

ARTICLE

Shortened food chain length in a fished versus unfished coral reef

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Abstract

Direct exploitation through fishing is driving dramatic declines of wildlife populations in ocean environments, particularly for predatory and large-bodied taxa. Despite wide recognition of this pattern and well-established consequences of such trophic downgrading on ecosystem function, there have been few empirical studies examining the effects of fishing on whole system trophic architecture. Understanding these kinds of structural impacts is especially important in coral reef ecosystems—often heavily fished and facing multiple stressors. Given the often high dietary flexibility and numerous functional redundancies in diverse ecosystems such as coral reefs, it is important to establish whether web architecture is strongly impacted by fishing pressure or whether it might be resilient, at least to moderate-intensity pressure. To examine this question, we used a combination of bulk and compound-specific stable isotope analyses measured across a range of predatory and low-trophic-level consumers between two coral reef ecosystems that differed with respect to fishing pressure but otherwise remained largely similar. We found that even in a high-diversity system with relatively modest fishing pressure, there were strong reductions in the trophic position (TP) of the three highest TP consumers examined in the fished system but no effects on the TP of lower-level consumers. We saw no evidence that this shortening of the affected food webs was being driven by changes in basal resource consumption, for example, through changes in the spatial location of foraging by consumers. Instead, this likely reflected internal changes in food web architecture, suggesting that even in diverse systems and with relatively modest pressure, human harvest causes significant compressions in food chain length. This observed shortening of these food webs may have many important emergent ecological consequences for the functioning of ecosystems impacted by fishing or hunting. Such important structural shifts may be widespread but unnoticed by traditional surveys. This insight may also be useful for applied ecosystem managers grappling with choices about the relative importance of protection for remote and pristine areas and the value of strict no-take areas to protect not just the raw constituents of systems affected by fishing and hunting but also the health and functionality of whole systems.

KEYWORDS

compound-specific, coral reef, food chain length, food web, sharks, stable isotopes, trophic position

INTRODUCTION

Wildlife is declining in both aquatic and terrestrial ecosystems around the world (Dirzo et al., 2014; McCauley et al., 2015), with recent estimates noting a 65% decline in vertebrate populations (Murali et al., 2022) and 69% declines in total wildlife in the last half century (Westveer et al., 2022). In marine habitats, direct exploitation through fishing is one of the most serious threats to wildlife populations (Halpern et al., 2015).

A primary driver of wildlife declines in coral reef ecosystems is fishing (Paddack et al., 2009; Williams et al., 2010). For instance, exposure to fishing reduced the biomass of herbivorous fish on coral reefs globally to about half the biomass recorded on unfished reefs (Edwards et al., 2014). The loss of both herbivorous and predatory fish on coral reefs has been shown to lead to state changes, including transition from coral to algal dominated cover (Edwards et al., 2014; Hughes et al., 2007; Mumby et al., 2006; Ruppert et al., 2013). The loss of fish also exacerbates the effects of other stressors including bleaching and disease (Harborne et al., 2017).

Considerable focus on the effects of defaunation on coral reefs has centered around declines of herbivorous species, given their important role in influencing algal-coral state transitions (e.g., Bellwood et al., 2012; Edwards et al., 2014). However, globally, large and predatory species are often among the first and most impacted by human perturbations such as fragmentation, hunting, or land-use change (Capdevila et al., 2022; Duncan et al., 2002; Gilbert et al., 1998). This selective loss of predatory organisms, referred to as “trophic downgrading” (Estes et al., 2011), can have dramatic effects on community composition and ecosystem functioning (Ferretti et al., 2010; Heithaus et al., 2008). This broad pattern has been observed in coral reef ecosystems, with the biomass and abundance of predatory fish typically declining dramatically when humans are abundant and close to reefs (Cinner et al., 2018; Friedlander & DeMartini, 2002; Sandin et al., 2008; Stallings, 2009; Valdivia et al., 2017). Predatory sharks have been especially impacted (Robbins et al., 2006; Sherman et al., 2023). Sharks are now considered one of the most threatened marine vertebrate groups, with 37% of shark and rays now listed as threatened with extinction by the International Union for Conservation of Nature (IUCN) (Dulvy et al., 2021).

Trophic downgrading is certainly not the only way fishing impacts ecosystems, for example, (Essington et al., 2006), as fishing typically occurs across multiple trophic levels, especially as fishing intensity increases (e.g., Graham et al., 2017). Yet it appears to be a common way that reef ecosystems are impacted by fishing, especially early in the fishing trajectory (e.g., Cinner et al., 2018; Pikitch et al., 2004; Sandin et al., 2008). Data documenting and describing such patterns of trophic downgrading (Friedlander & DeMartini, 2002; Pauly et al., 1998; Sandin et al., 2008; Zgliczynski & Sandin, 2017) have now facilitated new work on the emergent consequences of these shifts. Notably, it is now clear that trophic downgrading can impact change in multiple aspects of the architecture of marine food webs, including the flow of energy in these systems (Eddy et al., 2021; Edwards et al., 2020; Maureaud et al., 2017).

Aspects of food web architecture that may be strongly impacted by fishing, and specifically the selective fishing of predators, but for which there are relatively little data are the food chain position of individual consumers and overall food chain length—the trophic distance between basal and apex consumers in a community (Edwards et al., 2020; Maureaud et al., 2017). While there are few empirical data on this phenomenon, fishing could reduce total food chain length in multiple ways. Most simply, it could reduce the average number of trophic exchanges simply by removing a trophic level in a system, either by entirely removing a species or by merely removing largest individuals of a species. Even partial reductions in predators could result in a lower average number of trophic exchanges as energy may be more likely to complete a cycle without being consumed by a high-level predator. Fishing could also affect food chain length in other less visible ways. For instance, changes in fishing pressure could change the foraging ecology of the remaining consumers across multiple trophic levels, including both diet choice and movement, as has been observed in fish communities experiencing other forms of disturbance (Guerra et al., 2020, 2023; Madin, Gaines, & Warner, 2010).

Changes in foraging ecology, for example reducing intraguild predation among higher-level predators, reducing the average size of prey (without changing species of prey), or increasing omnivory, might all cause reductions in total food chain length. For instance, in a terrestrial system, changes in the diet of mesopredators and omnivores seem to primarily explain variation in measured

food chain length, rather than changes in the abundance or diet of top predators (Kuile et al., 2022). Some (but not all) other studies on coral reefs have indeed noted changes in the diets of reef consumers in response to disturbance, although not specifically to fishing degradation (Briones-Fourzán et al., 2019; Dell et al., 2015; Hempson et al., 2017).

Theory and data from other systems suggest that reductions in biodiversity will typically correlate with reduced trophic complexity and reduced food chain length (Kondoh & Ninomiya, 2009; Schriever & Dudley Williams, 2013; Vander Zanden et al., 1999). However, changes in trophic pathways and trophic structure may not always result in changes in food chain length. Where there are high levels of functional redundancy in a web, such as might be expected in a diverse coral reef system with many mesopredatory species, other species may be able to compensate for changing trophic roles. This may help buffer the trophic impact of fishing and explain why some studies show limited effects of fishing on predator or prey species (Casey et al., 2017; Loreau, 2004; Morillo-Velarde et al., 2018). Cumulatively, these results suggest that changes in the behavior or relative abundance of remaining, less targeted, consumers may be able to minimize trophic impacts, a result consistent with model predictions (Kondoh & Ninomiya, 2009). However, other studies have shown that behavioral changes in prey species in response to increased fishing can drive major trophic changes, at least in herbivores, with large cascading ecosystem effects (Guerra et al., 2020; Madin et al., 2016; Madin, Gaines, Madin, & Warner, 2010; Salomon et al., 2010). Overall, these studies suggest that behavioral changes could magnify as well as dampen the effects of fishing on trophic structure and overall food chain length.

In this study, we investigated whether and how moderate human harvesting in coral reef ecosystems altered the food chain length and trophic architecture of coral reef communities, even in systems where human density and fishing pressure is relatively low and apex predators remain present. To do this, we used a combination of ecological surveys and stable isotopic analyses across two atolls in the Central Pacific, Palmyra Atoll and Tabuaeran Atoll. Both systems retain a full suite of reef predators (i.e., no top predators have been driven locally extinct), but they varied in degrees of fishing pressure, from nearly pristine to lightly fished. We compared trophic position (TP) and food chain length in these systems using stable isotopes of nitrogen and carbon, an important toolset for understanding the trophic ecology of coral reefs (Hussey et al., 2014; Skinner et al., 2022; Wyatt et al., 2012). Specifically, we looked at changes in stable isotopic composition across a suite of predator species including (1) two common species of reef-associated sharks, high-

level mesopredators in these reef systems—gray reef sharks (*Carcharhinus amblyrhynchos*) and Galapagos sharks (*Carcharhinus galapagensis*); (2) three teleost mesopredator species that encompassed a range of size classes, mobility, and dietary preferences: a large jack (bluefin trevally, *Caranx melampygus*), a medium-sized grouper (peacock grouper, *Cephalopholis argus*), and a small snapper (blacktail snapper, *Lutjanus fulvus*); and (3) two low-trophic-level consumers: a herbivorous surgeonfish (white cheeked surgeonfish, *Acanthurus nigricans*) and a coral (*Porites lutea*), the latter of which was included as it allowed us to integrate an isotopic baseline over long time periods.

We used a combination of bulk $\delta^{15}\text{N}$ and compound-specific nitrogen isotope analysis of individual amino acids (CSSIA-AAAs) to identify TP changes within each focal organism and to estimate total food chain length. For bulk isotope analyses, we used $\delta^{13}\text{C}$ to control for potential differences in pelagic versus benthic sourcing of nutrients.

To examine the effects of fishing on reef communities, we first tested to confirm that (1) as a result of differences in human population density, the two communities would vary strongly in biomass and composition of fish community, with lower densities of large and predatory fish in the fished system, but would otherwise be similar in benthic structure and composition. We then tested the hypothesis that (2) the TP of predatory fish, but not basal consumers, would be lower in the fished compared to the unfished site and that this would be observed by both lower bulk $\delta^{15}\text{N}$ and smaller differences between trophic and source amino acids using CSSIA measurements of the higher-level predators in our fished versus unfished reef samples. Finally, we tested the hypotheses that (3) there would be minimal differences in $\delta^{13}\text{C}$ values, indicating that the changes in bulk and CSSIA $\delta^{15}\text{N}$ ratios were driven by differences in TP rather than changes in sourcing of carbon to the trophic web and (4) there would be a reduction in niche width within species in response to disturbance, providing insights into the mechanisms by which fishing may impact food chain length.

METHODS

Sites and species

This work was conducted in the northern line islands in the central Pacific between 2006 and 2009. All samples were collected from Palmyra Atoll National Wildlife Refuge (5°53' N, 162°05' W), a US outlying island, and Tabuaeran (3°51' N, 159°21' W), part of the nation of Kiribati

(Figure 1A). These two tropical coral reef atolls are situated in marine regions with similar sea surface temperatures (27.9°C vs. 27.5°C, respectively) and have similar coral cover (20.4% and 19.5%, respectively; Sandin et al., 2008). Palmyra is largely uninhabited (population of six to 25), and, since it is a marine protected area, fishing is almost entirely prohibited within 50 nautical miles. Tabuaeran at the time of this survey had a population density of approximately >60 humans per kilometer of reef (2500 total) and allowed both commercial and artisanal fishing. The majority of the impact had occurred only since the 1980s when government resettlement dramatically increased the resident population (Sandin et al., 2008). Previous studies showed that fish biomass was approximately a third lower on Tabuaeran than Palmyra, likely due to significant fishing pressures from the human population (Sandin et al., 2008; Zgliczynski & Sandin, 2017). Large apex predators in particular (groupers, sharks, snappers, and large jacks) made up 56% of the measured total fish biomass in Palmyra but, while present, comprised only 3% on Tabuaeran (Stevenson et al., 2007), a pattern seen in multiple studies (Zgliczynski & Sandin, 2017). The relative similarity of Palmyra and Tabuaeran, save for these differences in

fishing, has made this a commonly utilized interisland setting for the examination of the ecological impacts of fishing (Madin, Gaines, & Warner, 2010; McCauley, Hoffmann, et al., 2012).

