

Review Article

Emerging insights on effects of sharks and other top predators on coral reefs

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Predation is ubiquitous on coral reefs. Among the most charismatic group of reef predators are the top predatory fishes, including sharks and large-bodied bony fishes. Despite the threat presented by top predators, data describing their realized effects on reef community structure and functioning are challenging to produce. Many innovative studies have capitalized on natural experimental conditions to explore predator effects on reefs. Gradients in predator density have been created by spatial patterning of fisheries management. Evidence of prey release has been observed across some reefs, namely that potential prey increase in density when predator density is reduced. While such studies search for evidence of prey release among broad groups or guilds of potential prey, a subset of studies have sought evidence of release at finer population levels. We find that some groups of fishes are particularly vulnerable to the effects of predators and more able to capitalize demographically when predator density is reduced. For example, territorial damselfish appear to realize reliable population expansion with the reduction in predator density, likely because their aggressive, defensive behavior makes them distinctly vulnerable to predation. Relatedly, individual fishes that suffer from debilitating conditions, such as heavy parasite loads, appear to realize relatively stronger levels of prey release with reduced predator density. Studying the effects of predators on coral reefs remains a timely pursuit, and we argue that efforts to focus on the specifics of vulnerability to predation among potential prey and other context-specific dimensions of mortality hold promise to expand our knowledge.

Introduction

Predation is a dominant force defining the structure and dynamics of coral reef fish assemblages [1]. For most species of reef fish, the threat of predation begins at the earliest life stages, as fish recruiting to the reef face an intensive ‘predation gauntlet’. For example, a review of studies suggests that over 50% of individual fish settling from a pelagic-associated larval stage to a reef-associated juvenile phase die within 2 days of arrival [2]. The instantaneous threat of predation for a surviving individual drops with time, associated with an increase in experience and in body size [3]. For a fish living on a coral reef, among the most critical type of experience is the understanding of the landscape of shelter; for diurnally active reef fish, an intensive competition for shelter dominates at dusk as each fish searches for a hole, crevice, or other reef space where the individual can survive the night [4]. And, as with many marine taxa, the probability of predation per unit time among coral reef fishes is highest for the smallest individuals [1,3,5].

Although the instantaneous probability of predation tends to decrease through the life of an individual fish, the threat is never gone. In fact, predation remains a ubiquitous threat for reef fishes of all types and sizes. Consider the myriad somatic and behavioral adaptations of most coral reef fishes that are linked putatively with predator avoidance — cryptic coloration [6,7], aggregation or schooling [8,9], and morphological changes [10]. Even those fishes thought to be among the most dominant predators,

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for example large-bodied sharks and groupers, can fall victim to predation themselves [11,12]. As such, the study of predator effects on coral reefs is less of an investigation of the binary categorization of ‘vulnerable’ vs ‘invulnerable’ to predation, but instead is one of relative levels of risk.

The management of coral reefs often includes a goal to support viable populations of large predators [13,14]. One goal of management is motivated by simple existence value especially of culturally important or charismatic species [14–16]. However, a complementary goal is to maintain the ecosystem services of these taxa. Here, we consider the roles played by sharks and other top predators on the ecological workings of coral reefs. We focus this investigation on some emerging observations of predator effects, with an emphasis on case studies that highlight potential pathways for expanding our mechanistic understanding of predator effects in reef ecosystems.

What is a ‘top predator’ on a coral reef?

Predators are organisms that eat other organisms; at the simplest, ‘top predators’ are those that occupy the highest trophic levels within an ecological community. Simplified trophic models oftentimes present top predators as those that consume other predatory species, while having few (or no) predators themselves. Such constrained definitions of the top predator role have been challenged in the context of coral reef fish food webs. Reef sharks, for example, have been documented foraging on taxa across a range of trophic levels, including nearshore pelagic fishes [17] and lower trophic level fish and invertebrates in the reef habitat [18]. Similarly, the diet of the predatory two-spot snapper (*Lutjanus bohar*) across the Line Islands has been shown to converge on an estimated trophic level similar to that of smaller bodied teleost predators [19]. Given such evidence, it has been proposed that reef sharks and other large-bodied predatory fishes on coral reefs be designated as ‘mesopredators’ [18,20]. However, there is a distinct role played by the large-bodied predators on a coral reef, most importantly being their capacity to predate upon a particularly wide range of potential prey.

