure. We documented the benthic community in the sampling area using five haphazardly deployed 25 cm × 25 cm photoquadrats to examine potential relationships between the benthic community and cryptobenthic fishes. We then enclosed the entire sampling area with a weighted bell-shaped, fine-mesh net, covered the net with a weighted impermeable tarpaulin, and slowly injected two-liter clove-oil: ethanol solution (1:5) area using spray bottles. After waiting approximately three minutes for the anesthetic to take full effect, we removed the tarpaulin and collected all anesthetized fishes using forceps and plastic bags, slowly peeling back the net in the process. Sampling was concluded when five minutes were spent without retrieving additional fishes, and all fishes were brought to the surface, where they were placed on ice and transported to the laboratory for processing. In the laboratory, all fishes were photographed, weighed, measured, and preserved in ethanol or frozen for stable isotope analyses. While our collections also included species from families (e.g., Scorpaenidae, Serranidae, Pomacentridae, Labridae) beyond the 17 families nominally designated as cryptobenthic fishes (sensu [Brandl et al., 2018]), we refer to communities as "cryptobenthic" throughout the manuscript given that most sampled individuals (e.g., genera *Sebastapistes*, *Pseudogramma*, *Plectranthias*) are small-bodied and have a cryptic lifestyle.

We collected source materials for stable isotope analyses in 2016, including seawater samples collected from the open ocean and several groups of benthic algae, including the genera *Halimeda*, *Dictyota*, *Galaxaura*, *Turbinaria*, and turf algal mats, collected opportunistically around the island from both the forereef and backreef. Previous research has shown relatively stable differentiation in isotopic carbon signatures for benthic algae and seawater on coral reefs (Briand et al., 2015; Skinner et al., 2022), suggesting that the slight temporal mismatch between source and consumer collections does not affect our comparisons.

Laboratory processing

Depending on the size and shape of the individual, we used either whole specimens, the posterior half of the body (posterior to the anus), or the dorso-posterior quarter (from the posterior origin of the anal fin to the midpoint of the dorsal fin) for stable isotope analyses. For very small species with adults weighing less than 0.1 g (e.g., genus *Eviota*), up to five individuals from the same station were combined for a single sample. All samples (including source materials) were lyophilized in the field and brought to the Centre de Recherches Insulaires et Observatoire de l'Environnement (CRIOBE) in Perpignan, France. At CRIOBE, alimentary tracts and any large ossified and calcified structures were removed, and samples were homogenized using a bead mill. The samples were then separated into two parts: one part was decalcified for $\delta^{13}C$ analyses and the other was retained for $\delta^{15}N$ analyses. The decalcification samples were decalcified using 1% hydrochloric acid for 24 h. After decalcification, samples were centrifuged and the supernatant was removed via pipetting. Pellets were rinsed three times with MilliQ water, and this process was repeated at least three times (until all gases were released). Samples were then dried and homogenized once more, and all samples were sent to the Cornell University Stable Isotope Laboratory (COIL) for bulk stable isotope analyses of $\delta^{15}N$ and $\delta^{13}C$ on a Thermo Delta V isotope ratio mass spectrometer (IRMS). All samples were run according to COIL standard procedures, including quality checks performed against internal animal standards and expression of isotope ratios against Atmospheric Air for nitrogen (N) and Vienna Pee Dee Belemnite for carbon (C).

To characterize the benthic composition among sampling stations, we used photographs of the five haphazard 0.25 m × 0.25 m quadrats. We cropped and overlaid each photograph with a 5 × 5 uniform grid (25 points/quadrat) using the online machine learning platform, CoralNet (Beijbom et al., 2015; Chen et al., 2021). We quantified the substrate under each point (see Appendix S1: Table S2), and quadrat percent cover was calculated for each taxonomic group by dividing the number of points classified as a given taxon by the total number of points in the quadrat. We calculated percent cover of each cover type at a site as the average percent covers from all five quadrats.

Statistical analyses

We removed all individuals weighing more than 25 g from the dataset (28 out of 2569 individuals; 1%) as these individuals commonly do not permanently reside within the sampled area and were likely caught incidentally. We then summarized the collection data for each species and collection site (i.e., total abundance and biomass per species per site as well as species richness per site) and examined the cryptobenthic fish community composition and structure using multivariate statistics and Bayesian linear regression techniques. Specifically, we assessed differences between the forereef and backreef communities using a distance-based redundancy analysis (dbRDA) on the Bray–Curtis dissimilarity of the fish survey data, using the benthic cover of live corals and turf algae as constraints. We visualized the results in a bivariate ordination, including convex hulls and ellipses for the two habitats and the location of the two constrained axes, with only species with the highest absolute loadings superimposed on the plot. To test for differences in the abundance and species richness of cryptobenthic fishes across the two habitats and the potential effect of the benthic configuration, we ran four Bayesian Generalized Linear Models (GLMs). The models were formulated to examine the effect of habitat type (forereef vs. backreef) and coral cover or turf algal cover, respectively, on the abundance (negative binomial error distribution due to over-dispersed count data) and species richness (Poisson error distribution). We chose to primarily focus on live coral (across growth forms) and turf algae due to their benthic dominance (65.1% of combined total cover) and clear linkages with cryptobenthic fishes as food and habitat (Brandl et al., 2018). Furthermore, we examined differences in the benthic community across the two habitats using a principal coordinate analysis (PCoA) on the Manhattan distance of relative benthic cover across organismal groups. Finally, we examined patterns of community structure and composition across all four sampling years and tested for relationships between the whole benthic community as a latent variable (via the PCoA scores) and cryptobenthic fish abundance and species richness.

To understand the trophic structure of cryptobenthic fishes, we investigated the size spectra of communities on the forereef and backreef (Trebilco et al., 2013), which, despite occupying a limited size range among coral reef fishes more broadly, spanned wet weight estimates across more than four orders of magnitude (from 0.001 to 25 g). Size spectrum analyses provide comparisons of energetic or trophic profiles across communities, which can be used to assess the ecological mechanisms by which resources are distributed throughout food webs. For example, harvesting of large individuals can steepen the size spectrum slope, while external energetic subsidies can lead to disproportionately higher abundances in larger size classes, thus flattening or inverting the size spectrum slope (Blanchard et al., 2005; Trebilco et al., 2013). Notably, while size spectra are most powerful when applied across all consumer species in a food web, this is arguably rarely achieved. On coral reefs, virtually all previous studies focus on communities of large, mobile fishes (e.g., Graham et al., 2005; Robinson et al., 2017; Rogers et al., 2014), ignoring the community of small, cryptic species that are closely associated with the benthos. Here, we focus on this typically neglected component of the coral reef fish community, which exhibits tight internal trophic linkages (Goatley et al., 2017) and forms a distinct compartment in the wider coral reef food web. We used the normalized biomass size spectrum as it corrects for unequal size class bin widths and produces more accurate estimates compared with other regression techniques (Edwards et al., 2017). For each sample (i.e., station), we parsed all cryptobenthic fishes into equal log2 biomass bins and calculated the summed biomass of each bin. We then normalized the biomass of each bin by dividing it by its respective bin width (Trebilco et al., 2013). To generate the size spectra, we performed a Bayesian linear mixed-effects model (LMM) with log10-transformed biomass as the response variable, the interaction between log10 bin midpoints (centered) and habitat type (forereef vs. backreef) as the explanatory variables, and sampling station as a random effect, using a Gaussian distribution.

To examine how isotopic profiles varied among stations and habitats, we combined the stable isotope database with our survey data. Since 13.4% of individual observations in the survey data lacked species-specific isotope values, we employed a taxonomic approach to complete the database. In brief, we computed mean isotope values for all genera and families in the isotope database and then used the respective values to interpolate isotope values for unrepresented species and genera. While this is likely to obscure fine-scale differences in resource use that are prevalent in coral reef fish genera and families (Brandl & Bellwood, 2014; Casey et al., 2019; Leray et al., 2015; Nicholson & Clements, 2021), broader trophic categories are generally well preserved in reef fish families, and dietary shifts are rare (Parravicini et al., 2020; Siqueira et al., 2019). This process resulted in almost complete coverage, with only 3.8% of observations lacking genus-level isotope values, and <1% of observations lacking family-level values (seven species across the families Dinematichthyidae, Soleidae, Platycephalidae, Moringuidae, Samaridae, and Pseudochromidae); these observations were removed from the subsequent analyses. We then used the combined dataset to calculate the mean isotopic profile, its associated uncertainty, and the range of δ^{15}N values for each station's community. We plotted the mean values and analyzed differences in mean δ^{15}N values, mean δ^{13}C values, and food chain length (δ^{15}N range) using three Bayesian linear regression models with habitat type (backreef vs. forereef) as the explanatory variable with a Gaussian error structure.

Finally, to gain a better understanding of the origin and transfer of carbon through cryptobenthic fish communities, we combined Bayesian isotope mixing models (Parnell et al., 2013; Parnell & Inger, 2016) with demographic models of growth and mortality (Brandl et al., 2019; Morais & Bellwood, 2020), resulting in isotopically informed estimates of productivity. To do so, we calculated the mean δ^{13}C values for source materials, dividing them into samples indicative of pelagic productivity (seawater samples) and benthic productivity (algal samples). We then used these source estimates alongside the δ^{13}C values of fish species in Bayesian stable isotope mixing models to obtain relative values of source utilization for each species (Parnell et al., 2013), including those for which isotope values were estimated based on their genus or family. Using the mixing model outputs alongside the individual weight of each fish collected on the reef, we computed the mass obtained from pelagic versus benthic sources. We then used individual-based models of growth and mortality to estimate the biomass production via somatic growth of cryptobenthic fish communities. In short, this method combines species' identities, abundances, and body sizes with estimates of somatic growth rates (Morais & Bellwood, 2018) to predict the net biomass gains of all individuals of a given sample over the course of one day (Morais & Bellwood, 2020). From these models, we generated estimates of total biomass production, consumed biomass (i.e., from daily mortality rates; see Morais & Bellwood, 2020), and biomass turnover. Here, turnover is described as the ratio between the produced and standing biomass (% day^{-1}) and is indicative of the flow rate of particles moving through a system (Brandl et al., 2019). For all four metrics (i.e., standing biomass, produced biomass, consumed biomass, and turnover), we ran individual Bayesian GLMs with habitat (forereef vs. backreef) and carbon source (pelagic vs. benthic) interacting. Models were specified using either a Gamma error distribution with a log link (standing biomass, produced biomass, and consumed biomass) or a Beta error distribution with a logit link (turnover). All models were run using four chains, 6000 iterations, and a warmup of 3000 iterations, using the default non-informative priors as part of the brms v 2.16.4 package (Bürkner, 2017). Models were assessed via posterior predictive checks, simulated residuals, and visual evaluations of chain convergence. We used the vegan package (Oksanen et al., 2007) for all multivariate techniques and the simmr package (Govan et al., 2023) for isotope mixing models. All analyses were done in R v 4.1.0 (R Core Team, 2022), using the tidyverse package (Wickham et al., 2019).