Reef fish species diversity at both Palmyra and Tabuaeran stands at approximately 230–250 species (Sandin et al., 2008). The two species of sharks of focal interest in this study are gray reef sharks (*C. amblyrhynchos*) and Galapagos sharks (*C. galapagensis*), but other common shark species in the region include blacktip reef sharks (*Carcharhinus melanopterus*), whitetip reef sharks (*Triaenodon obesus*), lemon sharks (*Negaprion brevirostris*), scalloped hammerhead sharks (*Sphyrna lewini*), and tiger sharks (*Galeocerdo cuvier*) (Papastamatiou et al., 2014). To understand changes in food chain length in this study, we focused on a suite of common species in these systems, including two sharks (*C. amblyrhynchos* and *C. galapagensis*), three common mesopredatory teleost fishes—bluefin trevally (*C. melampyus*), peacock grouper (*C. argus*), and blacktail snapper (*L. fulvus*)—and one grazing teleost fish, the white cheeked surgeonfish (*A. nigricans*), and a mound-forming coral (*P. lutea*).

Both reef sharks are considered to be high-level mesopredators (Frisch et al., 2016; Roff et al., 2016).

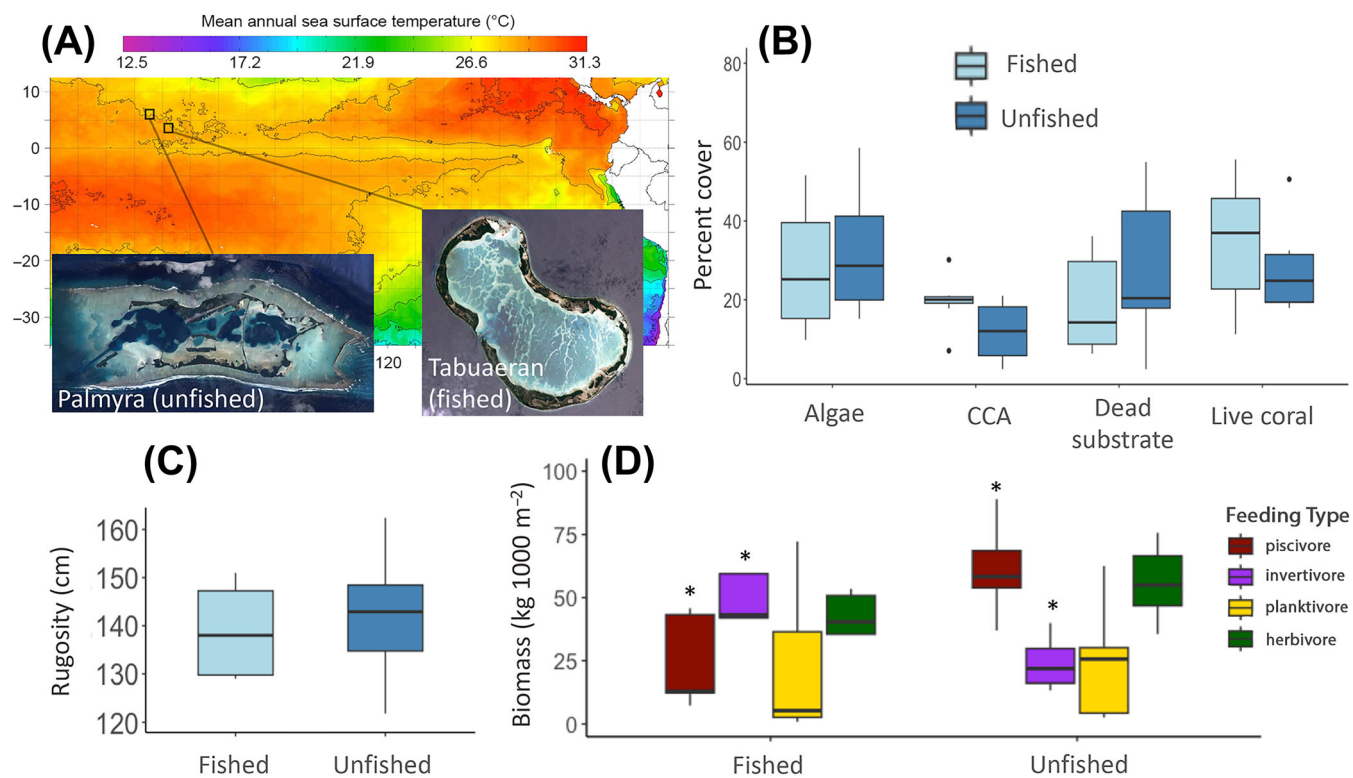


FIGURE 1 (A) Palmyra Atoll and Tabuaeran Atoll are located in relatively close physical proximity (~350 km distance) within the mid-equatorial Pacific in similar oceanic environments. (B) There were no significant differences in general classes of benthic cover observed across sites surveyed. (C) There were also no significant differences in rugosity or benthic structure. (D) However, there were strong and significant reductions in fish biomass from the unfished atoll (Palmyra) and the fished atoll (Tabuaeran), with significant effects observed for total biomass, herbivore biomass, and predator biomass.

The diet of *C. amblyrhynchos* and *C. galapagensis* has been reported to be composed largely of teleost fishes with some invertebrates. For *C. amblyrhynchos* teleost fish were found in 82% of individuals surveyed and included a wide variety of taxa including large numbers of Muraenidae (Moray eels) and Holocentridae (squirrelfish) (Wetherbee et al., 1997). Common invertebrates included cephalopods (in 30%) as well as a small number of crustaceans (5%) (Papastamatiou et al., 2006; Wetherbee et al., 1997). The diet of *C. galapagensis* is similar but consists of slightly fewer teleost fishes (67.7%) and more mollusks (26.5%) and crustaceans (18.7%); 13.5% of individuals also consumed elasmobranchs (Papastamatiou et al., 2006; Wetherbee et al., 1996). Notably, while *C. amblyrhynchos* and *C. galapagensis* are commonly observed on reef slopes, evidence from *C. amblyrhynchos* in this system suggests that much of their diet likely comes from pelagic ecosystems (McCauley, Young, et al., 2012); movement data from *C. galapagensis* from other systems likewise suggest they frequently forage at depth and off-shore (Meyer et al., 2010).

Both *C. argus* and *C. melampygyus* are almost exclusively predators of reef fish (Dierking et al., 2009; Sudekum, 1991), with *C. argus* being highly site-attached and sedentary, whereas *C. melampygyus* is a roving mobile species. The diet of *L. fulvus* is predominantly composed of crabs, with the remainder composed of small fish (DeFelice & Parrish, 2003; Nanami & Shimose, 2013). As a common grazer we used *A. nigricans*. Detailed dietary analysis on this species shows that it is an obligate herbivore, feeding almost exclusively on red thalassal algae and green and red filamentous species (Choat et al., 2002). *Porites lutea* was used as another low-trophic-level species that, through the use of coral cores, allowed for an integrated signal over very long time periods—allowing us to search for potential differences in baseline isotopes over time that might explain any patterns across atolls.

Characterization of reef communities

Fish communities were characterized at nine locations at Palmyra and five locations at Tabuaeran. These sites were distributed evenly, approximately 2 km apart from each other at random coordinates in shallow water (3–12 m) with replicate surveys conducted. Given the importance of the structural complexity of reefs on fish density and biomass (Graham & Nash, 2013), we also characterized benthic rugosity and benthic cover for each island to confirm they were similar at both atolls. Benthic complexity was measured by a rugosity index calculated by laying a 2-m chain against the reef surface and measuring the distance between two end points; the ratio of the length of

this chain as laid against the reef surface to the actual length of the chain was the rugosity index. Given the lack of SCUBA support at Tabuaeran, benthic cover and rugosity were characterized at more inshore depth ranges of our fish survey ranges for both islands and included six locations at Palmyra and eight locations at Tabuaeran (although rugosity was missed at one site at Tabuaeran). Benthic cover was surveyed by estimating percentage cover by cover type across a series of 10 gridded quadrats at each site; each 1-m² quadrat was distributed at 5-m intervals along a 50-m transect. Prior to analysis all cover data were pooled per site and binned in general categories: algae (both turf and macroalgae), living coral, dead substrate (sand, rock, rubble, and dead coral), and other (which predominantly included crustose coralline algae and other invertebrates). Benthic data from the 10 quadrats were then pooled by site for all subsequent analyses.

While benthic habitats were surveyed at only a single time point, fish surveys were conducted four times each at Tabuaeran (along the western and southern coastlines, March–April 2007) and seven times each at Palmyra (both northern and southern coastlines, June–August 2006). Fish communities at both sites were surveyed using belt transect surveys conducted in daytime. At each site a fish survey was composed of four belt transects, their dimensions tailored to the size (total length [TL]) of the fish being surveyed: fish of ≥ 50 cm TL were counted along a 50 \times 8-m transect; 30–49 cm TL fish along a 50 \times 4-m transect; 15–29 cm TL fish along a 50 \times 4-m transect; and fish of < 15 cm TL were surveyed along a 25 \times 2-m transect. Biomass was then scaled to area surveyed. Within each transect, a pair of observers was responsible for identifying, counting, and estimating the total length of each individual fish. The same pair of divers was responsible for all surveys across both atolls. Estimation of fish biomass was then derived from the survey data, using length–weight conversion constants sourced from FishBase (Froese & Pauly, 2010) or other scholarly publications. Further details are provided in (McCauley, Hoffmann, et al., 2012).

Fish were placed into one of four basic trophic classifications for subsequent analyses: predator, invertivore, herbivore, and planktivore. Trophic classifications were made based on the dominant diet type as assessed via review of diet information in Fishbase (Froese & Pauly, 2010), as well as a review of the literature on species diet for these species from this region of the Pacific. We note, however, that such simplistic categorical trophic classifications based on dominant diet type obscure the reality that many species are interguild consumers (e.g., mesopredators that are both piscivores and invertivores) and may diet switch across their lifespan.

Isotopic sample collection

We used isotopes to identify changes in TP and foraging ecology. Bulk $\delta^{15}\text{N}$ was used to identify TP changes within each focal organism, as ^{15}N typically fractionates at every transmission point in a food chain, such that it becomes enriched with each rise within a trophic web. We used the $\delta^{15}\text{N}$ of top predators (sharks and large trevally) to estimate total food chain length.

In contrast to $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ does not enrich substantially with trophic interactions, and we instead used this isotope to search for systematic differences in the source of the carbon consumed across species. Variation in $\delta^{13}\text{C}$ in this system can be used to identify benthic versus pelagic sourcing of nutrients and, sometimes relatedly, inshore versus offshore foraging (McCauley, Young, et al., 2012; Young et al., 2010).

Although such controlled measurements of nitrogen isotopes are useful for assays of dietary niche or food chain position, variation in isoscape over space and time and in isotopic fractionation extent across species can make comparisons challenging. As a second complementary measure of food chain position, we thus used compound-specific nitrogen isotope analysis of individual amino acids (CSSIA-AAAs) in one predatory shark species (gray reef shark, *C. amblyrhynchos*). Because certain trophic amino acids in consumers fractionate trophically while others (“source” or nontrophic amino acids) show little tendency for trophic fractionation, the differences between these amino acids can be used to calculate TP for an organism without the need for establishing a baseline using additional taxa (McClelland & Montoya, 2002; Popp et al., 2007). The difference between trophic and source $\delta^{15}\text{N}$ values in top predators can thus be used to provide a standalone estimate of the food chain length for a system (Chikaraishi et al., 2009).

All fish species used for isotopic analyses were collected using hook and line or via pole spear and sized at time of capture. *Lutjanus fulvus* were collected from lagoonal reefs at depths between 2 and 6 m. *Acanthurus nigricans*, *C. argus*, and *C. melampygus* were collected from forereef habitats at depths between 7 and 18 m. *Carcharhinus amblyrhynchos* and *C. galapagensis* were collected in waters 0.1–3 km offshore of the forereef habitats. All fish samples were collected between 2006 and 2009. A sample of white muscle tissue was removed from the dorsal region of all fish, frozen, and subsequently freeze-dried.