When considering the role played by predators, it is important to consider what the predator can consume and what the predator does consume. Many aspects of body shape and physiology determine what a predator can consume. Based on general limitations of predation among fishes, larger fishes tend to be able to consume larger prey [21,22]. Furthermore, fish that can swim faster, react more quickly, and capture prey within armored mouths are capable of consuming more types of prey. But the capacity to consume a particular type of prey does not equate directly to the regular consumption of this prey [23]. What a predator actually consumes depends upon many contextual (e.g. relative abundance of prey, history of consumption, breeding state) and behavioral cues (e.g. danger avoidance, territoriality), as well as elements of life history (e.g. ontogeny). Indeed, it has been a challenge to provide a consensus definition of top predators on coral reefs, a topic which has been debated and explored elsewhere [23,24]; here, we consider the role of predatory fish across contexts, and as such we use a working definition of ‘top predator’ based upon the extent of the potential prey base. On coral reefs, the predatory fishes with the broadest potential prey base are principally species of reef sharks (Carcharhinidae), groupers (Serranidae), jacks (Carangidae), and snappers (Lutjanidae), among others (Table 1 and Figure 1).

Effects of top predators on coral reef fish assemblage structure

Marine top predators are known to affect the structure of marine ecosystems in many ways, including the direct effects of predation and indirect effects including behavioral modification [25–28]. On coral reefs, the effects of fishing have been shown to lead to reductions in total fish biomass with disproportionate reductions in the biomass of top predatory fishes [29–36]. Many of the most common fishing techniques on coral reefs select for predatory species [37], with larger-bodied taxa typically more affected due to competitive dominance (e.g. competition among fish for bait) or preferential harvest (e.g. targeting by spearfishers).

Survey-based studies have revealed evidence that removal of predators can result in prey release across coral reefs. In comparisons of reef fish assemblages across a gradient of predator density, some studies reveal systematic shifts in the density of populations of putative prey [30,38–41]. For example in northwestern Australia, there were higher densities of mesopredatory carnivores observed on reefs with lower shark densities (here, mainly silvertip [*Carcharhinus albimarginatus*] and grey reef [*C. amblyrhynchos*] sharks) [42]. Across areas of the Great Barrier Reef (GBR), a large-bodied predatory grouper, *Plectropomus leopardus*, was observed in higher densities in zones afforded more fisheries protections while the density of the smaller-bodied fishes were

Table 1 Density metrics of five top predators by region from underwater visual surveys

Region	Family	Species	Biomass (grams/m ²)	Abundance (individuals/m ²)
Central Pacific (Line and Phoenix Islands)	Carcharhinidae	<i>Carcharhinus amblyrhynchos</i>	59.9	0.003
	Lutjanidae	<i>Lutjanus bohar</i>	35.6	0.040
	Carcharhinidae	<i>Carcharhinus melanopterus</i>	15.8	0.001
	Carcharhinidae	<i>Triaenodon obesus</i>	9.8	<0.001
	Carangidae	<i>Caranx melampygus</i>	5.0	0.007
Indian Ocean (Maldives)	Labridae	<i>Cheilinus undulatus</i>	2.7	<0.001
	Carcharhinidae	<i>Triaenodon obesus</i>	2.7	<0.001
	Carangidae	<i>Caranx melampygus</i>	1.1	0.005
	Lutjanidae	<i>Lutjanus gibbus</i>	1.0	0.044
	Serranidae	<i>Plectropomus laevis</i>	0.9	<0.001
Caribbean ¹ (Curaçao and Aruba)	Lutjanidae	<i>Lutjanus apodus</i>	5.3	0.015
	Lutjanidae	<i>Lutjanus mahogoni</i>	2.1	0.010
	Carangidae	<i>Caranx ruber</i>	1.9	0.007
	Muraenidae	<i>Gymnothorax funebris</i>	1.8	<0.001
	Sphyraenidae	<i>Sphyraena barracuda</i>	1.4	0.001