RESULTS

There were noticeable differences in cryptobenthic fish communities between the forereef and backreef in Mo'orea. The dbRDA showed a deep split in community composition ($p = 0.002$; Figure 1), with backreef communities characterized by species in the families Gobiidae, Blenniidae, and Apogonidae, while forereef communities were characterized by *Cirripectes* blennies, triplefins, pomacentrids, and small predatory fishes in the families Cirrhitidae and Serranidae. Backreef communities were associated with a higher prevalence of turf algae in the

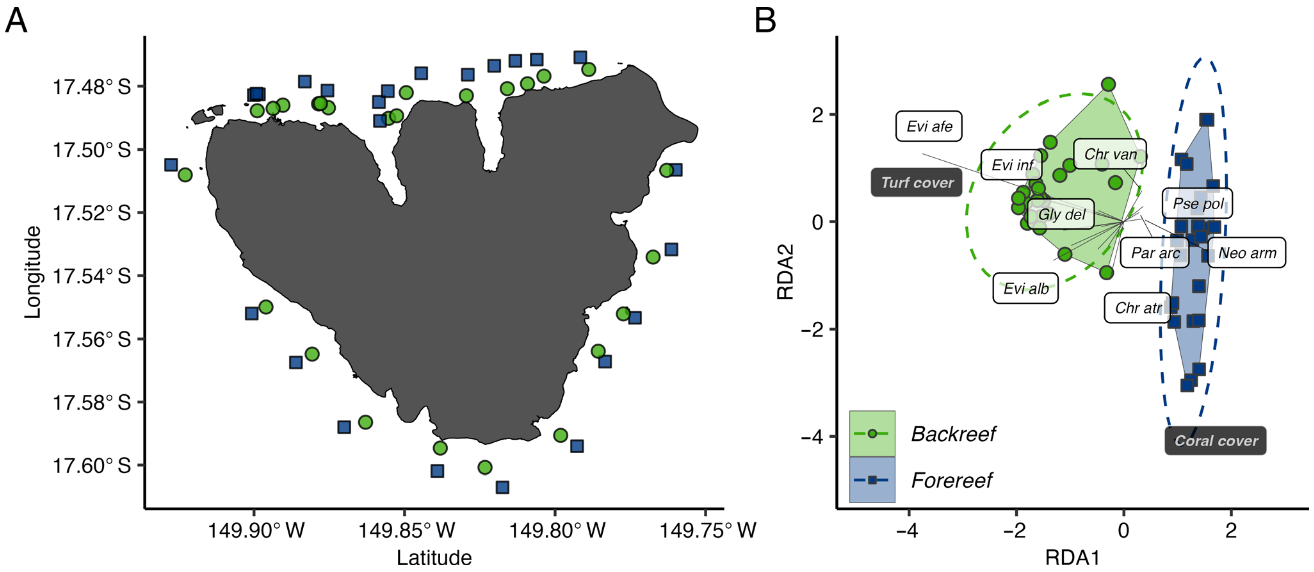

FIGURE 1 Map of sampling sites (A) and community composition of cryptobenthic fishes in Mo'orea, French Polynesia (B). The ordination (B) shows the distribution of sampling stations based on their abundance-weighted species composition in a distance-based redundancy analysis (dbRDA), where the percent cover of live corals and turf algae were specified as constraints. The two primary unconstrained axes (RDA1 and RDA2) explained 26.2% and 7.4% of the variability in the data. Convex hulls and ellipses show the spread and 95% confidence ellipses, respectively (green = backreef; blue = forereef). Thin vectors and labels denote the species loadings, while labels for "Turf cover" and "Coral cover" mark the influence of the constraints on the multivariate data distribution. Evi afe = *Eviota afelei*, Evi inf = *Eviota infulata*, Evi alb = *Eviota albolineata*, Gly del = *Glyptoparus delicatulus*, Chr van = *Chromis vanderbilti*, Pse pol = *Pseudogramma polyacantha*, Chr atr = *Chromis atripectoralis*, Par arc = *Paracirrhites arcatus*, Neo arm = *Neocirrhites armatus*.

benthic community, while forereef communities were associated with high live coral cover, specifically by branching corals. In terms of community structure, fish on the forereef were invariably less abundant than on the backreef ($>$99% estimated probability of the parameter estimate [β] for the forereef $<$0), but there were no notable differences in species richness (64% probability of $\beta < 0$) (Figure 2). After accounting for different reef zones, we found no strong evidence for coral cover affecting both abundance (45% probability of $\beta > 0$) and species richness (72% probability of $\beta > 0$), likely owing to the strong differences in coral cover across the two habitats. In contrast, there was robust indication of a positive relationship between turf algal cover and fish abundance ($>$90% probability of $\beta > 0$) and a negative relationship between turf algal cover and fish species richness ($>$95% probability of $\beta < 0$) on the backreef, while the forereef showed no discernible relationships. The benthic community differed between the forereef and backreef, with the backreef characterized by turf algae and invertebrates, while the forereef was mostly characterized by crustose coralline algae, dead coral, and live branching coral (Appendix S1: Figure S1). When using the PCoA scores as predictors of cryptobenthic fish community structure, there was indication of a negative relationship between PCoA scores on the first axis (Dim1) and cryptobenthic fish abundance on the backreef (93% probability of $\beta < 0$), a positive relationship between Dim1 and fish diversity on the backreef (94% probability of $\beta > 0$), and a negative relationship between Dim1 and fish diversity on the forereef (98% probability of $\beta < 0$) (Appendix S1: Figure S2). No relationships were found for the second dimension of the PCoA. We found no indication of notable changes in fish community structure or composition over the four years, despite the occurrence of a bleaching event in 2019 (Appendix S1: Figures S3 and S4).

The size spectrum analyses revealed striking differences between cryptobenthic fish communities on the forereef and backreef (Figure 3). There was a negative

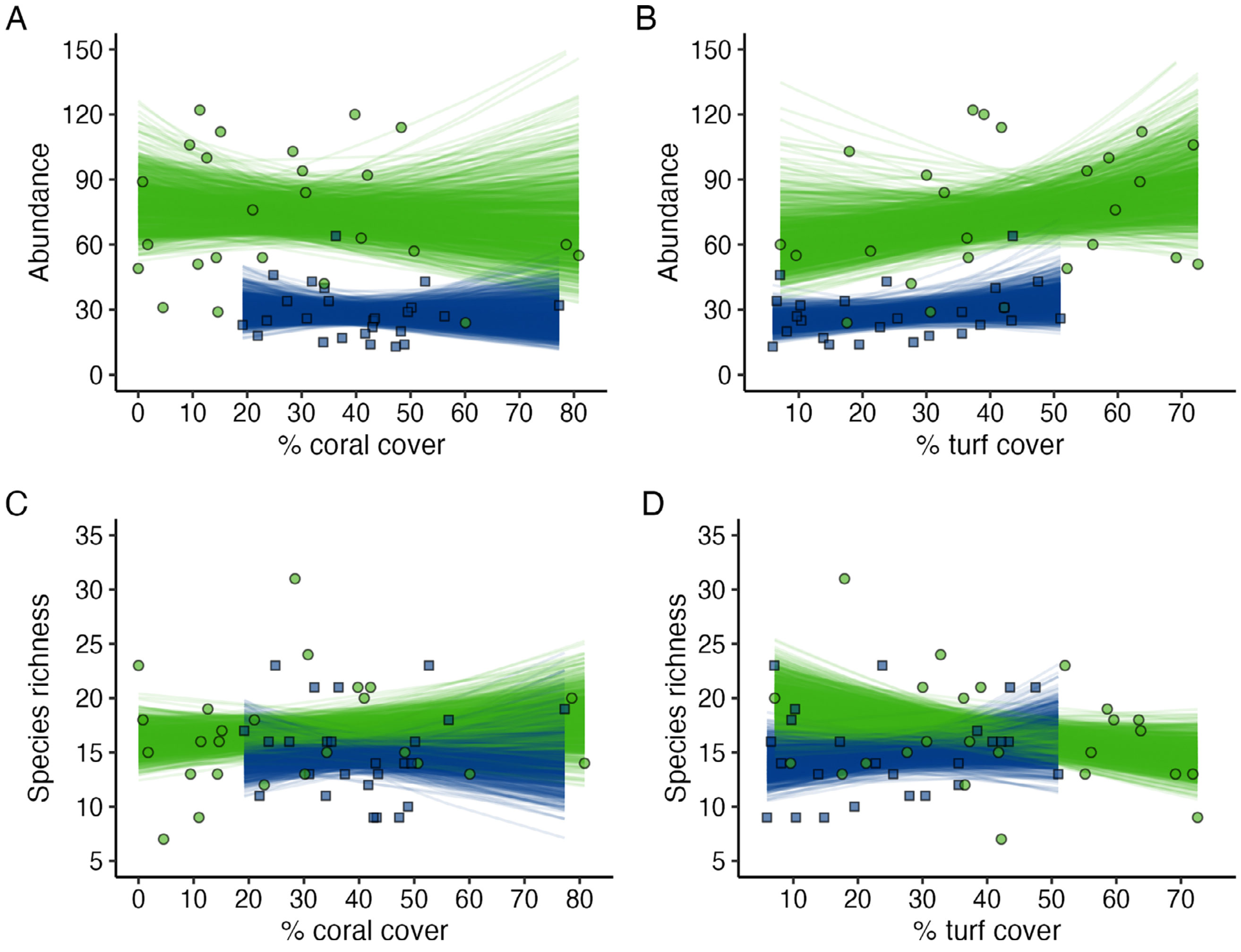

FIGURE 2 Abundance (A and B) and species richness (C and D) of cryptobenthic fishes in Mo'orea, French Polynesia. Plots show the raw data (symbols) and 1000 predicted posterior fits (lines) from Bayesian Generalized Linear Models examining the effects of habitat (green = backreef, blue = forereef) and percent cover of live corals (A and C) and turf algae (B and D) on the two community metrics.

relationship between the summed biomass in each bin and biomass bin midpoints in backreef communities ($\beta = -0.20$ [95% credible interval: −0.25, −0.15]), which suggests higher biomass in smaller size classes. In sharp contrast, the slope for forereef communities showed no decline, instead exhibiting a slope that is indistinguishable from zero ($\beta = 0.02$ [−0.04, 0.08]). This indicates that forereef habitats deviate from classic trophic pyramids and do not show size-based structuring; instead, medium- and large-bodied individuals are disproportionately abundant.