To obtain a long-term basal isotopic signature from the bottom of these food webs, we collected and analyzed tissues of one common coral species, *P. lutea*. Measurements were made of the coral-derived organic matter stored in the skeletal lattice of live *P. lutea* coral cores

collected at Palmyra (on 2 June 2005 from a 1.5-m-high colony at a depth of 10 m [$5^{\circ}51.85' \text{ N}$, $162^{\circ}06.89' \text{ W}$] and on 4 June 2007 from a 2-m-high colony at a depth of 5 m [$5^{\circ}52.015' \text{ N}$, $162^{\circ}07.092' \text{ W}$]) and Tabuaeran in September 1997 at a depth of 11 m on the forereef ($3^{\circ}54'32'' \text{ N}$, $159^{\circ}18'88'' \text{ W}$). After recovery, cores were rinsed in fresh water and air dried. Slabs were cut from cores using a double-bladed diamond tile saw, cleaned in deionized water, and dried. Annual density bands were visualized using X-radiographs and the age of bands were confirmed using $\delta^{18}\text{O}$ chronologies and bomb radiocarbon stratigraphies (Druffel-Rodriguez et al., 2012; Grottoli et al., 2003; Nurhati et al., 2009). Slabs were subsampled at selected time intervals below the surface tissue layer, with two replicate samples collected at every time point.

In total, we used 235 samples across seven species in bulk isotopic analyses.

Sample preparation and analyses

In the lab, all fish tissue samples were freeze dried and then ground to a homogenized powder. Coral subsamples were prepared for analysis following Marion et al. (2005); briefly, samples were cleaned by complete surface grinding and dust removal, pulverized, exposed to 30% H_2O_2 for 48 h, rinsed in deionized water, dried, and acidified repeatedly with HCl. The acid-insoluble residue was glass fiber filtered ($0.7 \mu\text{mol L}^{-1}$ pore size), rinsed two or three times with 50 mL deionized water, dried at 40°C for 24 h, and analyzed. All fish and coral samples were analyzed for bulk isotopes of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) at the Stanford Stable Isotope Biogeochemistry Facility using a Carlo Erba/ConFlo II elemental analyzer Thermo-Delta Finnigan Delta-Plus isotope ratio mass spectrometry (IRMS). Based on replicate and standards analysis the reproducibility and precision is better than 0.15‰ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (and typically better than 0.10‰).

For *C. amblyrhynchos* a subset of 11 individuals (six from Palmyra, five from Tabuaeran) were also analyzed for compound-specific stable isotopes. At UC Davis, freeze-dried tissue samples were acid-hydrolyzed using 6 M HCl at 150°C and derivatized using methoxycarbonylation esterification (Walsh et al., 2014; Yarnes & Herszage, 2017). Gas chromatography–combustion IRMS (GC-IRMS) was used to gather $\delta^{15}\text{N}$ values of individual derivatized AAs. The specific AAs that can be accurately quantified varies based on tissue AA content as well as preparation techniques (Ohkouchi et al., 2017). While we gathered data on 10 AA, several of the AAs were not measured in some samples, so we only used the following AAs in our analyses: alanine (Ala), leucine (Leu), proline

(Pro), valine (Val), aspartic acid (Asp; from asparagine), glutamic acid (Glu), glycine (Gly), and phenylalanine (Phe).

Calculations of trophic position

Given the strong potential for local and regional spatial variation in $\delta^{15}\text{N}$ (e.g., via differential effects of seabird guano accumulation across sites), we characterized the $\delta^{15}\text{N}$ baseline at the bottom of the food web at both Palmyra and Tabuaeran in multiple ways. To control for this, we used multiple integrated measures, all collected on the forereef where water mixing was higher. Specifically, we use samples collected from (1) a 15-year time series of massive *P. lutea* corals, thereby allowing integration over time, (2) a roving, grazing reef fish, *A. nigricans*, which should integrate over space, and, as detailed below, (3) CSSIA-AA. Notably, given the high variation in discrimination factors observed across fish species and even within elasmobranchs for bulk SIA values (e.g., Mill et al., 2007; Olin et al., 2013; Wyatt et al., 2019) and the lack of species-specific research on discrimination factors for the species in this study, we did not use bulk isotopes to attempt to calculate and compare absolute trophic position (TP) across species for this study but instead focused on relative differences across sites within a species.

To calculate TP from compound-specific analyses (*C. amblyrhynchos* only), we used a comparison of trophic amino acids (TAAs) and source amino acids (SAAs). Two of the AAs consistently measured for $\delta^{15}\text{N}$ are typically considered to have little fractionation with trophic transfer: glycine and phenylalanine (McClelland & Montoya, 2002; Seminoff et al., 2012). These SAAs can thus be used to help correct for variable baselines across sites, serving as a within-individual internal reference baseline. While phenylalanine (Phe) is frequently used as a SAA, recent work in other top marine predators has suggested that trophic enrichment of this AA is not negligible and leads to erroneous estimates of TP (Matthews et al., 2020). Given this and that previous work showed a strong correlation between $\delta^{15}\text{N}$ of Gly and Phe (e.g., Seminoff et al., 2012), we chose to use Gly rather than Phe as a SAA (as in Popp et al., 2007). Of the other AAs typically considered to be TAAs, glutamic acid is most commonly used as it typically shows the highest and most reliable fractionation. However, other AAs that have been shown to fractionate trophically (e.g., [Lemons et al., 2020; McClelland & Montoya, 2002; Seminoff et al., 2012]) and for which we recovered nearly complete data on from our samples were Ala, Val, Leu, Pro, and Asp.

While many calculations of TP have focused purely on a Glu-to-Phe comparison, recent reviews and meta-analyses have highlighted the high variability in these

numbers and suggested using a multiple-AA comparison (McMahon & McCarthy, 2016; Ohkouchi et al., 2017). Because of this, we used as our primary method a comparison of all putative TAAs (Glu, Ala, Val, Leu, Pro, Asp) versus both putative SAAs (Phe and Gly) (Ohkouchi et al., 2017). However, given the lack of clear consensus on the best way to calculate TP, we also provide TP estimates using a comparison of all TAAs compared with Gly (e.g., Popp et al., 2007) and a comparison of Glu versus Gly. Glu data were not recovered in one sample from Palmyra, bringing the maximum total number of samples included in any analysis to five per site; additionally, for the all-TAA versus all-SAA analysis, we removed one additional sample for which we did not have complete data on another AA. In all of these calculations of TP, we used a value of 3.4 as an average estimate of the difference between TAAs and SAAs in nonvascular primary producers (Chikaraishi et al., 2009). While a value of 7.6 is most commonly used as a trophic discrimination factor in such calculations (Chikaraishi et al., 2009), based on elasmobranch work by Dale et al. (2011), we instead used a value of 5. While this adjustment may make these values more accurate, without an estimate of discrimination factors specifically for these species and these AAs, we strongly caution that the absolute values of TP are merely estimates, and the focus of our study is on relative TP. There remain many sources of uncertainty that are associated with trophic discrimination factors and relative fractionation of SAAs versus TAAs across AAs as well as measurement errors. Notably, we do propagate error based on measurement error as the contribution to measurement error is likely overshadowed by other sources of uncertainty and so would not bound the real error in our estimates of TP. Based both on these limitations and caveats, and the relatively small sample size (especially compared to bulk isotopes), we thus caution against overinterpretation of these compound-specific results by themselves and strongly suggest they be considered only as a source of insight to supplement patterns from bulk isotopic analyses. Figures shown in the main text report the data with all TAAs versus all SAAs, and results from the other two calculations of TP are shown in Appendix S1: Figure S1.

DATA ANALYSIS

The attributes of reef fish communities were compared using generalized linear models with biomass per 1000 m² per day as a response variable and atoll identity, feeding guild (invertivore, planktivore, herbivore, or piscivore) and their interaction as predictor variables. Replication within sites across days was not included in

the models; rather, we used a single pooled average biomass value per day for these responses. We compared reef rugosity between sites using Student's t -tests across atolls. Reef cover across sites was compared using permutational multivariate ANOVA (PERMANOVA) analyses.

Comparison of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ bulk isotope values within species across atolls was conducted using two-tailed t -tests for each species, with Benjamini–Hochberg adjustment to correct for multiple tests across species. To compare trophic niche areas between these atolls, we used Bayesian standard ellipse area corrected for small sample size (SEAc) using the SSIAR package in R (Parnell & Jackson, 2013).

To compare species-specific changes in niche width for each species, we used SEAc values; standard ellipse area reported included 40% of the data for each species (although 95% ellipse area plots are also shown in the figures). The corrected standard ellipses were generated using Markov chain Monte Carlo simulations (Jackson et al., 2011) in the SIBER package in R. Percentage niche overlap was calculated using the sample size-corrected ellipse value by species (Parnell & Jackson, 2013). The probability that two SEAc values were different was determined using Bayesian inference based on 10,000 draws.

RESULTS

Reef characterization

Consistent with previous observations (Sandin et al., 2008; Stevenson et al., 2007), we found that the measurements

of general attributes of the benthic structure of the reef at our sampling sites did not significantly differ between atolls. PERMANOVA showed no significant differences in cover type between atolls ($F(3, 48) = 1.40$, $R^2 = 0.07$, $p = 0.22$; Figure 1B). Likewise, the rugosity of the reef substrates was statistically indistinguishable between the two atolls ($t = 1.12$, $df = 11$, $p = 0.3$; Figure 1C).

Fish community change

We found significant differences in total fish biomass between Tabuaeran and Palmyra atolls ($F = -13.96$, $p < 0.001$; Figure 1D), with average biomass (mean \pm SE) declining from 175 ± 22 kg/1000 m² at Palmyra Atoll to 141 ± 34 kg/1000 m² at Tabuaeran Atoll. Notably, there were also strong interactions between atolls and feeding guild ($F = 3.89$, $p = 0.01$); predators declined 63% on average on fished atolls ($t = 3.395$, $p = 0.001$), while invertivores actually increased 33% in the fished site ($t = 2.84$, $p < 0.01$); while both herbivores and planktivores were lower in average biomass in fished versus unfished sites, there were no significant differences.

Trophic position and niche across sites

There were significant differences in $\delta^{15}\text{N}$ values by species ($F(6, 222) = 116.72$, $p < 0.0001$; Figure 2) as well as species by atoll interactions ($F(7, 222) = 14.35$, $p < 0.0001$). Comparing $\delta^{15}\text{N}$ for each of the seven fish species across atolls, we found no significant difference

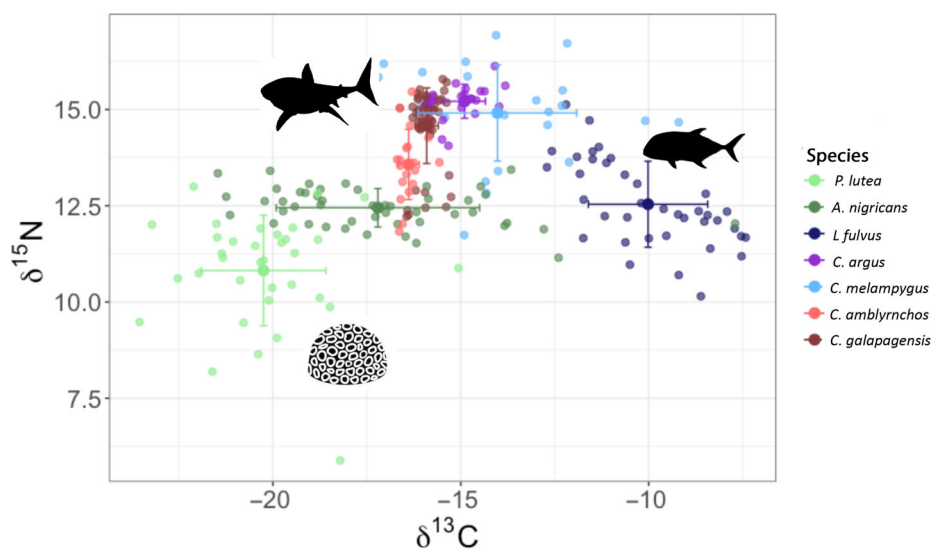


FIGURE 2 Comparisons of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ across both sites of lower trophic-level organisms (*Porites* sp. and *A. nigricans*, greens), teleost fish mesopredators (*C. argus*, *C. melampygyus*, *L. fulvus*, blues), and sharks (*C. amblyrhynchos* and *C. galapagensis*, reds). Higher $\delta^{15}\text{N}$ values typically represent higher trophic position, while $\delta^{13}\text{C}$ values show carbon sources.