Underwater visual survey data were collected between 2005–2021 and the five top predatory species (by biomass) observed in each region are presented. All surveys were conducted in forereef habitats along the 10 m isobath. Data collected by authors.¹The Caribbean reef shark (*Carcharhinus perezi*) is a significant top predator for the region but was not within the top five species according to mean biomass as assessed via underwater visual surveys.

observed in lower densities in protected areas [43]. In a comparison of fish assemblage structure across management zones of the GBR, a consistent signature existed with higher densities of multiple piscivorous fishes and lower densities of prey fishes within protected relative to less-protected areas [44]. Such evidence of prey



Figure 1. Images of the five top predators by biomass by three representative regions from underwater visual surveys (2005–2021). Data from the Caribbean were from Curaçao and Aruba. Data from Indian Ocean is from the Maldives and data from the Central Pacific is from the Line and Phoenix Islands. The images of *Caranx melampygus*, *Carcharhinus amblyrhynchos*, *Caranx ruber*, *Lutjanus gibbus*, *Sphyraena barracuda*, *Cheilinus undulatus*, and *Plectropomus laevis* were adapted from photos by Jack. E. Randall and are licensed under a Creative Commons Attribution-Noncommercial 3.0 Unported License, obtained from FishBase. The image of *Lutjanus mahogoni* was adapted from a photo by Roger Rittmaster and is licensed under Attribution-NonCommercial 4.0 International (CC BY-NC 4.0). The images of *Lutjanus apodus* and *Triaenodon obesus* were adapted with permissions from photographs by Carlos Estapeand Giuseppe Mazza, respectively. The remaining images were adapted from photographs by the author (BJZ).

release is consistent with the hypothesis that the combination of direct and indirect effects of predation can limit the size of prey populations on coral reefs.

Although survey-based studies reveal evidence that predators can affect populations of prey, there is much less consensus regarding the potential for cascading effects of predators across other functional groups on the coral reef. Evidence of trophic cascades on coral reefs is limited, likely due to the high diversity of species and relative functional redundancy among coral reef taxa [41,45]. Models suggesting that changes in density of sharks on coral reefs can create a trophic cascade (i.e. through the release of mesopredatory prey and the concomitant decrease in lower trophic level prey) have been challenged based upon similar considerations of high trophic complexity of most reef food webs [18,46]. However, recent evidence suggests that the diets of mesopredators (i.e. those that are potential prey of sharks) can differ across a gradient of shark density, with gut contents shifting from containing more fish when fewer sharks are around to more invertebrates when there are more sharks [47]. Furthermore, observations suggest that these diet shifts may be linked to shifts in the relative abundances of smaller prey species, consistent with a shark-induced trophic cascade [48].

Importantly, the limited ability to control covariates in natural experiments will confound our ability to find ‘clean’ data of potential cascading effects associated with shifts in predator abundance at guild or assemblage levels [49–51]. Multiple studies looking at guild-level data of reef fishes have not found evidence of either prey release or trophic cascades [45,52]. Opportunity exists, however, to focus upon some targeted patterns of predation in our goal to expand our understanding of the effects of top predators on coral reefs.

Some prey species are particularly vulnerable to top predators

Most models of prey release and trophic cascades consider targeted prey species as those in particular size classes or trophic guilds. However, given the high diversity of fish species (with associated variation in shape, swimming capabilities, coloration, and behavior) on most reefs, we may expect there to be species-specific variation in vulnerability even within size classes or trophic guilds. It is thus plausible that while predators may increase mean mortality rates on a larger group of fish (e.g. of a particular trophic group), the effects of changes in predator density may contribute to predictable shifts in the relative survival, and ultimately relative abundance, of individual taxa of fish.