Our stable isotope analyses revealed clear differences in mean $\delta^{15}N$ values, mean $\delta^{13}C$ values, and $\delta^{15}N$ ranges of cryptobenthic fish communities between the two habitat types (Figure 4). Specifically, communities on the forereef had markedly higher $\delta^{15}N$ values (forereef: $\beta = 1.12$ [0.96, 1.28]) and markedly lower $\delta^{13}C$ values (forereef: $\beta = -2.85$ [−3.22, −2.47]) compared with backreef communities, while exhibiting lower $\delta^{15}N$ ranges (forereef: $\beta = -2.08$ [−2.50, −1.68]), indicating shorter internal food chains. Furthermore, the isotopically informed demographic models revealed fundamentally different energetic dynamics between the two habitats (Figure 5). There were no differences in net standing biomass between the two habitats (forereef: $\beta = -0.34$ [−1.02, 0.36]; 288 g on the backreef vs. 151 g on the forereef), but backreef communities supported less standing biomass derived from pelagic carbon than from benthic carbon (pelagic: $\beta = -0.48$ [−0.62, −0.35]), while forereef communities showed the opposite trend (forereef-pelagic: $\beta = 0.82$ [0.63, 1.02]). These patterns intensified when considering the demographic dynamics between the two communities; backreef communities far exceeded forereef communities in both net produced biomass (forereef: $\beta = -1.28$ [−1.89, −0.64]; 6.27 vs. 1.28 g day^{-1}) and consumed biomass (forereef: $\beta = -1.50$ [−2.05, −0.93]; 7.75 vs. 1.66 g day^{-1}). In both of these metrics, the two habitats showed a widening dichotomy between benthic and pelagic productivity, with backreef communities producing biomass largely from benthic carbon (pelagic: $\beta = -0.63$ [−0.76, −0.51] and − 0.66 [−0.79, −0.54] for produced and consumed biomass, respectively), while the opposite was true for forereef communities (forereef-pelagic: $\beta = 0.98$ [0.82, 1.15] and 1.00 [0.82, 1.18] for produced and consumed biomass, respectively). Finally, biomass turnover was much higher in backreef communities (forereef: $\beta = -1.08$ [−1.36, −0.81]; 6.61% vs. 2.46%) and again dominated by benthic carbon turnover (pelagic: $\beta = -0.16$ [−0.24, −0.08]). In turn, while biomass turnover was still slightly higher for pelagically derived carbon on the forereef, the discrepancy between benthic and pelagic carbon turnover was less clear (forereef-pelagic: $\beta = 0.15$ [0.00, 0.29]).

DISCUSSION

The sources and pathways of energy in animal communities are a central topic of ecological investigation. Focusing on small consumers on tropical coral reefs, we

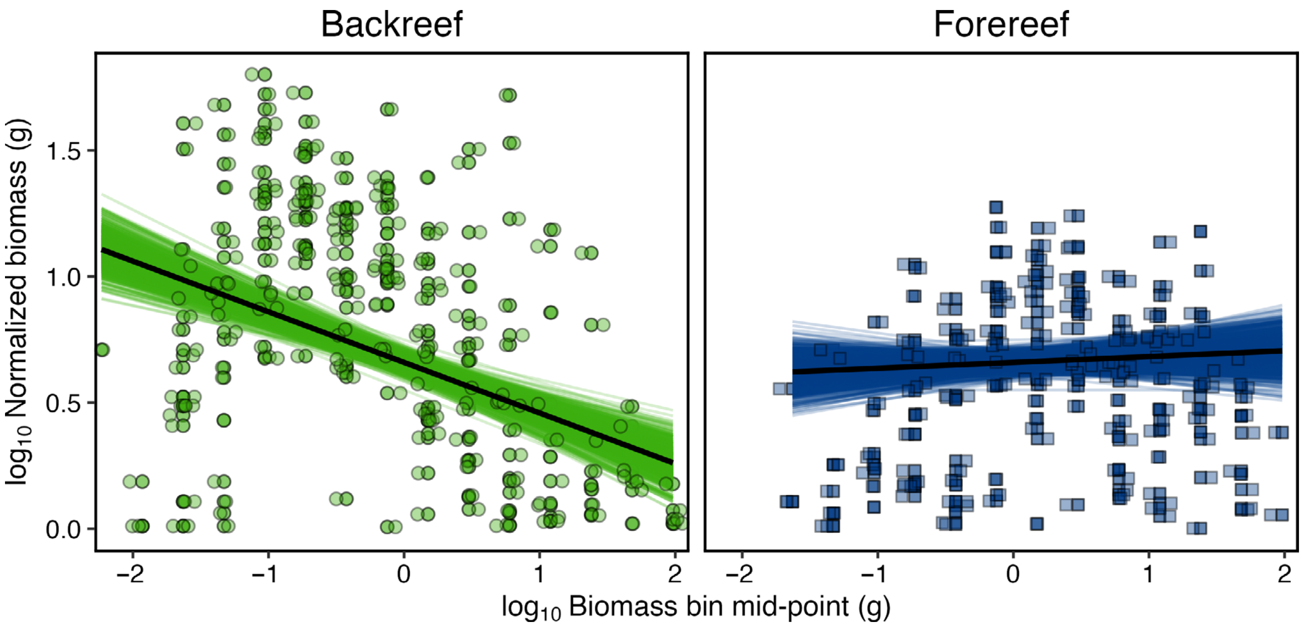

FIGURE 3 Size spectrum analysis of cryptobenthic fish communities from Mo'orea, French Polynesia. Points and lines show the cumulative representation of size bins (*x*-axis) and their respective normalized biomass (*y*-axis) across stations (marginalized over the random effect). Thin colored lines denote the predicted fit from a Bayesian linear mixed-effects model, while the thick black lines denote the mean fit between the two habitats (green = backreef; blue = forereef).

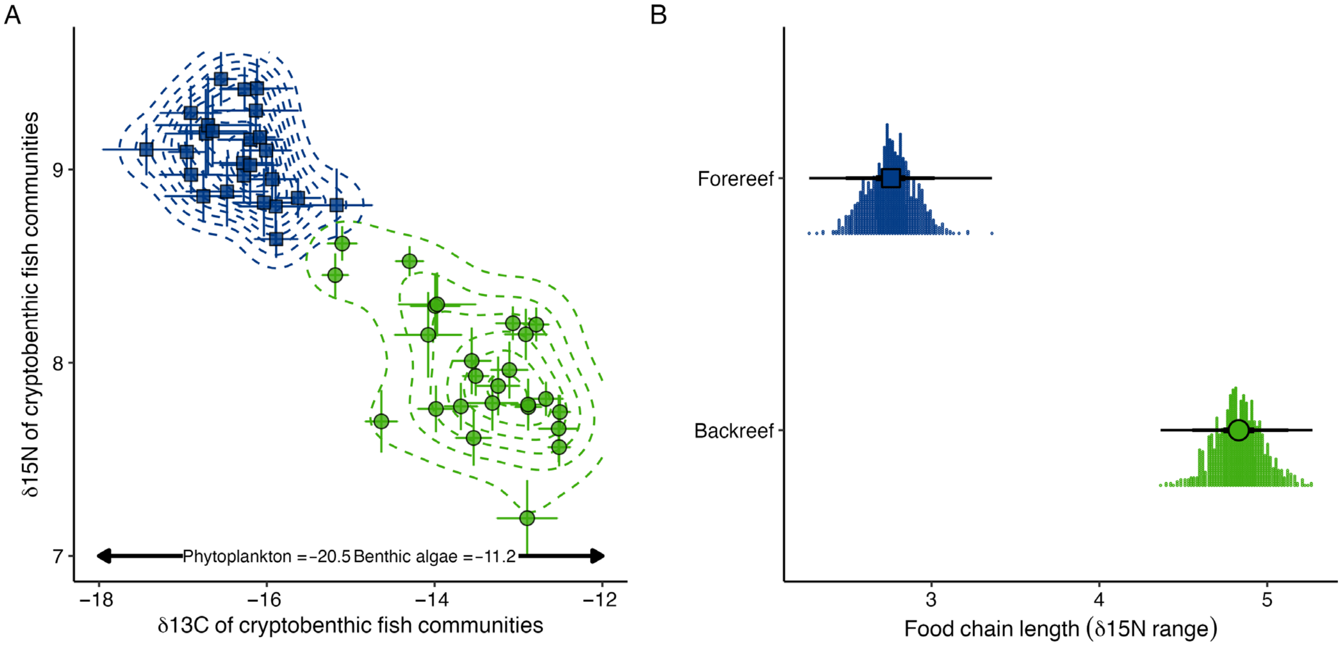

FIGURE 4 Community-scale isotopic profiles of cryptobenthic fish communities from Mo'orea, French Polynesia. (A) Relationship between community-scale δ^{13}C and δ^{15}N values, separated by habitat (green = backreef; blue = forereef). Horizontal and vertical error bars denote the associated SE in each community, while isopleths highlight the spread of the data within the two habitats. Black arrows and text highlight the δ^{13}C values of the two source materials (phytoplankton and benthic algae). (B) Differences in food chain length (derived from the range of δ^{15}N values within a single community) across the two habitats. Distributions and caterpillar plots show the full distribution of posterior predicted values and their median, 50%, and 95% credible intervals, respectively.

