Emerging Topics in Life Sciences (2022) **6** 57–65
https://doi.org/10.1042/ETLS20210238

PORTLAND PRESS

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,

Received: 11 September 2021
Revised: 23 December 2021
Accepted: 17 January 2022

Version of Record published:
8 March 2022

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 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	*Carcharhinus amblyrhynchos*	59.9	0.003
	Lutjanidae	*Lutjanus bohar*	35.6	0.040
	Carcharhinidae	*Carcharhinus melanopterus*	15.8	0.001
	Carcharhinidae	*Triaenodon obesus*	9.8	<0.001
	Carangidae	*Caranx melampygus*	5.0	0.007
Indian Ocean (Maldives)	Labridae	*Cheilinus undulatus*	2.7	<0.001
	Carcharhinidae	*Triaenodon obesus*	2.7	<0.001
	Carangidae	*Caranx melampygus*	1.1	0.005
	Lutjanidae	*Lutjanus gibbus*	1.0	0.044
	Serranidae	*Plectropomus laevis*	0.9	<0.001
Caribbean[1] (Curaçao and Aruba)	Lutjanidae	*Lutjanus apodus*	5.3	0.015
	Lutjanidae	*Lutjanus mahogoni*	2.1	0.010
	Carangidae	*Caranx ruber*	1.9	0.007
	Muraenidae	*Gymnothorax funebris*	1.8	<0.001
	Sphyraenidae	*Sphyraena barracuda*	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. [1]The 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

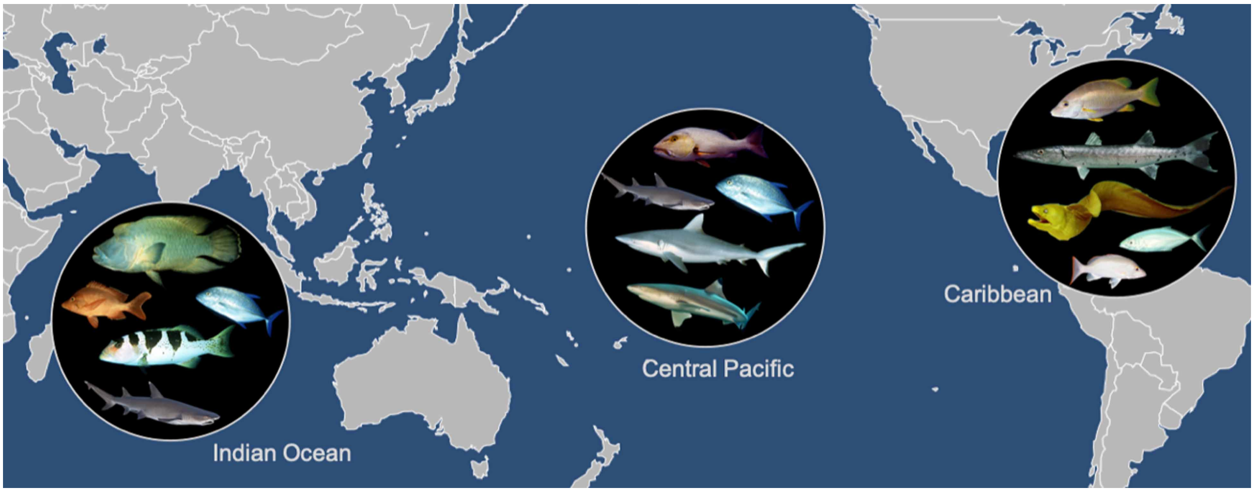

Figure 1. Images of the five top predators by biomass by three representative regions from underwater visual surveys (2005–2021).
Data from the Caribbean were from Curaçao and Aruba. Data from Indian Ocean is from the Maldives and data from the Central Pacific is from the Line and Phoenix Islands. The 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,

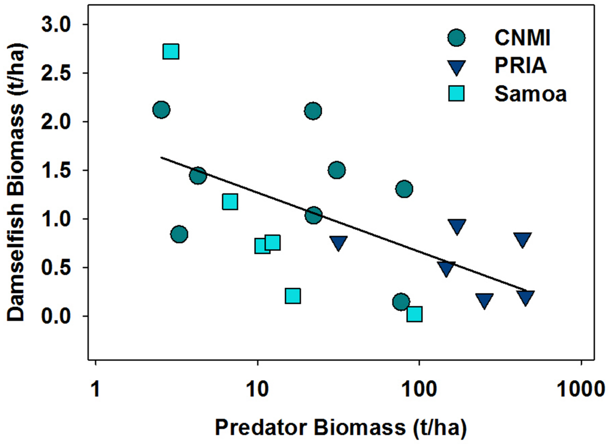

Figure 2. The relationship of biomass of territorial, herbivorous damselfish and top predatory fishes across the coral reefs of 20 islands in the U.S.-affiliated tropical Pacific.
Data from islands are coded by region, including the Commonwealth of the Northern Mariana Islands (CNMI), the Pacific Remote 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.

Emerging Topics in Life Sciences (2022) **6** 57–65
https://doi.org/10.1042/ETLS20210238

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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Open access for this article was enabled through a transformative open access agreement between Portland Press and the University of California.

Author Contributions

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

Acknowledgements

We would like to thank our colleagues and partners in the 100 Island Challenge effort for sharing insights and observations about reef systems. In particular, Mark Vermeij offered some early criticism that helped challenge our foundation for this manuscript and two anonymous reviewers helped to focus the goals of the contribution.