in $\delta^{15}\text{N}$ values observed between atolls for the herbivorous fish *A. nigricans* ($t(19.51) = -0.93, p = 0.4$) or the two smaller and more sedentary mesopredatory fish *L. fulvus* ($t(26.85) = -1.80, p = 0.08$) and *C. argus* ($t(6.34) = -0.78, p = 0.47$; Figure 3). Results from coral

cores also showed no significant difference in $\delta^{15}\text{N}$ across atolls ($t(28.34) = 1.34, p = 0.2$). However, the three highest trophic-level species all showed significant difference in bulk $\delta^{15}\text{N}$ values between atolls (*C. melampyus*: $t(8.37) = -2.84, p = 0.02$, *C. galapagensis*: $t(5.21) = -4.13, p < 0.01$, and *C. amblyrhynchos* $t(11.73) = -18.49, p < 0.001$; Figure 3). For all three of these predatory species Tabuaeran Atoll showed a lower mean $\delta^{15}\text{N}$ value compared to Palmyra atoll. Only one species, *A. nigricans*, showed significant differences in $\delta^{13}\text{C}$ values across atolls ($t = 7.153, df = 18.5, p < 0.001$), with significantly less-negative values in Tabuaeran compared with Palmyra Atoll.

Beyond these single-isotope comparisons, we also saw differences in niche width comparisons. Using 95% confidence intervals for trophic niche characterization of species, we found the following amounts of trophic niche overlap between the two sites (proportion of overlap compared to nonoverlapping areas) in order from least to most overlap: *C. amblyrhynchos* (<0.00), *C. galapagensis* (0.14), *C. argus* (0.17), *C. melampyus* (0.19), *L. fulvus* (0.37), *A. nigricans* (0.22), *Porites* (0.55). Patterns of effects of atoll on trophic area (TA) and SEAc varied widely by species (Table 1). However, both shark species showed a larger TA at Palmyra.

CSSIA analysis of trophic position

Consistent with findings from bulk isotopic analysis, TP as determined by CSSIA with *C. amblyrhynchos* revealed that these species occupy a significantly higher TP at Palmyra than at Tabuaeran Atoll using a comparison of all TAAs to all SAAs ($t = -2.9, df = 5.9, p = 0.03$; Figure 3B). Despite the uncertainty concerning the best metrics to use for these species, this result was consistent regardless of whether we calculated TP using comparisons of Glu to Gly ($t = -2.8, df = 5.3, p = 0.05$), or using comparison of all TAAs to Gly ($t = 3.8, df = 6.6, p < 0.01$).

DISCUSSION

Although the two atolls, one unfished and one modestly fished, were indistinguishable with respect to their benthic cover and general coral reef structure, there were significant differences in total fish biomass, presumably arising from the higher human fishing pressure at Tabuaeran Atoll. These declines were especially pronounced for piscivorous fishes, likely explained by preferential selection of the relatively large-bodied predatory fish species. Invertebrates actually increased in these fished

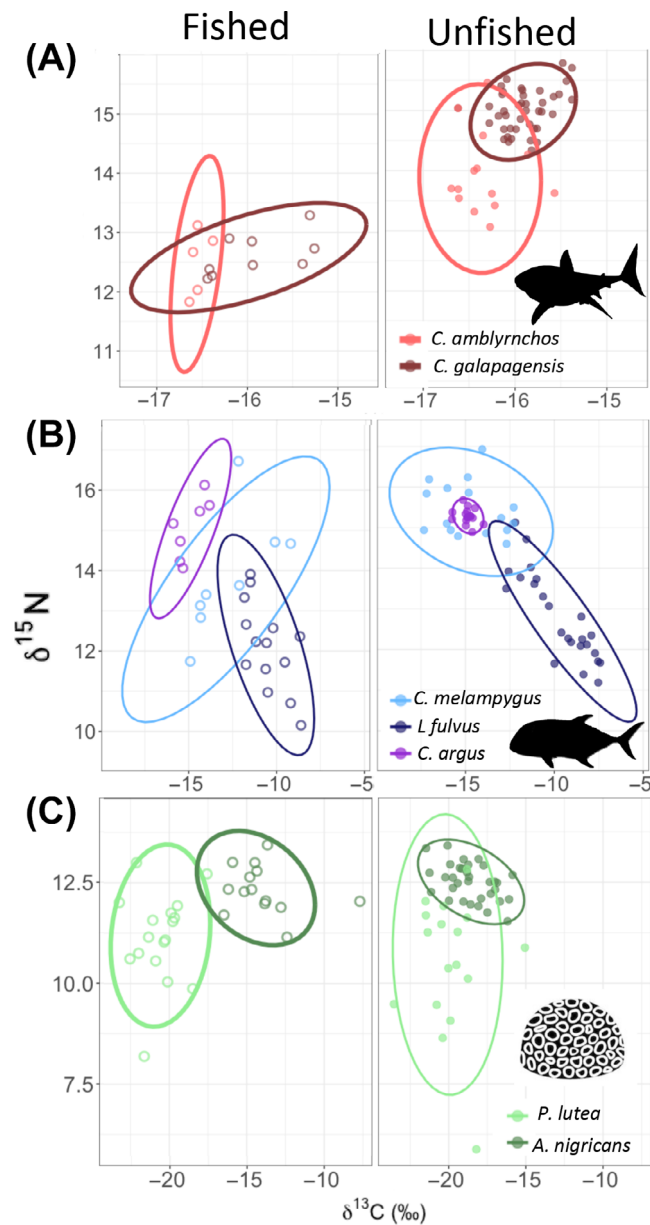


FIGURE 3 The 95% ellipse values of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in (A) top predators, (B) meso predators, and (C) lower trophic position consumers/producers at unfished (closed) and fished (open) atolls. There were no differences in $\delta^{15}\text{N}$ in either of the low-trophic-position consumers/producers (C), or in two of three mesopredators; there were significant changes in $\delta^{15}\text{N}$ in both shark species and in *C. melampyus*. Only *A. nigricans* showed significant shifts in $\delta^{13}\text{C}$ between atolls. Changes in trophic area and ellipse area were not consistent across atolls (see also Table 1). Note that while axes are identical within a panel pair, they vary between panels (A), (B), and (C) in order to allow better visualization of all data.

TABLE 1 Measurements of trophic area (TA) and corrected standard ellipse area (SEAc) by species and atoll.

Species	Species	Status	TA	SEAc
Basal consumers	<i>Porites</i>	Fished	17.48	5.52
	<i>lutea</i>	Unfished	32.5	10.01
	<i>Acanthurus nigricans</i>	Fished	11.6	4.3
		Unfished	6.69	1.97
Teleost mesopredators	<i>Lutjanus</i>	Fished	7.23	3.27
	<i>fulvus</i>	Unfished	8.76	3.05
	<i>Cephalophis argus</i>	Fished	1.9	1.57
		Unfished	0.8	0.27
	<i>Caranx melampygus</i>	Fished	10.69	8.91
		Unfished	8.16	3.86
Sharks	<i>Carcharhinus galapagensis</i>	Fished	0.15	0.2
		Unfished	1.55	0.71
	<i>Carcharhinus amblyrhynchos</i>	Fished	0.73	0.5
		Unfished	1	0.29

Note: These are grouped by low-trophic-level species (a coral and an herbivorous fish), teleost mesopredators, and shark predators. Bolded values simply indicate the higher value within species across the atoll for ease of comparison.

systems. While there was a 1-year offset in sampling at the two atolls, the magnitude of decline of fish community biomass was fairly similar, although somewhat more modest than that reported in previous studies (e.g., ~37% declines reported in Sandin et al., 2008), such that it seems unlikely that interannual variation would explain these patterns. The disproportionate declines in predatory fish are also consistent with effects from typical fishing practices and with results from other studies in this system (e.g., Sandin et al. [2008] reports changes from 65% to 24% of biomass composed of piscivores in Palmyra and Tabuaeran, respectively) and other coral reefs.

Relative TP (based on bulk $\delta^{15}\text{N}$ values) did not vary across atolls for the lower-trophic-level and smaller fish species. Coral results also showed no differences in baseline $\delta^{15}\text{N}$ values, even across long time periods that encompassed both before and after intensive fishing impacts at Tabuaeran. However, both shark species and the largest of the mesopredators (*C. melampygus*) showed significant decreases in trophic level at fished Tabuaeran compared to unfished Palmyra Atoll. Results from CSSIA analysis within *C. amblyrhynchos* provided strong evidence that these effects were due to the changing TP of these higher-trophic-level predators rather than variation in the baseline of $\delta^{15}\text{N}$ between Palmyra and Tabuaeran. While our CSSIA data are limited by the small sample size and several other sources of error, the relative change in TP across sites from CSSIA estimates ranged from 0.25 to 1.0 trophic levels; while the low-end estimate of change is rather modest, we highlight that even

this difference in TP between sites for *C. amblyrhynchos* is as large as the entire range of TP estimates within an island, suggesting that, while numerically small, such a change could still be ecologically meaningful.

Notably, the sharks in this study had $\delta^{15}\text{N}$ values similar to those of two of the three mesopredators examined (*C. argus*, *C. melampygus*), suggestive of similar TPs. This result is similar to that of other recent studies (Bond et al., 2018; Frisch et al., 2016) that, based on both stomach contents and stable isotopes, found that reef sharks occupied functional roles similar to those of other high-level mesopredators such as snappers, groupers, and emperor fish. Importantly, we emphasize that there could be species-specific discrimination factor differences across species not considered. While this should not strongly affect comparison of relative changes in TP, it could limit our ability to compare absolute TP variation across species.

Interestingly, we saw very little evidence for shifts in carbon sourcing across fish species. Only the obligate herbivore *A. nigricans* showed significant differences in carbon sourcing across systems. This is consistent with other studies that showed changes in herbivore diet across fishing pressures (Leitão et al., 2023) and studies that showed changes in herbivore behavior in response to declines in predators (Madin, Gaines, Madin, & Warner, 2010; Rasher et al., 2017). Such changes in the diets of herbivores may have important ecological consequences in this system beyond the scope of this study. However, for the purpose of answering the questions posed in this study, it is notable

that there were no changes in the $\delta^{15}\text{N}$ of herbivores, suggesting no shift in baseline $\delta^{15}\text{N}$ across sites. Also, the observed lack of difference of a $\delta^{13}\text{C}$ shift for all predatory species, combined with the CSSIA results discussed earlier, suggests that changes in $\delta^{15}\text{N}$ across larger predatory species is unlikely to be due to spatial changes in the foraging ecology of these species.

Multiple possible mechanisms might explain how fishing may have reduced the TP of top consumers (a metric of food chain length). First, the observed and pronounced abundance declines of the largest fishes at our fished sites might have forced the remaining predators to feed with greater frequency on the remaining smaller-bodied or lower-trophic-level prey species. This may be due to reduced intraguild foraging (e.g., more feeding on herbivores and less on other mesopredators). While other studies found evidence of predator prey species switching diets in response to fishing (e.g., Barley et al., 2017; Dierking et al., 2009), this may be more difficult for smaller mesopredator species (e.g., *L. fulvus*) or more resident species that may have less ability to switch prey. This explanation is somewhat supported by the patterns we observed; the three largest and most mobile species show changes in TP, while smaller and more resident mesopredators (and basal consumers) did not. However, if ability or need to prey switch is the only driver, it is surprising that *C. argus* did not change TPs. Other studies have shown that *C. argus* is very good at prey switching in degraded reefs, making it surprising that they would not also show these patterns if prey switching capability were the primary driver (Karkarey et al., 2017). However, if *C. argus* tends to target smaller prey than the other species, it may have less need to prey switch since smaller-bodied prey are minimally impacted in this system. Notably, the lack of significant shifts in $\delta^{13}\text{C}$ across these species suggests that any change in diet is likely due to changes in prey choice and not changes in foraging location.