show that these dynamics depend strongly on whether a reef habitat is facing the open ocean or located in an enclosed lagoon, even if the two habitats are separated by less than a few hundred meters. On coral reefs in Mo'orea, French Polynesia, cryptobenthic fish communities in the sheltered lagoonal backreef are compositionally distinct and more abundant than those on the nearby seaward-facing forereef and exhibit drastically different size structuring, carbon source use, and productivity dynamics. Specifically, backreef communities of small consumers exhibit a classic size-structured trophic pyramid, in which small-bodied species rapidly produce and transfer biomass to larger consumers, largely fueled by benthic carbon derived from algal sources. Despite comparable standing stock biomass, the trophic structure of forereef communities suggests that they are supported by allochthonous subsidies, which is evident in the dominant contribution of pelagically derived carbon to standing biomass and productivity. Yet, the latter falls short of the productivity in backreef communities. These findings suggest strong dichotomies in not only community structure and energy sources, but also the trophic functioning of coral reef fish communities across very small spatial scales, which may extend to a variety of ecosystem dynamics, including those that underpin services to human societies. As such, our results call for a better integration of habitat-specific dynamics into our interpretation of coral reef ecosystem functioning and highlight the utility of integrative approaches in diverse and well-connected marine ecosystems.

Habitat-mediated differences in fish community structure

The zonation of coral reefs can create distinct breaks in community structure and ecological processes (Darling et al., 2017; Fox & Bellwood, 2007; Friedlander et al., 2010; Hay, 1981). Previous work suggests this occurs for both fish community composition and ecological dynamics, such as coral–macroalgal phase shifts, in Mo'orea (Galzin, 1987; Schmitt et al., 2019). We also found this to be true for cryptobenthic fishes. Cryptobenthic fish community composition differs strongly among reef habitats in various bioregions (Brandl et al., 2020; Depczynski & Bellwood, 2005b; Greenfield, 2003; Harborne et al., 2012), but the importance of exposure to the open ocean relative to other biotic and abiotic controls can vary. For example, wave exposure superseded the importance of microhabitat composition across an exposure gradient on Lizard Island, Australia, where, similar to our study, shallow exposed forereef sites exhibited depauperate communities made up of fewer,

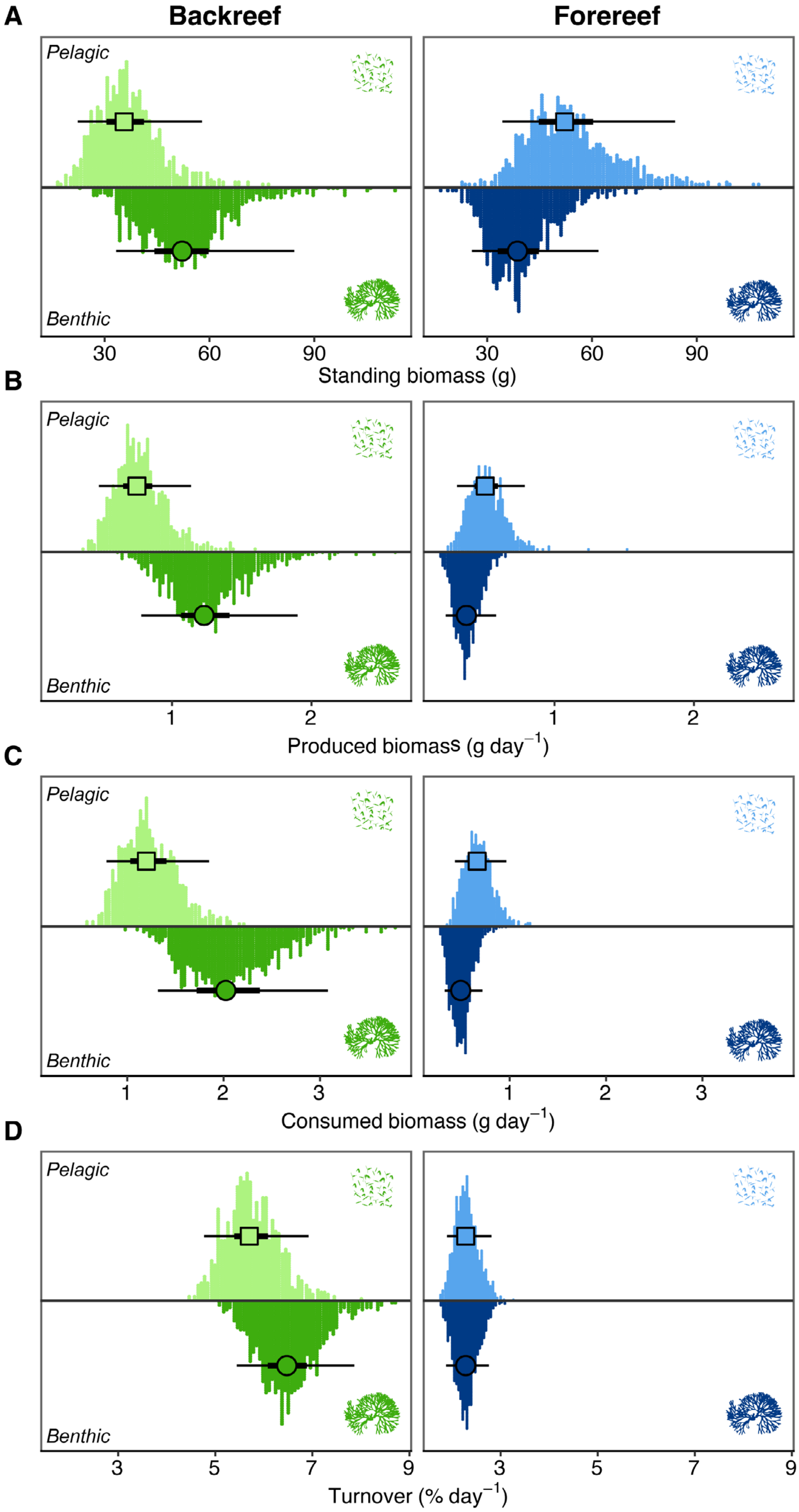

FIGURE 5 Legend on next page.

larger individuals that may be better suited to withstand wave action (Depczynski & Bellwood, 2005b). Similarly, wave exposure shaped cryptobenthic fish communities on the Belizean Barrier Reef (Brandl et al., 2020). In contrast, on Caribbean reefs surrounding the US Virgin Islands, the availability of dead coral substrate was more important than the exposure regime for predicting cryptobenthic fish assemblages (Harborne et al., 2012). In our study, the weak (or even absent) correlations between the two most dominant benthic components (live coral at 34.0% mean cover and turf algae at 31.4% mean cover across all stations) and cryptobenthic fish abundance and species richness support the notion that seascape effects may be stronger than the influence of fine-scale habitat variability.

Benthic cover by live coral by itself, in particular, had no notable effects on cryptobenthic fish abundance or richness. Live coral is often cited as crucial habitat for small fishes (Pratchett et al., 2011), but a comparatively small number of cryptobenthic reef fishes (e.g., *Gobiodon*, *Paragobiodon*, and *Pleurosicya*) directly depend on live coral habitat for food or shelter (Brandl et al., 2018; Coker et al., 2014). Most of these (except *Pleurosicya*) favor branching coral, which was abundantly available on the forereef. While the abundances of these species are generally low compared with other cryptobenthic species (Depczynski & Bellwood, 2004), they can significantly contribute to species richness due to their high microhabitat specificity (Munday et al., 1997). Yet, given the remote location of French Polynesia, Mo'orea's history of multiple sequential disturbances (Pérez-Rosales et al., 2021), and the strong impact of multiple disturbances on coral goby populations (Bellwood et al., 2012; Froehlich et al., 2021; Munday, 2004), the community of coral-dwelling gobies around Mo'orea may already be depleted, which could explain the lack of correlation between live coral cover and cryptobenthic fish community structure. In turn, akin to the strong positive correlation between cryptobenthic fishes and dead coral in the Caribbean (Harborne et al., 2012), we found a positive correlation between turf algal cover and cryptobenthic fish abundance. Many species of cryptobenthic fishes feed on filamentous algae, detritus, and turf-associated meiofauna such as copepods (Brandl et al., 2018; Depczynski & Bellwood, 2003). Thus, the correlation between turf algal cover and cryptobenthic fish abundance suggests a direct energetic link between resources and consumers, which is strengthened by a detailed investigation of the trophic structure and dynamics in the two communities. In turn, the weak relationship between turf cover and richness may indicate diminished microhabitat heterogeneity, which precludes the existence of some specialist species. This is further supported by the diametrically opposed correlations between species richness and the positioning of stations in the benthic PCoA (Appendix S1: Figure S2), which suggests that more extreme and ostensibly homogeneous benthic configurations on both the back- and the forereef reduce cryptobenthic fish diversity.

Energy fluxes through cryptobenthic fish communities

The size structure of consumer communities can reveal critical insights into the transfer of energy and nutrients across biomes (Graham et al., 2005; Potapov, Klarner, et al., 2019). Body size distribution is generally a powerful predictor of ecological dynamics in marine ecosystems (Blanchard et al., 2017), but within fish communities, this structure can be highly compartmentalized (i.e., present only within certain sub-sections of the entire community) (Jennings et al., 2001). Our results show that, as a compartment of the wider reef fish community that is typically ignored in size spectrum analyses, lagoonal cryptobenthic fish communities form a typical bottom-heavy trophic pyramid, while forereef communities of small consumers show no perceptible differences in biomass across size classes. These patterns, alongside the isotopic results, help us understand the energetic dynamics that operate in small consumer communities in the two habitats.