As a case study, let us consider how predation affects one notable trophic group on coral reefs, the herbivorous fishes [53–57]. When considering herbivorous fishes as a guild, there have been inconsistent reports relating herbivore composition and predator abundance. In some cases, the density (or biomass) of herbivorous fish was shown to be related negatively to the density of predators [44], consistent with models of prey release. In others, the relationship was positive [58] or insignificant between density of predators and herbivores [30,35]. Given that fishing activity can affect the density of both predators and large-bodied herbivores, it is not surprising that correlative studies show inconsistent relationships; the relative amount of extraction of predatory fish and large-bodied herbivorous fish is itself inconsistent across locations [37,55]. Perhaps by focusing our attention on herbivores that are not targeted, it may be possible to expand our understanding of effects of predators on coral reefs.

Herbivorous, territorial damselfish present an interesting case study for exploring the effects of predators on coral reef prey. Despite a lack of consistent variation in total herbivore biomass across a dramatic gradient of predator biomass in the northern Line Islands, there was strong evidence of prey release among the subset of herbivorous damselfish [30]. Similar negative associations of predators and territorial damselfish have been observed across a within-island gradient in Bonaire [59], a multi-region study of the GBR [44], and through survey years on Moorea [60]. Indeed, across a broad gradient of fisheries activity in the tropical Pacific, areas with more fisheries protections (and, ostensibly, higher predator densities) support lower densities of herbivorous damselfish [61]. When combining data on the biomass of territorial herbivorous damselfish directly with estimates of predator biomass, we find a strong negative relationship between biomass of predators and herbivorous damselfish (Figure 2).

Territorial damselfish are a well-studied group on most coral reefs, often typified by particularly aggressive behavior especially considering their generally diminutive size [62]. It is not uncommon for such small-bodied damselfish (generally 10–100 g body mass) to defend their territories with postures and strikes toward invading competitors that are 10–100 times their body mass. Such aggressive behaviors, however, are not constrained simply to potential resource competitors, but appear targeted towards any invader. In behavioral observations,

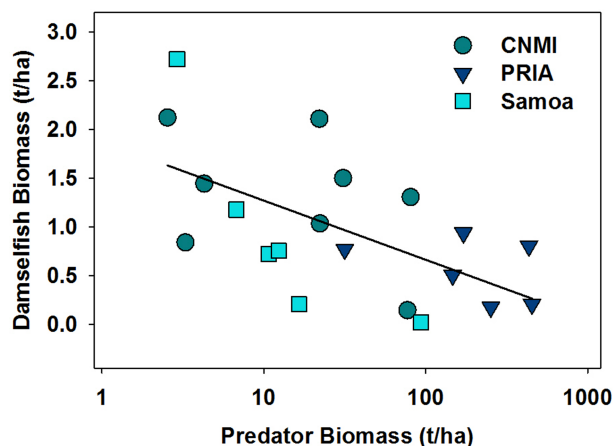


Figure 2. The relationship of biomass of territorial, herbivorous damselfish and top predatory fishes across the coral reefs of 20 islands in the U.S.-affiliated tropical Pacific.

Data from islands are coded by region, including the Commonwealth of the Northern Mariana Islands (CNMI), the Pacific Remote Island Area (PRIA), and American Samoa (Samoa). Data were collected by the Pacific Islands Fisheries Science Center (U.S. National Oceanic and Atmospheric Administration), using belt-transect surveys along forereef habitats. Islands were included if a minimum of eight sites were surveyed. Data are a subset of those published in related reports [37,61].

notable studies have indicated that some species of territorial damselfish do not modify their behavior as a function of predator density [63] or predation risk [64]. Seemingly, these territorial damselfish will only survive in the presence of abundant predators when they have sufficient shelter to support their overtly aggressive defensive behaviors. With fewer predators, their range can expand to habitats that are sub-optimal for survival (i.e. areas of reef with less shelter) but where they can still create and defend algal gardens. The aggressive behavior of territorial damselfish may thus lead to extremely constrained distributions with predators present, but perhaps may be particularly advantageous for prodigious range extension (through establishment of algal gardens across all parts of the reefscape) in the relative absence of predators. An opportunity exists to consider more closely the responses of fish species individually to shifts in predator abundances; the specificity of predation pathways may result in more predictability in species-specific, rather than guild-specific, responses to shifts in predator density.