The predators themselves might also be getting smaller, such that even if individuals of a given body size are not changing diets across atolls, the species as a group is eating smaller prey because the species as a group have shrunk in size. This may be especially true of teleost fish, which are more gape-limited than sharks. However, at least for sharks, we did not see any correlation between body size and trophic level relationship consistent with that pattern (Figure 4C). Given that tropical sharks are experiencing substantial declines in body size, this suggests that this change alone may not show major differences in the trophic architecture of communities (Roff et al., 2018). However, it should be noted that this conclusion applies only to adult sharks, as sampled in this study. Other studies have observed dramatic changes in

diet in sharks across their full ontogeny; however, many of the most dramatic shifts occur in much smaller size classes (Wetherbee et al., 1996).

An alternative (and not mutually exclusive) hypothesis to the higher-level predators (e.g., sharks) having been reduced in size is that the intermediate-level predators (e.g., snappers) themselves may have been reduced in size. Such size changes would result in these intermediate predators now targeting different species, ratcheting down food chain length, without any differences in the species of prey the higher-level predators eat. Such patterns have been seen in terrestrial environments, where trophic changes observed isotopically in top predators actually seem to be driven by changes in the diet of prey species or in smaller individuals of the same species (Kuile et al., 2022). This is consistent with a widespread pattern of decreasing body size of fish in response to fishing pressure, including in response to shark removal and on coral reef communities (Hammerschlag et al., 2018; Robinson et al., 2017; Zgliczynski & Sandin, 2017). We notably did not see changes in TP in smaller or lower-level predators, which could be consistent with this explanation, as smaller prey and, in particular, invertebrate prey would be less likely to have size distributions impacted by human fishing pressure, such that these mesopredators would not be expected to show such changes. However, for the species that do change TP across fish contexts, we do not see any consistent shrinking in SEAc across predators between fished and unfished areas for predatory species, as has been seen in other studies (Layman, Albrey Arrington, et al., 2007) and as might be expected if the trophic range available to them were consistently shrinking.

Another possible explanation is the otherwise highly intact condition of the focal unfished reef (Palmyra) utilized in our study. Caribbean reefs have been experiencing multiple stressors for much longer periods of time and present a sharp contrast to highly remote Palmyra Atoll. Notably, they have experienced regional fishing impacts, and particularly high reductions in large and predatory fish (including sharks), for many decades (Dillon et al., 2021; Pandolfi et al., 2003; Rioja-Nieto & Álvarez-Filip, 2019; Schmitter-Soto et al., 2018). Even relatively intact Caribbean reefs, such as those examined by Morillo-Velarde et al. (2018), may have already lost many players, so there may have been less flexibility for predators (or mesopredators) to shift diet in response to further disturbance. Caribbean reefs are also relatively low in diversity (Roff & Mumby, 2012), potentially leaving less potential for prey switching in these systems.

The significant change in TP for reef sharks is particularly notable given that previous work suggested that these reef sharks might source as little as 20% of their

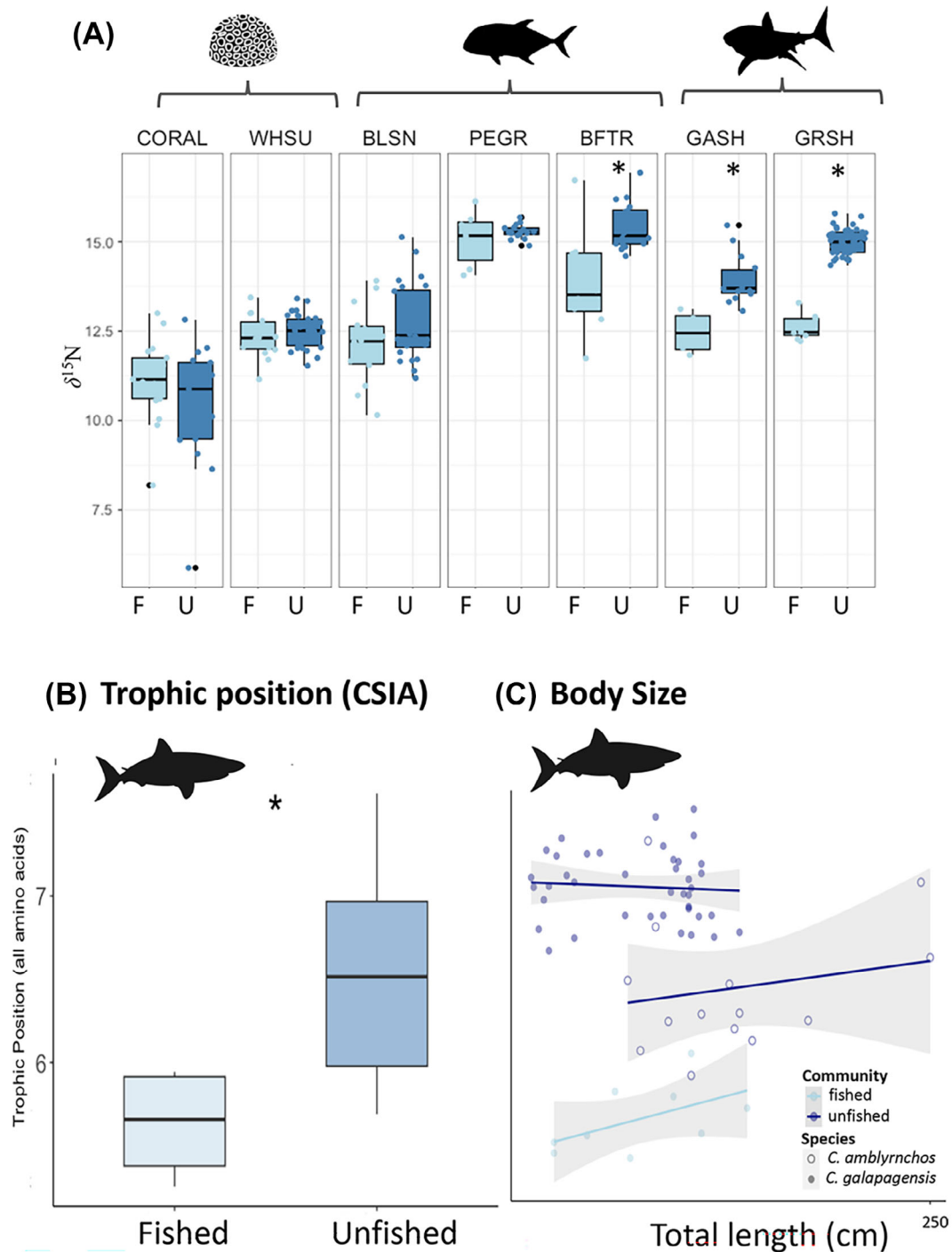


FIGURE 4 (A) Focusing on bulk $\delta^{15}\text{N}$ values, there were significant shifts to lower values in fished (F) Tabuaeran Atoll compared to unfished (U) Palmyra Atoll only in the two sharks (A) and one mesopredator (*C. melampyrgus*). Lower-trophic-level organisms (coral, surgeonfish) and smaller predators (snapper and grouper) showed no significant differences. (B) Compound-specific stable isotope results for *C. amblyrhynchos* showed values similar to those suggested by bulk amino analyses (using all trophic and source amino acids), suggesting that the observed differences in $\delta^{15}\text{N}$ values represented a shift in trophic position to higher trophic levels in unfished sites compared to fished sites. (C) Notably, there was no relationship between body size (total length) and $\delta^{15}\text{N}$ in the adult sharks used in this study.

nutrients from reef-derived productivity (McCauley, Young, et al., 2012). This makes it particularly surprising to see differences in TP without changes in carbon sourcing. We suggest at least three non-mutually exclusive

potential mechanisms that could give rise to the changes in TP we observed: (1) While we have not directly measured fishing pressure in this system, this pressure may well extend into the “near” pelagic zone, and this fishing

may also be “fishing down” the size structure (or trophic structure) of these pelagic systems. Such impacts have been hypothesized in other pelagic systems. The pelagic area near Tabuaeran Atoll is known to be used by resident fishers as well as intermittently by commercial fishers pursuing pelagic prey; so we might expect fish like *C. amblyrhynchos* that appear to source nutrients from pelagic environments (while still staying in close proximity to the reef) to be affected by any size class reductions from these fisheries operating in both areas where they feed. (2) Although a large contribution of source carbon to *C. amblyrhynchos* is pelagic, it may be that this “pelagic” carbon is captured and transferred through reef-based fish, such that they are not actually eating as much pelagic food as previous analyses suggested. If *C. amblyrhynchos* (or, more realistically, their intermediate prey) were eating mostly planktivorous fish on the reef, they would still look pelagic while being more impacted by reef-centric fishing pressures. Recent work emphasizing the importance of pelagically sourced nutrients even in obligately reef-dwelling fishes suggest that this interpretation requires consideration (Brandl et al., 2019; Skinner et al., 2021). Finally, (3) if there are sufficiently strong changes to the food chain length of the community on the reef (as suggested by studies describing impacts of fishing on reef fish biomass in this study archipelago), those changes, even if they only effect 20% of their diet, could very well manifest as a significant change in TP.

Understanding the effects of selective fishing of large predatory species including sharks is critical. Nearly two-thirds of coral reef-associated sharks and rays are threatened with extinction (Bradley & Gaines, 2014; Dulvy et al., 2021; Letessier et al., 2019; Williams et al., 2010). Tropical sharks have declined 74%–92% (Roff et al., 2018), and reef sharks are now totally absent on 20% of the world’s coral reefs (MacNeil et al., 2020). *Charcharhinus amblyrhynchos*, once highly abundant and composing large proportions of the total biomass at upper trophic levels of coral reef ecosystems, has moved from least concern to endangered in 20 years (Simpfendorfer et al., 2020). These sharks are a major component of predator biomass in tropical pelagic and reef environments and have been postulated to play an important role in reef ecosystem health, functioning, and behavioral processes on reefs (Jorgensen et al., 2022; Roff et al., 2016); however, our understanding of their full influence on such ecosystems has been debated and remains a subject of inquiry and an area needing additional research (Jorgensen et al., 2022; Roff et al., 2016). While in this study we did not see the reef sharks operating at a substantially higher TP than the larger teleost mesopredators, they did occupy trophic niches that were distinct among them and vis-à-vis any of the teleost fish when both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were

included. This suggests low dietary overlap and, thus, perhaps, different functional roles. As in other recent reviews of sharks, this may hint at a low functional redundancy between sharks and other species, suggesting unique roles and important impacts their loss may have on ecosystems (Hussey et al., 2015; McCauley et al., 2010; McCauley, Young, et al., 2012).

Conclusions

While there is extensive literature on the effects of fishing on the biomass, body size distributions, diversity, and behavior of affected coral reef and other marine communities, very little work has been done to examine how such fishing affects functionally critical, but more difficult to measure, structural properties of ecosystems, such as food chain length. Here we highlight how even relatively modest harvest appears to strongly alter the fundamental properties of food web architecture and trophic ecology, including by cryptically shortening food chain length and changing the trophic ecology of the highest-level consumers—without local or regional extirpation of these consumers. Such alterations and associated losses of interaction and function may be among the most insidious and important impacts resulting from human change (Jordano, 2016).

There is also significant applied management utility of these results in the context of coral reefs, as well as other systems. For example, the enhanced spatial protection conferred on our unfished reefs in the protected Pacific Remote Islands Marine National Monument Area appears to have preserved facets of food chain architecture in Palmyra’s ecosystems—adding more depth to our understanding of the diverse benefits conferred by such protected areas. Such results are especially timely in light of emerging conversations on expanding protected areas to manage the integrity of whole ecosystems on land and in the ocean (e.g., Convention on Biological Diversity 30 × 30 agreement; UNEP, 2022). These observations of the impacts of fishing on food chain length are equally germane to considerations of how to use fisheries management tools, in the majority of the ocean outside of protected areas, to minimize food web disruptions—and contribute to and enlarge the concept of ecosystem-based management (Pikitch et al., 2004).