Given the abundance of a highly productive primary producer in shallow, lagoonal habitats (filamentous turf algae) that is available to small consumers (Hatcher, 1988; Steneck & Dethier, 1994), it is intuitive that these systems are energetically driven by bottom-up dynamics, resulting in a traditional trophic pyramid. In contrast, the horizontal slope for size spectrum analyses on the forereef suggests limited size structuring, akin to a trophic stack or diamond (Woodson et al., 2018). This pattern could be explained by incomplete sampling of the community or the influence of an allochthonous resource (Trebilco et al., 2013). Both are possible in our case. First, the community of small fishes on the forereef featured many small, cryptic predators.

FIGURE 5 Energy fluxes through cryptobenthic fish communities (A = standing biomass; B = produced biomass; C = consumed biomass; D = turnover) on the backreef (green) and forereef (blue) in Mo'orea, French Polynesia, divided into carbon derived from pelagic sources (light color = seawater) and benthic sources (dark = benthic algae). Density curves show the distribution of the fitted values from Bayesian generalized linear mixed-effects models, while caterpillar plots indicate the mean as well as the 50% (thick line) and 95% (thin line) credible intervals. Illustrations by Simon J. Brandl.

These predators (largely composed of cirrhitids, serranids, and scorpaenids) regularly prey on macroinvertebrates such as caridean shrimp or brachyuran crabs (Casey et al., 2019; Leray et al., 2015), which were not considered in the present study but represent a substantial biomass reservoir at low trophic levels (Heather et al., 2021; Wolfe et al., 2020). Furthermore, larger bodied and more mobile predators (e.g., medium-sized groupers) are likely to escape from the area during sampling. Second, given the expansive interface between forereefs and the open ocean and the prevalence of plankton-feeding species, it is likely that trophic subsidies in the form of pelagically derived plankton underpin the energetic dynamics in the forereef community (Morais & Bellwood, 2019). These subsidies are unlikely to be easily accessible for the smallest size classes of cryptobenthic fishes (e.g., dwarf gobies in the genus *Eviota*), since these fishes are unable to withstand hydrodynamic forcing in high-flow environments and rely on strong associations with the benthos for survival (Brandl et al., 2018; Miller, 1996). As a consequence, cryptobenthic fish communities on the forereef around Mo'orea lack the high numbers of small cryptobenthic species that are characteristic of the lagoonal communities.

This, in turn, begets different energy fluxes through the two communities. Our stable isotope analyses revealed a clear dichotomy in the use of benthic versus pelagic resources across the two communities, despite the limited spatial separation. As expected, given the trophic structuring, forereef communities relied more heavily on pelagically derived carbon and showed higher trophic positioning and shorter food chains. In contrast, backreef communities were fueled by benthic carbon and supported longer food chains and lower trophic levels. Previous research has shown a shift in the reliance of reef fishes on pelagic versus benthic productivity across a reefscape (from the exposed forereef to the lagoonal backreef) (Wyatt et al., 2012), which is likely related to the rapid depletion of zooplankton on the reef crest by planktivorous organisms (Hamner et al., 1988). This is further supported by research showing an increasing importance of benthic primary production toward the center of reef flat habitats (Davis et al., 2015). Indeed, measurements of carbon availability on a transect from the reef crest to the shoreline in Mo'orea have shown that the vast majority of new production in the lagoon comes from benthic autotrophs (Alldredge et al., 2013).

Collectively, these dynamics profoundly affect the transfer of carbon to higher-level consumers, as revealed by our isotopically informed demographic models. Specifically, while communities in both habitats boast comparable standing biomass, cryptobenthic fish communities in the lagoon exhibit much higher production, transfer (i.e., consumed biomass), and turnover of biomass, which is predominantly fueled by carbon derived from benthic autotrophs. The high production of fish biomass on coral reefs has been a subject of interest to ecologists since the 1950s (Hatcher, 1997; Odum & Odum, 1955; Sargent & Austin, 1954), and various sources and conduits have been highlighted as important for maintaining coral reef productivity (Brandl et al., 2019; De Goeij et al., 2013; Morais & Bellwood, 2019; Skinner et al., 2021; Wild et al., 2004). Our results suggest that, at least in a Pacific reef system,

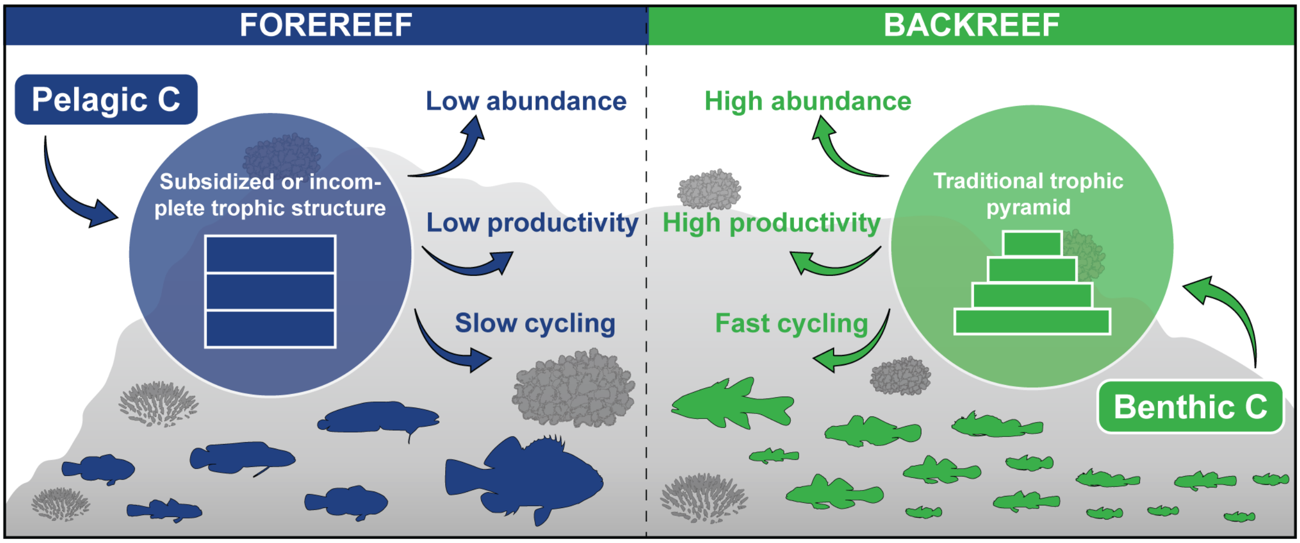

FIGURE 6 Conceptual summary of the dichotomy in the role of cryptobenthic communities across coral reef habitats. On the forereef, pelagic carbon fuels a non-size-structured community that has high-standing biomass, but low abundance, productivity, and turnover. In contrast, the backreef harbors a traditional trophic pyramid of small consumers. These communities are sustained by benthic carbon and exhibit high abundance, productivity, and biomass turnover, with comparable standing stock to slope communities. Illustrations by Simon J. Brandl.

there is a clear dichotomy in the primary energetic channels that underpin reef fish productivity at a relatively small spatial scale (Figure 6): by harnessing benthic-derived carbon and passing it to higher trophic levels, cryptobenthic fishes promote the sequestration and transfer of benthic production to higher trophic levels in the lagoon, while they play a minimal role in the capture and transfer of pelagic primary production on the forereef. This highlights the deep context-dependency of ecological dynamics in ecosystems with strong spatial partitioning and calls for caution in deriving conclusions from case studies across a limited number of sites or habitats.

Beyond coral reefs, our results showcase the potential of combining multiple techniques to trace energy and nutrient fluxes in complex marine, freshwater, and terrestrial ecosystems. While size spectra and stable isotope analyses have a long history of impactful application in marine systems (Blanchard et al., 2017; Eddy et al., 2021) and modeling of energy and nutrient fluxes has gained popularity in recent years (Allgeier et al., 2017; Schiettekatte et al., 2020), the various methods at our disposal have rarely been used in concert (Robinson et al., 2023). As a consequence, we still lack a thorough understanding of (1) what food web compartments and energy channels underpin the productivity of most coastal marine ecosystems and (2) what drivers mediate the importance of different energy sources for large consumer species across environmental gradients. In terrestrial systems, the integration of multiple approaches has revealed some of these dynamics (Potapov et al., 2021), including critical information about changes in energy flow following human interference (Pollierer et al., 2023; Potapov, Klarner, et al., 2019). As coastal marine ecosystems continue to change, a better and more generalized comprehension of when, where, and why a given suite of sources and consumers emerge as critical energy and nutrient channels remains an important challenge.

AUTHOR CONTRIBUTIONS

Simon J. Brandl conceived the study with Isabelle M. Côté and Valeriano Parravicini. Simon J. Brandl, Jordan M. Casey, Nina M. D. Schiettekatte, Helen F. Yan, Valeriano Parravicini, and Alexandre Mercière performed the field collections. Julianna J. Renzi, Nina M. D. Schiettekatte, Alexandre Mercière, and Fabien Morat performed the laboratory work and image processing. Simon J. Brandl and Helen F. Yan performed the statistical analyses. Simon J. Brandl wrote the first draft of the paper, and all coauthors contributed thereafter.

ACKNOWLEDGMENTS

This work was funded by the BNP Paribas Foundation (REEF-Services), the Agence Nationale pour la Recherche (REEFLUX; ANR-17-CE32-0006), the Natural Sciences and Engineering Research Council of Canada (NSERC) (Discovery Grant RGPIN/03933-2017), and the Institut des Récifs Coralliens du Pacifique (IRCP). Simon J. Brandl was supported by an NSERC Vanier-Banting Fellowship. Additional support comes from a National Science Foundation Graduate Research Fellowship (DGE-1650114; Julianna J. Renzi), Australian Research Council Laureate Scholarship and NSERC Postgraduate Doctoral Scholarship (Helen F. Yan) and Make Our Planet Great Again Postdoctoral Grant (mopga-pdf-0000000144; Jordan M. Casey). Collections were performed using permit number 681/MCE/ENV and under Simon Fraser University Animal Care approval 1254B-17. We thank Samuel Degregori, Jason Vii, and the staff of CRIOBE in Mo'orea for field and laboratory assistance.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Brandl, 2025) are available in Figshare at https://doi.org/10.6084/m9.figshare.28400828.v1.