Some prey individuals are particularly vulnerable to top predators

Predators do not operate in a vacuum; the effects of top predators on relative survival across individuals and across species will interact with other effects on prey condition and function. Parasites constitute one such impact on prey condition that is a particularly interesting case, as parasites often exert sublethal effects on their host including modifications of physiology, condition, and even behavior [65] and can reach high biomass in marine communities [66].

Certainly, one might expect prey with substantial numbers or impacts from parasites to be more vulnerable to predation. Parasites not only impose energetic costs, but in the marine environment, large ectoparasites might be expected to increase drag, reduce swimming performance, and overall decrease the ability of the prey to escape from predation. One of the most prevalent ectoparasites on coral reefs is gnathiid isopods. The direct energetic costs of these ectoparasites are not trivial; one gnathiid has been shown to consume up to 85% of the blood volume of a late-stage larval damselfish [67].

The evidence of behavioral changes with parasites in coral reef fish is decidedly more mixed and appears to vary with ontogeny, body size, and species identity [68–70]. The vulnerability to predation of fishes with such parasites is most certainly elevated relative to their unparasitized conspecifics. Notably, in our observations across gradients of predator density, fishes that are parasitized by ectoparasites are conspicuously absent when predators are abundant.

Modeling work has shown that removal of predators can lead to an increase in parasite abundance resulting in a reduction in the number of healthy individuals in the prey population [71]. This suggests that the overall fitness of the population might increase in the presence of predators, as those heavily infected fish are effectively removed from the ecosystem under the top-down control of predation. Indeed, reef fish communities with low abundance of large-bodied piscivores, such as those in the reefs of Curaçao, exhibit fish with a high incidence of dermal parasites when compared with other reef fish communities in the Caribbean, including Belize and Mexico [72].

Of course, parasites exhibit substantial functional and phylogenetic diversity, and impacts on prey populations are expected to differ depending on factors specific to the infecting parasites, including transmission strategy. There is a further interaction with fishing pressure, such that although the overall species richness of parasites is reduced on unfished compared with fished islands [73], the abundance of different groups of parasites have opposing responses depending on transmission strategy. Directly transmitted parasites are often more abundant on islands with greater fishing pressure, whereas trophically transmitted parasites tend to decrease in abundance [74]. Many trophically transmitted parasites use large apex predators as their final hosts. As these predators are particularly susceptible to human impacts, including fishing, the loss of obligate final hosts may result in a decrease in abundance of these trophically transmitted parasites. The loss of species richness of parasites itself seems to be related to the negative impacts of fishing on complex life cycle hosts [75]. Taken together, it is likely that decreases in top predator abundance will co-occur with corresponding increases in directly transmitted parasites, such as large ectoparasitic gnathiid isopods, and decreases in complex life cycle parasites, respectively. The indirect effects of the loss of top predators to the hidden biodiversity on reefs, including parasites, may therefore have potentially large implications for reef health.

Summary

- Top predatory fishes on coral reefs increase the mortality rate of many species of coral reef fish.
- The removal of predators from some coral reefs has been linked with the increase in density of many species of prey, though the specific taxa experiencing prey release vary across locations and there are few robust accounts of predator-induced trophic cascades from coral reefs.
- The effects of predators on coral reefs are noted reliably in some unique taxa (like territorial damselfish), in particular those with behaviors that may make them most vulnerable to predation.
- Predators affect the survival of individual fishes that are physiologically compromised, including some that suffer the effects of handicapping parasites.
- Coral reefs offer a strong opportunity to study the myriad effects of predators on community structure and dynamics, and studies designed by an understanding of prey vulnerability hold unique promise to expand our understanding of the predators' effects on emergent ecosystem health.

Competing Interests

The authors declare that there are no competing interests associated with the manuscript.

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Author Contributions

All authors contributed to the conceptualization and preparation of the manuscript.

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Abbreviations

GBR, Great Barrier Reef; PRIA, Pacific Remote Island Area.

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