Lastly, it is worth considering whether some of the methods communicated here (e.g., comparative surveys of natural abundance/compound-specific isotope signatures of top predators) could even offer a simple and relatively low-cost means of using predator chemistry as an indicator of ecosystem structural health and to assess recovery after intervention.

In sum, these results suggest the possibility that food chains and interaction length may have contracted as a result of harvest in ways that have gone largely unnoticed in many systems. Future research will help to illuminate the ubiquity of these potential structural shifts in marine systems and beyond and will shed light more definitively on the mechanisms underpinning these contractions.

AUTHOR CONTRIBUTIONS

Hillary S. Young and Finn O. McCauley contributed equally.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Young et al., 2024) are available in Dryad at <https://doi.org/10.5061/dryad.kpr4xhcg>.

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REFERENCES

- Barley, S. C., M. G. Meekan, and J. J. Meeuwig. 2017. "Species Diversity, Abundance, Biomass, Size and Trophic Structure of Fish on Coral Reefs in Relation to Shark Abundance." *Marine Ecology Progress Series* 565: 163–179.
- Bellwood, D. R., A. S. Hoey, and T. P. Hughes. 2012. "Human Activity Selectively Impacts the Ecosystem Roles of Parrotfishes on Coral Reefs." *Proceedings of the Royal Society B: Biological Sciences* 279(1733): 1621–29.
- Bond, M. E., J. Valentin-Albanese, E. A. Babcock, N. E. Hussey, M. R. Heithaus, and D. D. Chapman. 2018. "The Trophic Ecology of Caribbean Reef Sharks (*Carcharhinus perezi*) Relative to Other Large Teleost Predators on an Isolated Coral Atoll." *Marine Biology* 165: 1–13.
- Bradley, D., and S. D. Gaines. 2014. "Counting the Cost of Overfishing on Sharks and Rays." *eLife* 3: e02199.
- Brandl, S. J., L. Tornabene, C. H. R. Goatley, J. M. Casey, R. A. Morais, I. M. Côté, C. C. Baldwin, V. Parravicini, N. M. D. Schiettekatte, and D. R. Bellwood. 2019. "Demographic Dynamics of the Smallest Marine Vertebrates Fuel Coral Reef Ecosystem Functioning." *Science* 364(6446): 1189–92.
- Briones-Fourzán, P., L. Álvarez-Filip, C. Barradas-Ortíz, P. S. Morillo-Velarde, F. Negrete-Soto, I. Segura-García, A. Sánchez-González, and E. Lozano-Álvarez. 2019. "Coral Reef Degradation Differentially Alters Feeding Ecology of Co-Occurring Congeneric Spiny Lobsters." *Frontiers in Marine Science* 5: 516. <https://doi.org/10.3389/fmars.2018.00516>.
- Capdevila, P., N. Noviello, L. McRae, R. Freeman, and C. F. Clements. 2022. "Global Patterns of Resilience Decline in Vertebrate Populations." *Ecology Letters* 25(1): 240–251.
- Casey, J. M., A. H. Baird, S. J. Brandl, M. O. Hoogenboom, J. R. Rizzari, A. J. Frisch, C. E. Mirbach, and S. R. Connolly. 2017. "A Test of Trophic Cascade Theory: Fish and Benthic Assemblages across a Predator Density Gradient on Coral Reefs." *Oecologia* 183: 161–175.
- Chikaraishi, Y., N. O. Ogawa, Y. Kashiyama, Y. Takano, H. Suga, A. Tomitani, H. Miyashita, H. Kitazato, and N. Ohkouchi. 2009. "Determination of Aquatic Food-Web Structure Based on Compound-Specific Nitrogen Isotopic Composition of Amino Acids." *Limnology and Oceanography: Methods* 7(11): 740–750. <https://doi.org/10.4319/lom.2009.7.740>.
- Choat, J. H., K. D. Clements, and W. Robbins. 2002. "The Trophic Status of Herbivorous Fishes on Coral Reefs: 1: Dietary Analyses." *Marine Biology* 140: 613–623.
- Cinner, J. E., E. Maire, C. Huchery, M. A. MacNeil, N. A. J. Graham, C. Mora, T. R. McClanahan, M. L. Barnes, J. N. Kittinger, and C. C. Hicks. 2018. "Gravity of Human Impacts Mediates Coral Reef Conservation Gains." *Proceedings of the National Academy of Sciences* 115(27): E6116–E6125.
- Dale, J. J., N. J. Wallsgrave, B. N. Popp, and K. N. Holland. 2011. "Nursery Habitat Use and Foraging Ecology of the Brown Stingray *Dasyatis lata* Determined from Stomach Contents, Bulk and Amino Acid Stable Isotopes." *Marine Ecology Progress Series* 433: 221–236.
- DeFelice, R. C., and J. D. Parrish. 2003. "Importance of Benthic Prey for Fishes in Coral Reef-Associated Sediments." *Pacific Science* 57(4): 359–384.
- Dell, C., J. P. Montoya, and M. E. Hay. 2015. "Effect of Marine Protected Areas (MPAs) on Consumer Diet: MPA Fish Feed Higher in the Food Chain." *Marine Ecology Progress Series* 540: 227–234.
- Dierking, J., I. D. Williams, and W. J. Walsh. 2009. "Diet Composition and Prey Selection of the Introduced Grouper Species Peacock Hind (*Cephalopholis argus*) in Hawaii." *Fishery Bulletin* 107: 464–476.
- Dillon, E. M., D. J. McCauley, J. M. Morales-Saldaña, N. D. Leonard, J.-X. Zhao, and A. O'Dea. 2021. "Fossil Dermal Denticles Reveal the Preexploitation Baseline of a Caribbean Coral Reef Shark Community." *Proceedings of the National Academy of Sciences* 118(29): e2017735118.
- Dirzo, R., H. S. Young, M. Galetti, G. Ceballos, N. J. B. Isaac, and B. Collen. 2014. "Defaunation in the Anthropocene." *Science* 345(6195): 401–6. <https://doi.org/10.1126/science.1251817>.
- Druffel-Rodríguez, K. C., D. Vetter, S. Griffin, E. R. M. Druffel, R. B. Dunbar, D. A. Mucciarone, L. A. Ziolkowski, and J.-A. Sanchez-Cabeza. 2012. "Radiocarbon and Stable Isotopes in Palmyra Corals during the Past Century." *Geochimica et Cosmochimica Acta* 82: 154–162.
- Dulvy, N. K., N. Pacoureau, C. L. Rigby, R. A. Pollom, R. W. Jabado, D. A. Ebert, B. Finucci, et al. 2021. "Overfishing Drives over One-Third of all Sharks and Rays toward a Global Extinction Crisis." *Current Biology* 31(21): 4773–4787.e8. <https://doi.org/10.1016/j.cub.2021.08.062>.

- Duncan, R. P., T. M. Blackburn, and T. H. Worthy. 2002. "Prehistoric Bird Extinctions and Human Hunting." *Proceedings of the Royal Society of London. Series B: Biological Sciences* 269(1490): 517–521. <https://doi.org/10.1098/rspb.2001.1918>.
- Eddy, T. D., R. J. Bernhardt, J. L. Blanchard, W. L. Cheung, M. Colléter, H. D. A. Pontavice, E. A. Fulton et al. 2021. "Energy Flow Through Marine Ecosystems: Confronting Transfer Efficiency." *Trends in Ecology & Evolution* 36(1): 76–86.
- Edwards, C. B., A. M. Friedlander, A. G. Green, M. J. Hardt, E. Sala, H. P. Sweatman, I. D. Williams, B. Zgliczynski, S. A. Sandin, and J. E. Smith. 2014. "Global Assessment of the Status of Coral Reef Herbivorous Fishes: Evidence for Fishing Effects." *Proceedings of the Royal Society B: Biological Sciences* 281(1774): 20131835. <https://doi.org/10.1098/rspb.2013.1835>.
- Edwards, M., B. Konar, J.-H. Kim, S. Gabara, G. Sullaway, T. McHugh, M. Spector, and S. Small. 2020. "Marine Deforestation Leads to Widespread Loss of Ecosystem Function." *PLoS One* 15(3): e0226173.
- Essington, T. E., A. H. Beaudreau, and J. Wiedenmann. 2006. "Fishing through Marine Food Webs." *Proceedings of the National Academy of Sciences* 103(9): 3171–75.
- Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, et al. 2011. "Trophic Downgrading of Planet Earth." *Science* 333(6040): 301–6. <https://doi.org/10.1126/science.1205106>.
- Ferretti, F., B. Worm, G. L. Britten, M. R. Heithaus, and H. K. Lotze. 2010. "Patterns and Ecosystem Consequences of Shark Declines in the Ocean." *Ecology Letters* 13(8): 1055–71. <https://doi.org/10.1111/j.1461-0248.2010.01489.x>.
- Friedlander, A. M., and E. E. DeMartini. 2002. "Contrasts in Density, Size, and Biomass of Reef Fishes between the Northwestern and the Main Hawaiian Islands: The Effects of Fishing down Apex Predators." *Marine Ecology Progress Series* 230: 253–264. <https://doi.org/10.3354/meps230253>.
- 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(2): 459–472. <https://doi.org/10.1007/s00338-016-1415-2>.
- Froese, R., and D. Pauly. 2010. *FishBase*. Vancouver: Fisheries Centre, University of British Columbia.
- Gilbert, F., A. Gonzalez, and I. Evans-Freke. 1998. "Corridors Maintain Species Richness in the Fragmented Landscapes of a Microecosystem." *Proceedings of the Royal Society of London. Series B: Biological Sciences* 265(1396): 577–582. <https://doi.org/10.1098/rspb.1998.0333>.
- Graham, N. A. J., and K. L. Nash. 2013. "The Importance of Structural Complexity in Coral Reef Ecosystems." *Coral Reefs* 32(2): 315–326. <https://doi.org/10.1007/s00338-012-0984-y>.
- Graham, N. A. J., T. R. McClanahan, M. Aaron MacNeil, S. K. Wilson, J. E. Cinner, C. Huchery, and T. H. Holmes. 2017. "Human Disruption of Coral Reef Trophic Structure." *Current Biology* 27(2): 231–36.
- Grottoli, A. G., S. T. Gille, E. R. M. Druffel, and R. B. Dunbar. 2003. "Decadal Timescale Shift in the 14C Record of a Central Equatorial Pacific Coral." *Radiocarbon* 45(1): 91–99. <https://doi.org/10.1017/S0033822200032422>.
- Guerra, A. S., A. B. Kao, D. J. McCauley, and A. M. Berdahl. 2020. "Fisheries-Induced Selection against Schooling Behaviour in Marine Fishes." *Proceedings of the Royal Society B* 287(1935): 20201752.
- Guerra, A. S., J. C. Van Wert, A. J. Haupt, D. J. McCauley, E. J. Eliason, H. S. Young, D. Lecchini, T. D. White, and J. E. Caselle. 2023. "Differences in the Behavior and Diet between Shoaling and Solitary Surgeonfish (*Acanthurus Triostegus*)." *Ecology and Evolution* 13(1): e9686.
- Halpern, B. S., M. Frazier, J. Potapenko, K. S. Casey, K. Koenig, C. Longo, J. S. Lowndes, R. Cotton Rockwood, E. R. Selig, and K. A. Selkoe. 2015. "Spatial and Temporal Changes in Cumulative Human Impacts on the World's Ocean." *Nature Communications* 6(1): 1–7.
- Hammerslag, N., S. C. Barley, D. J. Irschick, J. J. Meeuwig, E. R. Nelson, and M. G. Meekan. 2018. "Predator Declines and Morphological Changes in Prey: Evidence from Coral Reefs Depleted of Sharks." *Marine Ecology Progress Series* 586: 127–139. <https://doi.org/10.3354/meps12426>.
- Harborne, A. R., A. Rogers, Y.-M. Bozec, and P. J. Mumby. 2017. "Multiple Stressors and the Functioning of Coral Reefs." *Annual Review of Marine Science* 9: 445–468.
- Heithaus, M. R., A. Frid, A. J. Wirsing, and B. Worm. 2008. "Predicting Ecological Consequences of Marine Top Predator Declines." *Trends in Ecology & Evolution* 23(4): 202–210. <https://doi.org/10.1016/j.tree.2008.01.003>.
- Hempson, T. N., N. A. J. Graham, M. A. MacNeil, D. H. Williamson, G. P. Jones, and G. R. Almany. 2017. "Coral Reef Mesopredators Switch Prey, Shortening Food Chains, in Response to Habitat Degradation." *Ecology and Evolution* 7(8): 2626–35. <https://doi.org/10.1002/ece3.2805>.
- Hughes, T. P., M. J. Rodrigues, D. R. Bellwood, D. Ceccarelli, O. Hoegh-Guldberg, L. McCook, N. Moltschanivskyj, M. S. Pratchett, R. S. Steneck, and B. Willis. 2007. "Phase Shifts, Herbivory, and the Resilience of Coral Reefs to Climate Change." *Current Biology* 17(4): 360–65.
- Hussey, N. E., M. Aaron MacNeil, B. C. McMeans, J. A. Olin, S. F. J. Dudley, G. Cliff, S. P. Wintner, S. T. Fennessy, and A. T. Fisk. 2014. "Rescaling the Trophic Structure of Marine Food Webs." *Ecology Letters* 17(2): 239–250. <https://doi.org/10.1111/ele.12226>.
- Hussey, N. E., M. Aaron MacNeil, M. C. Siple, B. N. Popp, S. F. J. Dudley, and A. T. Fisk. 2015. "Expanded Trophic Complexity among Large Sharks." *Food Webs* 4: 1–7. <https://doi.org/10.1016/j.fooweb.2015.04.002>.
- Jackson, A. L., R. Inger, A. C. Parnell, and S. Bearhop. 2011. "Comparing Isotopic Niche Widths among and within Communities: SIBER—Stable Isotope Bayesian Ellipses in R." *Journal of Animal Ecology* 80(3): 595–602. <https://doi.org/10.1111/j.1365-2656.2011.01806.x>.
- Jordano, P. 2016. "Chasing Ecological Interactions." *PLoS Biology* 14(9): e1002559.
- Jorgensen, S. J., F. Micheli, T. D. White, K. S. Van Houtan, J. Alfaro-Shigueto, S. Andrzejczek, N. S. Arnoldi, et al. 2022. "Emergent Research and Priorities for Shark and Ray Conservation." *Endangered Species Research* 47: 171–203. <https://doi.org/10.3354/esr01169>.
- Karkarey, R., T. Alcoverro, S. Kumar, and R. Arthur. 2017. "Coping with Catastrophe: Foraging Plasticity Enables a Benthic Predator to Survive in Rapidly Degrading Coral Reefs." *Animal Behaviour* 131: 13–22.