ORCID

Simon J. Brandl https://orcid.org/0000-0002-6649-2496
Helen F. Yan https://orcid.org/0000-0002-9428-9882
Nina M. D. Schiettekatte https://orcid.org/0000-0002-1925-3484
Julianna J. Renzi https://orcid.org/0000-0002-6187-8656
Fabien Morat https://orcid.org/0000-0002-9925-1437

REFERENCES

Adams, L. G., S. D. Farley, C. A. Stricker, D. J. Demma, G. H. Roffler, D. C. Miller, and R. O. Rye. 2010. "Are Inland Wolf–Ungulate Systems Influenced by Marine Subsidies of Pacific Salmon?" *Ecological Applications* 20: 251–262.

Alldredge, A. L., C. A. Carlson, and R. C. Carpenter. 2013. "Sources of Organic Carbon to Coral Reef Flats." *Oceanography* 26: 108–113.

Allen, D. C., and J. S. Wesner. 2016. "Synthesis: Comparing Effects of Resource and Consumer Fluxes into Recipient Food Webs Using Meta-Analysis." *Ecology* 97: 594–604.

Allgeier, J. E., D. E. Burkepile, and C. A. Layman. 2017. "Animal Pee in the Sea: Consumer-Mediated Nutrient Dynamics in the World's Changing Oceans." *Global Change Biology* 23: 2166–78.

Atkinson, C. L., K. A. Capps, A. T. Rugenski, and M. J. Vanni. 2017. "Consumer-Driven Nutrient Dynamics in Freshwater Ecosystems: From Individuals to Ecosystems." *Biological Reviews* 92: 2003–23.

Barnes, A. D., P. Weigelt, M. Jochum, D. Ott, D. Hodapp, N. F. Haneda, and U. Brose. 2016. "Species Richness and Biomass Explain Spatial Turnover in Ecosystem Functioning across Tropical and Temperate Ecosystems." *Philosophical Transactions of the Royal Society B: Biological Sciences* 371: 20150279.

Baxter, C. V., K. D. Fausch, and W. Carl Saunders. 2005. "Tangled Webs: Reciprocal Flows of Invertebrate Prey Link Streams and Riparian Zones." *Freshwater Biology* 50: 201–220.

Beijbom, O., P. J. Edmunds, C. Roelfsema, J. Smith, D. I. Kline, B. P. Neal, M. J. Dunlap, V. Moriarty, T.-Y. Fan, and C.-J. Tan. 2015. "Towards Automated Annotation of Benthic Survey Images: Variability of Human Experts and Operational Modes of Automation." *PLoS One* 10: e0130312.

Bellwood, D. R., A. H. Baird, M. Depczynski, A. González-Cabello, A. S. Hoey, C. D. Lefèvre, and J. K. Tanner. 2012. "Coral Recovery May Not Herald the Return of Fishes on Damaged Coral Reefs." *Oecologia* 170: 567–573.

Blanchard, J. L., N. K. Dulvy, S. Jennings, J. R. Ellis, J. K. Pinnegar, A. Tidd, and L. T. Kell. 2005. "Do Climate and Fishing Influence Size-Based Indicators of Celtic Sea Fish Community Structure?" *ICES Journal of Marine Science* 62: 405–411.

Blanchard, J. L., R. F. Heneghan, J. D. Everett, R. Trebilco, and A. J. Richardson. 2017. "From Bacteria to Whales: Using Functional Size Spectra to Model Marine Ecosystems." *Trends in Ecology & Evolution* 32: 174–186.

Brandl, S. J. 2025. "Data and Code for Brandl et al. (2025) A Seascape Dichotomy in the Role of Small Consumers for Coral Reef Energy Fluxes." Ecology. Figshare. https://doi.org/10.6084/m9.figshare.28400828.v1.

Brandl, S. J., and D. R. Bellwood. 2014. "Individual-Based Analyses Reveal Limited Functional Overlap in a Coral Reef Fish Community." *Journal of Animal Ecology* 83: 661–670.

Brandl, S. J., J. Carlot, R. D. Stuart-Smith, S. A. Keith, N. A. Graham, G. J. Edgar, J. Wicquart, S. K. Wilson, R. Karkarey, and M. K. Donovan. 2024. "Unifying Coral Reef States through Space and Time Reveals a Changing Ecosystem." *Global Ecology and Biogeography* 33: e13926.

Brandl, S. J., J. M. Casey, N. Knowlton, and J. E. Duffy. 2017. "Marine Dock Pilings Foster Diverse, Native Cryptobenthic Fish Assemblages across Bioregions." *Ecology and Evolution* 7: 7069–79.

Brandl, S. J., J. M. Casey, and C. P. Meyer. 2020. "Dietary and Habitat Niche Partitioning in Congeneric Cryptobenthic Reef Fish Species." *Coral Reefs* 39: 1–13.

Brandl, S. J., C. H. Goatley, D. R. Bellwood, and L. Tornabene. 2018. "The Hidden Half: Ecology and Evolution of Cryptobenthic Fishes on Coral Reefs." *Biological Reviews* 93: 1846–73.

Brandl, S. J., L. Tornabene, C. H. Goatley, J. M. Casey, R. A. Morais, I. M. Côté, C. C. Baldwin, V. Parravicini, N. M. Schiettekatte, and D. R. Bellwood. 2019. "Demographic Dynamics of the Smallest Marine Vertebrates Fuel Coral Reef Ecosystem Functioning." *Science* 364: 1189–92.

Briand, M. J., X. Bonnet, C. Goiran, G. Guillou, and Y. Letourneur. 2015. "Major Sources of Organic Matter in a Complex Coral Reef Lagoon: Identification from Isotopic Signatures (δ13C and δ15N)." *PLoS One* 10: e0131555.

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. "Toward a Metabolic Theory of Ecology." *Ecology* 85: 1771–89.

Bürkner, P.-C. 2017. "brms: An R Package for Bayesian Multilevel Models Using Stan." *Journal of Statistical Software* 80: 1–28.

Casey, J. M., C. P. Meyer, F. Morat, S. J. Brandl, S. Planes, and V. Parravicini. 2019. "Reconstructing Hyperdiverse Food Webs: Gut Content Metabarcoding as a Tool to Disentangle Trophic Interactions on Coral Reefs." *Methods in Ecology and Evolution* 10: 1157–70.

Chen, Q., O. Beijbom, S. Chan, J. Bouwmeester, and D. Kriegman. 2021. "A New Deep Learning Engine for Coralnet." 3693–3702 pp. https://openaccess.thecvf.com/content/ICCV2021W/OceanVision/html/Chen_A_New_Deep_Learning_Engine_for_CoralNet_ICCVW_2021_paper.html.

Christensen, V., and C. J. Walters. 2004. "Ecopath with Ecosim: Methods, Capabilities and Limitations." *Ecological Modelling* 172: 109–139.

Coker, D. J., S. K. Wilson, and M. S. Pratchett. 2014. "Importance of Live Coral Habitat for Reef Fishes." *Reviews in Fish Biology and Fisheries* 24: 89–126.

Darling, E. S., N. A. Graham, F. A. Januchowski-Hartley, K. L. Nash, M. S. Pratchett, and S. K. Wilson. 2017. "Relationships between Structural Complexity, Coral Traits, and Reef Fish Assemblages." *Coral Reefs* 36: 561–575.

Davis, J. P., K. A. Pitt, R. M. Connolly, and B. Fry. 2015. "Community Structure and Dietary Pathways for Invertebrates on Intertidal Coral Reef Flats." *Food Webs* 3: 7–16.

De Goeij, J. M., D. Van Oevelen, M. J. Vermeij, R. Osinga, J. J. Middelburg, A. F. de Goeij, and W. Admiraal. 2013. "Surviving in a Marine Desert: The Sponge Loop Retains Resources within Coral Reefs." *Science* 342: 108–110.

DeAngelis, D. L. 1980. "Energy Flow, Nutrient Cycling, and Ecosystem Resilience." *Ecology* 61: 764–771.

Depczynski, M., and D. Bellwood. 2004. "Microhabitat Utilisation Patterns in Cryptobenthic Coral Reef Fish Communities." *Marine Biology* 145: 455–463.

Depczynski, M., and D. R. Bellwood. 2003. "The Role of Cryptobenthic Reef Fishes in Coral Reef Trophodynamics." *Marine Ecology Progress Series* 256: 183–191.

Depczynski, M., and D. R. Bellwood. 2005a. "Shortest Recorded Vertebrate Lifespan Found in a Coral Reef Fish." *Current Biology* 15: R288–R289.

Depczynski, M., and D. R. Bellwood. 2005b. "Wave Energy and Spatial Variability in Community Structure of Small Cryptic Coral Reef Fishes." *Marine Ecology Progress Series* 303: 283–293.

Depczynski, M., and D. R. Bellwood. 2006. "Extremes, Plasticity, and Invariance in Vertebrate Life History Traits: Insights from Coral Reef Fishes." *Ecology* 87: 3119–27.

Eddy, T. D., J. R. Bernhardt, J. L. Blanchard, W. W. Cheung, M. Colléter, H. Du Pontavice, E. A. Fulton, D. Gascuel, K. A. Kearney, and C. M. Petrik. 2021. "Energy Flow through Marine Ecosystems: Confronting Transfer Efficiency." *Trends in Ecology & Evolution* 36: 76–86.

Edwards, A. M., J. P. Robinson, M. J. Plank, J. K. Baum, and J. L. Blanchard. 2017. "Testing and Recommending Methods for Fitting Size Spectra to Data." *Methods in Ecology and Evolution* 8: 57–67.

Elser, J., R. Sterner, E. Gorokhova, W. Fagan, T. Markow, J. Cotner, J. Harrison, S. Hobbie, G. Odell, and L. Weider. 2000. "Biological Stoichiometry from Genes to Ecosystems." *Ecology Letters* 3: 540–550.

Fox, R. J., and D. R. Bellwood. 2007. "Quantifying Herbivory across a Coral Reef Depth Gradient." *Marine Ecology Progress Series* 339: 49–59.

Friedlander, A. M., S. A. Sandin, E. E. DeMartini, and E. Sala. 2010. "Spatial Patterns of the Structure of Reef Fish Assemblages at a Pristine Atoll in the Central Pacific." *Marine Ecology Progress Series* 410: 219–231.

Frisch, A. J., M. Ireland, J. R. Rizzari, O. M. Lönnstedt, K. A. Magnenat, C. E. Mirbach, and J.-P. A. Hobbs. 2016. "Reassessing the Trophic Role of Reef Sharks as Apex Predators on Coral Reefs." *Coral Reefs* 35: 459–472.

Froehlich, C. Y., O. S. Klanten, M. L. Hing, M. Dowton, and M. Y. Wong. 2021. "Uneven Declines between Corals and Cryptobenthic Fish Symbionts from Multiple Disturbances." *Scientific Reports* 11: 1–10.

Galzin, R. 1987. "Structure of Fish Communities of French Polynesian Coral Reefs. 1. Spatial Scales. Marine Ecology Progress Series." *Oldendorf* 41: 129–136.

Goatley, C. H., A. González-Cabello, and D. R. Bellwood. 2017. "Small Cryptopredators Contribute to High Predation Rates on Coral Reefs." *Coral Reefs* 36: 207–212.

Goldsworthy, N. C., M. Srinivasan, P. Smallhorn-West, L. Cheah, P. L. Munday, and G. P. Jones. 2022. "Life-History Constraints, Short Adult Life Span and Reproductive Strategies in Coral Reef Gobies of the Genus *Trimma*." *Journal of Fish Biology* 101: 996–1007.

Govan, E., A. L. Jackson, R. Inger, S. Bearhop, and A. C. Parnell. 2023. "simmr: A Package for Fitting Stable Isotope Mixing Models in R." arXiv preprint arXiv:2306.07817. https://arxiv.org/abs/2306.07817.

Graham, N., N. Dulvy, S. Jennings, and N. Polunin. 2005. "Size-Spectra as Indicators of the Effects of Fishing on Coral Reef Fish Assemblages." *Coral Reefs* 24: 118–124.

Greenfield, D. W. 2003. "A Survey of the Small Reef Fishes of Kane'ohe Bay, O'ahu, Hawaiian Islands." *Pacific Science* 57: 45–76.

Hamner, W., M. Jones, J. Carleton, I. Hauri, and D. M. Williams. 1988. "Zooplankton, Planktivorous Fish, and Water Currents on a Windward Reef Face: Great Barrier Reef, Australia." *Bulletin of Marine Science* 42: 459–479.

Hanson, P. C., T. B. Johnson, D. E. Schindler, and J. F. Kitchell. 1997. "Fish Bioenergetics 3.0 for Windows." https://repository.library.noaa.gov/view/noaa/42424.

Harborne, A., H. Jelks, W. Smith-Vaniz, and L. Rocha. 2012. "Abiotic and Biotic Controls of Cryptobenthic Fish Assemblages across a Caribbean Seascape." *Coral Reefs* 31: 977–990.

Hatcher, B. 1997. "Coral Reef Ecosystems: How Much Greater Is the Whole than the Sum of the Parts?" *Coral Reefs* 16: S77–S91.

Hatcher, B. G. 1988. "Coral Reef Primary Productivity: A beggar's Banquet." *Trends in Ecology & Evolution* 3: 106–111.

Hay, M. E. 1981. "Herbivory, Algal Distribution, and the Maintenance of Between-Habitat Diversity on a Tropical Fringing Reef." *The American Naturalist* 118: 520–540.

Heather, F. J., J. L. Blanchard, G. J. Edgar, R. Trebilco, and R. D. Stuart-Smith. 2021. "Globally Consistent Reef Size Spectra Integrating Fishes and Invertebrates." *Ecology Letters* 24: 572–79.

Hernaman, V., and P. Munday. 2005. "Life-History Characteristics of Coral Reef Gobies. I. Growth and Life-Span." *Marine Ecology Progress Series* 290: 207–221.

Hernaman, V., P. Probert, and W. Robbins. 2009. "Trophic Ecology of Coral Reef Gobies: Interspecific, Ontogenetic, and Seasonal Comparison of Diet and Feeding Intensity." *Marine Biology* 156: 317–330.

Hilting, A. K., C. A. Currin, and R. K. Kosaki. 2013. "Evidence for Benthic Primary Production Support of an Apex Predator–Dominated Coral Reef Food Web." *Marine Biology* 160: 1681–95.

Hobson, K. A., J. F. Piatt, and J. Pitocchelli. 1994. "Using Stable Isotopes to Determine Seabird Trophic Relationships." *Journal of Animal Ecology* 63: 786–798.

Jennings, S., J. K. Pinnegar, N. V. Polunin, and T. W. Boon. 2001. "Weak Cross-Species Relationships between Body Size and Trophic Level Belie Powerful Size-Based Trophic Structuring in Fish Communities." *Journal of Animal Ecology* 70(6): 934–944. https://doi.org/10.1046/j.0021-8790.2001.00552.x.

Koltz, A. M., A. Asmus, L. Gough, Y. Pressler, and J. C. Moore. 2018. "The Detritus-Based Microbial-Invertebrate Food Web Contributes Disproportionately to Carbon and Nitrogen Cycling in the Arctic." *Polar Biology* 41: 1531–45.

Koltz, A. M., L. A. Burkle, Y. Pressler, J. E. Dell, M. C. Vidal, L. A. Richards, and S. M. Murphy. 2018. "Global Change and the Importance of Fire for the Ecology and Evolution of Insects." *Current Opinion in Insect Science* 29: 110–16.

Leray, M., C. P. Meyer, and S. C. Mills. 2015. "Metabarcoding Dietary Analysis of Coral Dwelling Predatory Fish Demonstrates the Minor Contribution of Coral Mutualists to their Highly Partitioned, Generalist Diet." *PeerJ* 3: e1047.

Manca, F., C. Mulà, C. Gustafsson, A. Mauri, T. Roslin, D. N. Thomas, L. Benedetti-Cecchi, A. Norkko, and G. Strona. 2022. "Unveiling the Complexity and Ecological Function of Aquatic Macrophyte–Animal Networks in Coastal Ecosystems." *Biological Reviews* 97: 1306–24.

McMahon, K. W., S. R. Thorrold, L. A. Houghton, and M. L. Berumen. 2016. "Tracing Carbon Flow through Coral Reef Food Webs Using a Compound-Specific Stable Isotope Approach." *Oecologia* 180: 809–821.

Miller, P. J. 1996. *Miniature Vertebrates. The Implications of Small Body Size*. New York: Oxford University Press.

Morais, R. A., and D. R. Bellwood. 2018. "Global Drivers of Reef Fish Growth." *Fish and Fisheries* 19: 874–889.

Morais, R. A., and D. R. Bellwood. 2019. "Pelagic Subsidies Underpin Fish Productivity on a Degraded Coral Reef." *Current Biology* 29: 1521–27.

Morais, R. A., and D. R. Bellwood. 2020. "Principles for Estimating Fish Productivity on Coral Reefs." *Coral Reefs* 39: 1221–31.

Munday, P. L. 2004. "Habitat Loss, Resource Specialization, and Extinction on Coral Reefs." *Global Change Biology* 10: 1642–47.

Munday, P. L., G. P. Jones, and M. J. Caley. 1997. "Habitat Specialisation and the Distribution and Abundance of Coral-Dwelling Gobies." *Marine Ecology Progress Series* 152: 227–239. https://doi.org/10.3354/meps152227.

Nakano, S., and M. Murakami. 2001. "Reciprocal Subsidies: Dynamic Interdependence between Terrestrial and Aquatic Food Webs." *Proceedings of the National Academy of Sciences of the United States of America* 98: 166–170.

Nicholson, G. M., and K. D. Clements. 2021. "Ecomorphological Divergence and Trophic Resource Partitioning in 15 Syntopic Indo-Pacific Parrotfishes (Labridae: Scarini)." *Biological Journal of the Linnean Society* 132: 590–611.

Nobre, R. L., L. S. Carneiro, S. E. Panek, M. J. González, and M. J. Vanni. 2019. "Fish, Including Their Carcasses, Are Net Nutrient Sources to the Water Column of a Eutrophic Lake." *Frontiers in Ecology and Evolution* 7: 340.

Norris, D. R., P. Arcese, D. Preikshot, D. F. Bertram, and T. K. Kyser. 2007. "Diet Reconstruction and Historic Population Dynamics in a Threatened Seabird." *Journal of Applied Ecology* 44: 875–884.

Odum, E. P. 1962. "Relationships between Structure and Function in the Ecosystem." *Japanese Journal of Ecology* 12: 108–118.

Odum, E. P. 1968. "Energy Flow in Ecosystems: A Historical Review." *American Zoologist* 8: 11–18.

Odum, H. T., and E. P. Odum. 1955. "Trophic Structure and Productivity of a Windward Coral Reef Community on Eniwetok Atoll." *Ecological Monographs* 25: 291–320.

Oksanen, J., R. Kindt, P. Legendre, B. O'Hara, M. H. H. Stevens, M. J. Oksanen, and M. Suggests. 2007. "The Vegan Package. Community Ecology Package 10." https://mirror.ibcp.fr/pub/CRAN/web/packages/vegan/vegan.pdf.

Parnell, A., and R. Inger. 2016. "Stable Isotope Mixing Models in R with simmr." https://cran.r-project.org/web/packages/simmr/vignettes/simmr.html.

Parnell, A. C., D. L. Phillips, S. Bearhop, B. X. Semmens, E. J. Ward, J. W. Moore, A. L. Jackson, J. Grey, D. J. Kelly, and R. Inger. 2013. "Bayesian Stable Isotope Mixing Models." *Environmetrics* 24: 387–399.