- Kondoh, M., and K. Ninomiya. 2009. "Food-Chain Length and Adaptive Foraging." *Proceedings of the Royal Society B: Biological Sciences* 276(1670): 3113–21.
- Kuile, M.-t., A. A. Ana, A. Bui, K. Butner, J. N. Childress, S. Copeland, B. P. DiFiore, et al. 2022. "Changes in Invertebrate Food Web Structure between High- and Low-Productivity Environments Are Driven by Intermediate but Not Top-Predator Diet Shifts." *Biology Letters* 18(10): 20220364. <https://doi.org/10.1098/rsbl.2022.0364>.
- Layman, C. A., D. Albrey Arrington, C. G. Montaña, and D. M. Post. 2007. "Can Stable Isotope Ratios Provide for Community-Wide Measures of Trophic Structure?" *Ecology* 88(1): 42–48.
- Leitão, M., C. W. Hackrad, Í. Lima, J. E. Ciancio, and F. C. Félix-Hackrad. 2023. "Effect of Human Impact on Coral Reef Herbivorous Fish Niche." *Marine Biology* 170(5): 59.
- Lemons, G. E., R. L. Lewison, J. A. Seminoff, C. M. Coppentrath, and B. N. Popp. 2020. "Nitrogen Isotope Fractionation of Amino Acids from a Controlled Study on the Green Turtle (*Chelonia mydas*): Expanding beyond Glx/Phe for Trophic Position." *Marine Biology* 167: 1–13.
- Letessier, T. B., D. Mouillot, P. J. Bouchet, L. Vigliola, M. C. Fernandes, C. Thompson, G. Boussarie, J. Turner, J.-B. Juhel, and E. Maire. 2019. "Remote Reefs and Seamounts Are the Last Refuges for Marine Predators across the Indo-Pacific." *PLoS Biology* 17(8): e3000366.
- Loreau, M. 2004. "Does Functional Redundancy Exist?" *Oikos* 104(3): 606–611.
- MacNeil, M. A., D. D. Chapman, M. Heupel, C. A. Simpfendorfer, M. Heithaus, M. Meekan, E. Harvey, J. Goetze, J. Kiszka, and M. E. Bond. 2020. "Global Status and Conservation Potential of Reef Sharks." *Nature* 583(7818): 801–6.
- Madin, E. M. P., L. M. Dill, A. D. Ridlon, M. R. Heithaus, and R. R. Warner. 2016. "Human Activities Change Marine Ecosystems by Altering Predation Risk." *Global Change Biology* 22(1): 44–60.
- Madin, E. M. P., S. D. Gaines, J. S. Madin, and R. R. Warner. 2010. "Fishing Indirectly Structures Macroalgal Assemblages by Altering Herbivore Behavior." *The American Naturalist* 176(6): 785–801.
- Madin, E. M. P., S. D. Gaines, and R. R. Warner. 2010. "Field Evidence for Pervasive Indirect Effects of Fishing on Prey Foraging Behavior." *Ecology* 91(12): 3563–71.
- Marion, G. S., R. B. Dunbar, D. A. Mucciarone, J. N. Kremer, J. Stephen Lansing, and A. Arthawiguna. 2005. "Coral Skeletal $\delta^{15}\text{N}$ Reveals Isotopic Traces of an Agricultural Revolution." *Marine Pollution Bulletin* 50(9): 931–944.
- Matthews, C. J. D., R. I. Ruiz-Cooley, C. Pomerleau, and S. H. Ferguson. 2020. "Amino Acid $\delta^{15}\text{N}$ Underestimation of Cetacean Trophic Positions Highlights Limited Understanding of Isotopic Fractionation in Higher Marine Consumers." *Ecology and Evolution* 10(7): 3450–62. <https://doi.org/10.1002/ece3.6142>.
- Maureaud, A., D. Gascuel, M. Colléter, M. L. D. Palomares, H. Du Pontavice, D. Pauly, and W. W. L. Cheung. 2017. "Global Change in the Trophic Functioning of Marine Food Webs." *PLoS One* 12(8): e0182826.
- McCauley, D. J., E. Hoffmann, H. S. Young, and F. Micheli. 2012. "Night Shift: Expansion of Temporal Niche Use Following Reductions in Predator Density." *PLoS One* 7(6): e38871. <https://doi.org/10.1371/journal.pone.0038871>.
- McCauley, D. J., F. Micheli, H. S. Young, D. P. Tittensor, D. R. Brumbaugh, E. M. P. Madin, K. E. Holmes, et al. 2010. "Acute Effects of Removing Large Fish from a Near-Pristine Coral Reef." *Marine Biology* 157(12): 2739–50. <https://doi.org/10.1007/s00227-010-1533-2>.
- McCauley, D. J., M. L. Pinsky, S. R. Palumbi, J. A. Estes, F. H. Joyce, and R. R. Warner. 2015. "Marine Defaunation: Animal Loss in the Global Ocean." *Science* 347(6219): 1255641.
- McCauley, D. J., H. S. Young, R. B. Dunbar, J. A. Estes, B. X. Semmens, and F. Micheli. 2012. "Assessing the Effects of Large Mobile Predators on Ecosystem Connectivity." *Ecological Applications* 22(6): 1711–17. <https://doi.org/10.1890/11-1653.1>.
- McClelland, J. W., and J. P. Montoya. 2002. "Trophic Relationships and the Nitrogen Isotopic Composition of Amino Acids in Plankton." *Ecology* 83(8): 2173–80.
- McMahon, K. W., and M. D. McCarthy. 2016. "Embracing Variability in Amino Acid $\delta^{15}\text{N}$ Fractionation: Mechanisms, Implications, and Applications for Trophic Ecology." *Ecosphere* 7(12): e01511. <https://doi.org/10.1002/ecs2.1511>.
- Meyer, C. G., Y. P. Papastamatiou, and K. N. Holland. 2010. "A Multiple Instrument Approach to Quantifying the Movement Patterns and Habitat Use of Tiger (*Galeocerdo cuvier*) and Galapagos Sharks (*Carcharhinus galapagensis*) at French Frigate Shoals, Hawaii." *Marine Biology* 157: 1857–68.
- Mill, A. C., J. K. Pinnegar, and N. V. C. Polunin. 2007. "Explaining Isotope Trophic-Step Fractionation: Why Herbivorous Fish Are Different." *Functional Ecology* 21: 1137–45.
- Morillo-Velarde, P. S., P. Briones-Fourzán, L. Álvarez-Filip, S. Aguiñiga-García, A. Sánchez-González, and E. Lozano-Álvarez. 2018. "Habitat Degradation Alters Trophic Pathways but Not Food Chain Length on Shallow Caribbean Coral Reefs." *Scientific Reports* 8(1): 4109. <https://doi.org/10.1038/s41598-018-22463-x>.
- Mumby, P. J., C. P. Dahlgren, A. R. Harborne, C. V. Kappel, F. Micheli, D. R. Brumbaugh, K. E. Holmes, et al. 2006. "Fishing, Trophic Cascades, and the Process of Grazing on Coral Reefs." *Science* 311(5757): 98–101. <https://doi.org/10.1126/science.1121129>.
- Murali, G., G. H. de Oliveira Caetano, G. Barki, S. Meiri, and U. Roll. 2022. "Emphasizing Declining Populations in the Living Planet Report." *Nature* 601(7894): E20–E24. <https://doi.org/10.1038/s41586-021-04165-z>.
- Nanami, A., and T. Shimose. 2013. "Interspecific Differences in Prey Items in Relation to Morphological Characteristics among Four Lutjanid Species (*Lutjanus decussatus*, *L. fulviflamma*, *L. fulvus* and *L. gibbus*)." *Environmental Biology of Fishes* 96(5): 591–602. <https://doi.org/10.1007/s10641-012-0049-7>.
- Nurhati, I. S., K. M. Cobb, C. D. Charles, and R. B. Dunbar. 2009. "Late 20th Century Warming and Freshening in the Central Tropical Pacific." *Geophysical Research Letters* 36(21): L21606. <https://doi.org/10.1029/2009GL040270>.
- Ohkouchi, N., Y. Chikaraishi, H. G. Close, B. Fry, T. Larsen, D. J. Madigan, M. D. McCarthy, et al. 2017. "Advances in the Application of Amino Acid Nitrogen Isotopic Analysis in Ecological and Biogeochemical Studies." *Organic Geochemistry* 113: 150–174. <https://doi.org/10.1016/j.orggeochem.2017.07.009>.
- Olin, J. A., N. E. Hussey, A. Grgicak-Mannion, M. W. Fritts, S. P. Wintner, and A. T. Fisk. 2013. "Variable $\delta^{15}\text{N}$ Diet-Tissue