Parravicini, V., J. M. Casey, N. M. Schiettekatte, S. J. Brandl, C. Pozas-Schacre, J. Carlot, G. J. Edgar, N. A. Graham, M. Harmelin-Vivien, and M. Kulbicki. 2020. "Delineating Reef Fish Trophic Guilds with Global Gut Content Data Synthesis and Phylogeny." *PLoS Biology* 18: e3000702.

Pérez-Rosales, G., S. J. Brandl, Y. Chancerelle, G. Siu, E. Martinez, V. Parravicini, and L. Hédouin. 2021. "Documenting Decadal Disturbance Dynamics Reveals Archipelago-Specific Recovery and Compositional Change on Polynesian Reefs." *Marine Pollution Bulletin* 170: 112659.

Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. "Toward an Integration of Landscape and Food Web Ecology: The Dynamics of Spatially Subsidized Food Webs." *Annual Review of Ecology and Systematics* 28: 289–316.

Polis, G. A., and D. R. Strong. 1996. "Food Web Complexity and Community Dynamics." *The American Naturalist* 147: 813–846.

Pollierer, M. M., J. Drescher, A. Potapov, Kasmiatun, A. Mawan, M. Mutiari, R. Nazarreta, P. Hidayat, D. Buchori, and S. Scheu. 2023. "Rainforest Conversion to Plantations Fundamentally Alters Energy Fluxes and Functions in Canopy Arthropod Food Webs." *Ecology Letters* 26: 1663–75.

Post, D. M., M. L. Pace, and N. G. Hairston. 2000. "Ecosystem Size Determines Food-Chain Length in Lakes." *Nature* 405: 1047–49.

Potapov, A. M. 2022. "Multifunctionality of Belowground Food Webs: Resource, Size and Spatial Energy Channels." *Biological Reviews* 97: 1691–1711.

Potapov, A. M., U. Brose, S. Scheu, and A. V. Tiunov. 2019. "Trophic Position of Consumers and Size Structure of Food Webs across Aquatic and Terrestrial Ecosystems." *The American Naturalist* 194: 823–839.

Potapov, A. M., B. Klarner, D. Sandmann, R. Widyastuti, and S. Scheu. 2019. "Linking Size Spectrum, Energy Flux and Trophic Multifunctionality in Soil Food Webs of Tropical Land-Use Systems." *Journal of Animal Ecology*. 88: 1845–59.

Potapov, A. M., O. L. Rozanova, E. E. Semenina, V. D. Leonov, O. I. Belyakova, V. Y. Bogatyreva, M. I. Degtyarev, A. S. Esaulov, A. Y. Korotkevich, and A. A. Kudrin. 2021. "Size Compartmentalization of Energy Channeling in Terrestrial Belowground Food Webs." *Ecology* 102: e03421.

Pratchett, M. S., A. S. Hoey, S. K. Wilson, V. Messmer, and N. A. Graham. 2011. "Changes in Biodiversity and Functioning of Reef Fish Assemblages Following Coral Bleaching and Coral Loss." *Diversity* 3: 424–452.

R Core Team. 2022. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. https://www.R-project.org/.

Ripple, W. J., C. Wolf, T. M. Newsome, M. Hoffmann, A. J. Wirsing, and D. J. McCauley. 2017. "Extinction Risk Is most Acute for the world's Largest and Smallest Vertebrates." *Proceedings of the National Academy of Sciences of the United States of America* 114: 10678–83.

Robinson, J. P., C. E. Benkwitt, E. Maire, R. Morais, N. M. Schiettekatte, C. Skinner, and S. J. Brandl. 2023. "Quantifying Energy and Nutrient Fluxes in Coral Reef Food Webs." *Trends in Ecology & Evolution* 39: 467–478.

Robinson, J. P., I. D. Williams, A. M. Edwards, J. McPherson, L. Yeager, L. Vigliola, R. E. Brainard, and J. K. Baum. 2017. "Fishing Degrades Size Structure of Coral Reef Fish Communities." *Global Change Biology* 23: 1009–22.

Rogers, A., J. L. Blanchard, and P. J. Mumby. 2014. "Vulnerability of Coral Reef Fisheries to a Loss of Structural Complexity." *Current Biology* 24: 1000–1005.

Rougerie, F., J. Fagerstrom, and C. Andrie. 1992. "Geothermal Endo-Upwelling: A Solution to the Reef Nutrient Paradox?" *Continental Shelf Research* 12: 785–798.

Sargent, M. C., and T. S. Austin. 1954. *Biologic Economy of Coral Reefs*, 293–300. U.S. Geological Survey Professional Paper 260-E.

Schiettekatte, N. M., D. R. Barneche, S. Villéger, J. E. Allgeier, D. E. Burkepile, S. J. Brandl, J. M. Casey, A. Mercière, K. S. Munsterman, and F. Morat. 2020. "Nutrient Limitation, Bioenergetics and Stoichiometry: A New Model to Predict Elemental Fluxes Mediated by Fishes." *Functional Ecology* 34: 1857–69.

Schmitt, R. J., S. J. Holbrook, S. L. Davis, A. J. Brooks, and T. C. Adam. 2019. "Experimental Support for Alternative Attractors on Coral Reefs." *Proceedings of the National Academy of Sciences of the United States of America* 116: 4372–81.

Siqueira, A. C., D. R. Bellwood, and P. F. Cowman. 2019. "The Evolution of Traits and Functions in Herbivorous Coral Reef Fishes through Space and Time." *Proceedings of the Royal Society B* 286: 20182672.

Skinner, C., M. Cobain, Y. Zhu, A. Wyatt, and N. Polunin. 2022. "Progress and Direction in the Use of Stable Isotopes to Understand Complex Coral Reef Ecosystems: A Review." *Oceanography and Marine Biology* 60: 373–432.

Skinner, C., A. C. Mill, M. D. Fox, S. P. Newman, Y. Zhu, A. Kuhl, and N. Polunin. 2021. "Offshore Pelagic Subsidies Dominate Carbon Inputs to Coral Reef Predators." *Science Advances* 7: eabf3792.

Spiller, D. A., J. Piovia-Scott, A. N. Wright, L. H. Yang, G. Takimoto, T. W. Schoener, and T. Iwata. 2010. "Marine Subsidies Have Multiple Effects on Coastal Food Webs." *Ecology* 91: 1424–34.

Steneck, R. S., and M. N. Dethier. 1994. “A Functional Group Approach to the Structure of Algal-Dominated Communities.” *Oikos* 69(3): 476–498. https://doi.org/10.2307/3545860.

Takimoto, G., D. A. Spiller, and D. M. Post. 2008. “Ecosystem Size, but Not Disturbance, Determines Food-Chain Length on Islands of The Bahamas.” *Ecology* 89: 3001–7.

Trebilco, R., J. K. Baum, A. K. Salomon, and N. K. Dulvy. 2013. “Ecosystem Ecology: Size-Based Constraints on the Pyramids of Life.” *Trends in Ecology & Evolution* 28: 423–431.

Vander Zanden, M. J., B. J. Shuter, N. Lester, and J. B. Rasmussen. 1999. “Patterns of Food Chain Length in Lakes: A Stable Isotope Study.” *The American Naturalist* 154: 406–416.

Vander Zanden, M. J., and Y. Vadeboncoeur. 2002. “Fishes as Integrators of Benthic and Pelagic Food Webs in Lakes.” *Ecology* 83: 2152–61.

Wagner, D. L., E. M. Grames, M. L. Forister, M. R. Berenbaum, and D. Stopak. 2021. “Insect Decline in the Anthropocene: Death by a Thousand Cuts.” *Proceedings of the National Academy of Sciences of the United States of America* 118: e2023989118.

White, E. P., S. M. Ernest, A. J. Kerkhoff, and B. J. Enquist. 2007. “Relationships between Body Size and Abundance in Ecology.” *Trends in Ecology & Evolution* 22: 323–330.

Whiteman, J. P., E. A. Elliott Smith, A. C. Besser, and S. D. Newsome. 2019. “A Guide to Using Compound-Specific Stable Isotope Analysis to Study the Fates of Molecules in Organisms and Ecosystems.” *Diversity* 11.

Wickham, H., M. Averick, J. Bryan, W. Chang, L. McGowan, R. François, G. Grolemund, A. Hayes, L. Henry, and J. Hester. 2019. “Welcome to the Tidyverse.” *Journal of Open Source Software* 4: 1686.

Wild, C., M. Huettel, A. Klueter, S. G. Kremb, M. Y. Rasheed, and B. B. Jørgensen. 2004. “Coral Mucus Functions as an Energy Carrier and Particle Trap in the Reef Ecosystem.” *Nature* 428: 66–70.

Wolfe, K., A. Desbiens, J. Stella, and P. J. Mumby. 2020. “Length–Weight Relationships to Quantify Biomass for Motile Coral Reef Cryptofauna.” *Coral Reefs* 39: 1649–60.

Woodson, C. B., J. R. Schramski, and S. B. Joye. 2018. “A Unifying Theory for Top-Heavy Ecosystem Structure in the Ocean.” *Nature Communications* 9: 23.

Wyatt, A. S., R. J. Lowe, S. Humphries, and A. M. Waite. 2013. “Particulate Nutrient Fluxes over a Fringing Coral Reef: Source-Sink Dynamics Inferred from Carbon to Nitrogen Ratios and Stable Isotopes.” *Limnology and Oceanography* 58: 409–427.

Wyatt, A. S., A. M. Waite, and S. Humphries. 2012. “Stable Isotope Analysis Reveals Community-Level Variation in Fish Trophodynamics across a Fringing Coral Reef.” *Coral Reefs* 31: 1029–44.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Brandl, Simon J., Helen F. Yan, Jordan M. Casey, Nina M. D. Schiettekatte, Julianna J. Renzi, Alexandre Mercière, Fabien Morat, Isabelle M. Côté, and Valeriano Parravicini. 2025. “A Seascape Dichotomy in the Role of Small Consumers for Coral Reef Energy Fluxes.” *Ecology* 106(3): e70065. https://doi.org/10.1002/ecy.70065