- Discrimination Factors among Sharks: Implications for Trophic Position, Diet and Food Web Models." *PLoS One* 8(10): e77567.
- Paddack, M. J., J. D. Reynolds, C. Aguilar, R. S. Appeldoorn, J. Beets, E. W. Burkett, P. M. Chittaro, K. Clarke, R. Esteves, and A. C. Fonseca. 2009. "Recent Region-Wide Declines in Caribbean Reef Fish Abundance." *Current Biology* 19(7): 590–95.
- Pandolfi, J. M., R. H. Bradbury, E. Sala, T. P. Hughes, K. A. Bjorndal, R. G. Cooke, D. McArdle, et al. 2003. "Global Trajectories of the Long-Term Decline of Coral Reef Ecosystems." *Science* 301(5635): 955–58. <https://doi.org/10.1126/science.1085706>.
- Papastamatiou, Y. P., C. L. Wood, D. Bradley, D. J. McCauley, A. L. Pollock, and J. E. Caselle. 2014. "First Records of the Sicklefin Lemon Shark, *Negaprion acutidens*, at Palmyra Atoll, Central Pacific: A Recent Colonization Event?" *Marine Biodiversity Records* 7: e114. <https://doi.org/10.1017/S175526721400116X>.
- Papastamatiou, Y., B. Wetherbee, C. Lowe, and G. Crow. 2006. "Distribution and Diet of Four Species of Carcharhinid Shark in the Hawaiian Islands: Evidence for Resource Partitioning and Competitive Exclusion." *Marine Ecology Progress Series* 320: 239–251. <https://doi.org/10.3354/meps320239>.
- Parnell, A., and A. Jackson. 2013. "Siar: Stable Isotope Analysis in R." R Package Version 4.2, CRAN. R-project.org/package=sia.
- Pauly, D., V. Christensen, J. Dalsgaard, R. Froese, and F. T. Jr. 1998. "Fishing Down Marine Food Webs." *Science* 279(5352): 860–63.
- Pikitch, E. K., S. Cristine, A. B. Elizabeth, B. Andrew, B. Ramon, O. C. David, D. Paul, D. Phaedra, D. Fulharthy, and B. Heneman. 2004. "Ecosystem-based fishery management." *Science* 305(5682): 346–47.
- Popp, B. N., B. S. Graham, R. J. Olson, C. C. S. Hannides, M. J. Lott, G. A. López-Ibarra, F. Galván-Magaña, and B. Fry. 2007. "Insight into the Trophic Ecology of Yellowfin Tuna, *Thunnus albacares*, from Compound-Specific Nitrogen Isotope Analysis of Proteinaceous Amino Acids." In *Stable Isotopes as Indicators of Ecological Change*. Terrestrial Ecology, edited by Todd E. Dawson and Rolf T. W. Siegwolf, Vol. 1, 173–190. San Diego, CA: Elsevier. [https://doi.org/10.1016/S1936-7961\(07\)01012-3](https://doi.org/10.1016/S1936-7961(07)01012-3).
- Rasher, D. B., A. S. Hoey, and M. E. Hay. 2017. "Cascading Predator Effects in a Fijian Coral Reef Ecosystem." *Scientific Reports* 7(1): 15684. <https://doi.org/10.1038/s41598-017-15679-w>.
- Rioja-Nieto, R., and L. Álvarez-Filip. 2019. "Coral Reef Systems of the Mexican Caribbean: Status, Recent Trends and Conservation." *Marine Pollution Bulletin* 140: 616–625.
- Robbins, W. D., M. Hisano, S. R. Connolly, and J. Howard Choat. 2006. "Ongoing Collapse of Coral-Reef Shark Populations." *Current Biology* 16(23): 2314–19.
- Robinson, J. P. W., 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(3): 1009–22.
- Roff, G., C. J. Brown, M. A. Priest, and P. J. Mumby. 2018. "Decline of Coastal Apex Shark Populations over the Past Half Century." *Communications Biology* 1: 223. <https://doi.org/10.1038/s42003-018-0233-1>.
- Roff, G., C. Doropoulos, A. Rogers, Y.-M. Bozec, N. C. Krueck, E. Aurellado, M. Priest, C. Birrell, and P. J. Mumby. 2016. "The Ecological Role of Sharks on Coral Reefs." *Trends in Ecology & Evolution* 31(5): 395–407. <https://doi.org/10.1016/j.tree.2016.02.014>.
- Roff, G., and P. J. Mumby. 2012. "Global Disparity in the Resilience of Coral Reefs." *Trends in Ecology & Evolution* 27(7): 404–413. <https://doi.org/10.1016/j.tree.2012.04.007>.
- Ruppert, J. L. W., M. J. Travers, L. L. Smith, M.-J. Fortin, and M. G. Meekan. 2013. "Caught in the Middle: Combined Impacts of Shark Removal and Coral Loss on the Fish Communities of Coral Reefs." *PLoS One* 8(9): e74648. <https://doi.org/10.1371/journal.pone.0074648>.
- Salomon, A. K., S. K. Gaichas, N. T. Shears, J. E. Smith, E. M. P. Madin, and S. D. Gaines. 2010. "Key Features and Context-Dependence of Fishery-Induced Trophic Cascades." *Conservation Biology* 24(2): 382–394.
- Sandin, S. A., J. E. Smith, E. E. DeMartini, E. A. Dinsdale, S. D. Donner, A. M. Friedlander, T. Konotchick, et al. 2008. "Baselines and Degradation of Coral Reefs in the Northern Line Islands." *PLoS One* 3(2): e1548. <https://doi.org/10.1371/journal.pone.0001548>.
- Schmitter-Soto, J. J., A. Aguilar-Perera, A. Cruz-Martínez, R. L. Herrera-Pavón, A. A. Morales-Aranda, and D. Cobián-Rojas. 2018. "Interdecadal Trends in Composition, Density, Size, and Mean Trophic Level of Fish Species and Guilds before and after Coastal Development in the Mexican Caribbean." *Biodiversity and Conservation* 27: 459–474.
- Schriever, T. A., and D. Dudley Williams. 2013. "Influence of Pond Hydroperiod, Size, and Community Richness on Food-Chain Length." *Freshwater Science* 32(3): 964–975.
- Seminoff, J. A., S. R. Benson, K. E. Arthur, T. Eguchi, P. H. Dutton, R. F. Tapilatu, and B. N. Popp. 2012. "Stable Isotope Tracking of Endangered Sea Turtles: Validation with Satellite Telemetry and $\delta^{15}\text{N}$ Analysis of Amino Acids." *PLoS One* 7(5): e37403.
- Sherman, C. S., C. A. Simpfendorfer, N. Pacoureaux, J. H. Matsushiba, H. F. Yan, R. H. L. Walls, C. L. Rigby, W. J. VanderWright, R. W. Jabado, and R. A. Pollom. 2023. "Half a Century of Rising Extinction Risk of Coral Reef Sharks and Rays." *Nature Communications* 14(1): 15.
- Simpfendorfer, C., R. R. Yuneni, D. Tanay, L. Seyha, A. B. Haque, F. B. A. Ali, D. Bineesh, K. K. Gautama, D. A. Maung, A. Sianipar, A. J. A. T. Utzurrum, and V. Q. Vo. 2020. "Carcharhinus melanopterus" (Quoy & Gaimard, 1824). *The IUCN Red List of Threatened Species*. <https://doi.org/10.2305/IUCN.UK.2020-3.RLTS.T39375A58303674.en>
- Skinner, C., A. C. Mill, M. D. Fox, S. P. Newman, Y. Zhu, A. Kuhl, and N. V. C. Polunin. 2021. "Offshore Pelagic Subsidies Dominate Carbon Inputs to Coral Reef Predators." *Science Advances* 7(8): eabf3792.
- Skinner, C., M. R. D. Cobain, Y. Zhu, A. S. J. Wyatt, and N. V. C. Polunin. 2022. "Progress and direction in the use of stable isotopes to understand complex coral reef ecosystems: A Review." *Oceanography and Marine Biology* 373–432.
- Stallings, C. D. 2009. "Fishery-Independent Data Reveal Negative Effect of Human Population Density on Caribbean Predatory Fish Communities." *PLoS One* 4(5): e5333.
- Stevenson, C., L. S. Katz, F. Micheli, B. Block, K. W. Heiman, C. Perle, K. Weng, R. Dunbar, and J. Witting. 2007. "High Apex Predator Biomass on Remote Pacific Islands." *Coral Reefs* 26(1): 47–51. <https://doi.org/10.1007/s00338-006-0158-x>.

- Sudekum, A. E. 1991. "Life History and Ecology of Large Jacks in Undisturbed, Shallow, Oceanic Communities." *Fish Bull* 89: 493–513 <https://cir.nii.ac.jp/crid/1572543024730147200>.
- UNEP, United Nations Environment Program. 2022. "Decision Adopted by the Conference of the Parties to the Convention on Biological Diversity: Kunming-Montreal Global Biodiversity Framework." <https://www.cbd.int/doc/decisions/cop-15/cop-15-dec-04-en.pdf>.
- Valdivia, A., C. E. Cox, and J. F. Bruno. 2017. "Predatory Fish Depletion and Recovery Potential on Caribbean Reefs." *Science Advances* 3(3): e1601303.
- Vander Zanden, M., B. J. Jake, N. L. Shuter, and J. B. Rasmussen. 1999. "Patterns of Food Chain Length in Lakes: A Stable Isotope Study." *The American Naturalist* 154(4): 406–416.
- Walsh, R. G., S. He, and C. T. Yarnes. 2014. "Compound-Specific $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ Analysis of Amino Acids: A Rapid, Chloroformate-Based Method for Ecological Studies." *Rapid Communications in Mass Spectrometry* 28(1): 96–108.
- Westveer, J., R. Freeman, L. McRae, V. Marconi, R. E. A. Almond, and M. Grooten. 2022. "A Deep Dive into the Living Planet Index: A Technical Report." WWF, Gland, Switzerland. Design and infographics by: Peer.
- Wetherbee, B., G. Crow, and C. Lowe. 1997. "Distribution, Reproduction and Diet of the Gray Reef Shark *Carcharhinus amblyrhynchos* in Hawaii." *Marine Ecology Progress Series* 151: 181–89. <https://doi.org/10.3354/meps151181>.
- Wetherbee, B. M., G. L. Crow, and C. G. Lowe. 1996. "Biology of the Galapagos Shark, *Carcharhinus galapagensis*, in Hawai'i." *Environmental Biology of Fishes* 45: 299–310.
- Williams, I. D., B. L. Richards, S. A. Sandin, J. K. Baum, R. E. Schroeder, M. O. Nadon, B. Zgliczynski, P. Craig, J. L. McIlwain, and R. E. Brainard. 2010. "Differences in Reef Fish Assemblages between Populated and Remote Reefs Spanning Multiple Archipelagos across the Central and Western Pacific." *Journal of Marine Sciences* 2011: e826234. <https://doi.org/10.1155/2011/826234>.
- Wyatt, A. S. J., R. Matsumoto, Y. Chikaraishi, Y. Miyairi, Y. Yokoyama, K. Sato, N. Ohkouchi, and T. Nagata. 2019. "Enhancing Insights into Foraging Specialization in the World's Largest Fish Using a Multi-Tissue, Multi-Isotope Approach." *Ecological Monographs* 89(1): e01339.
- Wyatt, A. S. J., 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.
- Yarnes, C. T., and J. Herszage. 2017. "The Relative Influence of Derivatization and Normalization Procedures on the Compound-Specific Stable Isotope Analysis of Nitrogen in Amino Acids." *Rapid Communications in Mass Spectrometry* 31(8): 693–704.
- Young, H. S., D. J. McCauley, R. Dirzo, R. B. Dunbar, and S. A. Shaffer. 2010. "Niche Partitioning among and within Sympatric Tropical Seabirds Revealed by Stable Isotope Analysis." *Marine Ecology Progress Series* 416: 285–294.
- Young, H. S., F. O. McCauley, F. Micheli, R. B. Dunbar, and D. J. McCauley. 2024. "Data from: Shortened Food Chain Length in a Fished Versus Unfished Coral Reef." Dryad, Dataset. <https://doi.org/10.5061/dryad.kpr4xhcg>.
- Zgliczynski, B. J., and S. A. Sandin. 2017. "Size-Structural Shifts Reveal Intensity of Exploitation in Coral Reef Fisheries." *Ecological Indicators* 73: 411–421. <https://doi.org/10.1016/j.ecolind.2016.09.045>.

SUPPORTING INFORMATION

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

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