Abbreviations

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

References

1 Hixon, M.A. (1991) Predation as a process structuring coral reef fish communities. In *The Ecology of Fishes on Coral Reefs* (Sale, P.F., ed.), pp. 475–508, Academic Press, Inc, San Diego
2 Almany, G.R. and Webster, M.S. (2006) The predation gauntlet: early post-settlement mortality in reef fishes. *Coral Reefs* **25**, 19–22 https://doi.org/10.1007/s00338-005-0044-y
3 Goatley, C.H.R. and Bellwood, D.R. (2016) Body size and mortality rates in coral reef fishes: a three-phase relationship. *Proc. R. Soc. B Biol. Sci.* **283**, 20161858 https://doi.org/10.1098/rspb.2016.1858
4 Shulman, M.J. (1985) Coral reef fish assemblages: intra-and interspecific competition for shelter sites. *Environ. Biol. Fishes* **13**, 81–92 https://doi.org/10.1007/BF00002576
5 Munday, P.L. and Jones, G.P. (1998) The ecological implications of small body size among coral-reef fishes. *Oceanogr. Mar. Biol.* **36**, 373–411
6 Phillips, G.A.C., How, M.J., Lange, J.E., Marshall, N.J. and Cheney, K.L. (2017) Disruptive colouration in reef fish: does matching the background reduce predation risk? *J. Exp. Biol.* **220**, 1962–1974 https://doi.org/10.1242/jeb.151480
7 Marshall, N.J. (2000) Communication and camouflage with the same 'bright' colours in reef fishes. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **355**, 1243–1248 https://doi.org/10.1098/rstb.2000.0676
8 White, J.W., Samhouri, J.F., Stier, A.C., Wormald, C.L., Hamilton, S.L. and Sandin, S.A. (2010) Synthesizing mechanisms of density dependence in reef fishes: behavior, habitat configuration, and observational scale. *Ecology* **91**, 1949–1961 https://doi.org/10.1890/09-0298.1
9 Sandin, S.A. and Pacala, S.W. (2005) Fish aggregation results in inversely density-dependent predation on continuous coral reefs. *Ecology* **86**, 1520–1530 https://doi.org/10.1890/03-0654
10 Hammerschlag, N., Barley, S.C., Irschick, D.J., Meeuwig, J.J., Nelson, E.R. and Meekan, M.G. (2018) Predator declines and morphological changes in prey: evidence from coral reefs depleted of sharks. *Mar. Ecol. Prog. Ser.* **586**, 127–139 https://doi.org/10.3354/meps12426
11 Mourier, J., Planes, S. and Buray, N. (2013) Trophic interactions at the top of the coral reef food chain. *Coral Reefs* **32**, 285 https://doi.org/10.1007/s00338-012-0976-y
12 Mourier, J., Maynard, J., Parravicini, V., Ballesta, L., Clua, E., Domeier, M.L. et al. (2016) Extreme inverted trophic pyramid of reef sharks supported by spawning groupers. *Curr. Biol.* **26**, 2011–2016 https://doi.org/10.1016/j.cub.2016.05.058
13 Nadon, M.O., Baum, J.K., Williams, I.D., McPherson, J.M., Zgliczynski, B.J., Richards, B.L. et al. (2012) Re-creating missing population baselines for Pacific reef sharks. *Conserv. Biol.* **26**, 493–503 https://doi.org/10.1111/j.1523-1739.2012.01835.x
14 MacNeil, M.A., Chapman, D.D., Heupel, M., Simpfendorfer, C.A., Heithaus, M., Meekan, M. et al. (2020) Global status and conservation potential of reef sharks. *Nature* **583**, 801–806 https://doi.org/10.1038/s41586-020-2519-y
15 Morris, A.V., Roberts, C.M. and Hawkins, J.P. (2000) The threatened status of groupers (Epinephelinae). *Biodivers. Conserv.* **9**, 919–942 https://doi.org/10.1023/A:1008996002822
16 Zgliczynski, B.J., Williams, I.D., Schroeder, R., Nadon, M.O., Richards, B.L. and Sandin, S.A. (2013) The IUCN red list of threatened species: an assessment of coral reef fishes in the US Pacific Islands. *Coral Reefs* **32**, 1966–1976 https://doi.org/10.1007/s00338-013-1018-0
17 McCauley, D.J., Young, H.S., Dunbar, R.B., Estes, J.A., Semmens, B.X. and Micheli, F. (2012) Assessing the effects of large mobile predators on ecosystem connectivity. *Ecol. Appl.* **22**, 1711–1717 https://doi.org/10.1890/11-1653.1
18 Roff, G., Doropoulos, C., Rogers, A., Bozec, Y.-M., Krueck, N.C., Aurellado, E. et al. (2016) The ecological role of sharks on coral reefs. *Trends Ecol. Evol.* **31**, 395–407 https://doi.org/10.1016/j.tree.2016.02.014
19 Zgliczynski, B.J., Williams, G.J., Hamilton, S.L., Cordner, E.G. Fox, M.D., Eynaud, Y. et al. (2019) Foraging consistency of coral reef fishes across environmental gradients in the central Pacific. *Oecologia* **191**, 433–445 https://doi.org/10.1007/s00442-019-04496-9
20 Frisch, A.J., Ireland, M., Rizzari, J.R., Lönnstedt, O.M., Magnenat, K.A., Mirbach, C.E. et al. (2016) Reassessing the trophic role of reef sharks as apex predators on coral reefs. *Coral Reefs* **35**, 459–472 https://doi.org/10.1007/s00338-016-1415-2
21 Wainwright, P.C. and Richard, B.A. (1995) Predicting patterns of prey use from morphology of fishes. *Environ. Biol. Fishes* **44**, 97–113 https://doi.org/10.1007/BF00005909
22 Mittelbach, G.G. and Persson, L. (1998) The ontogeny of piscivory and its ecological consequences. *Can. J. Fish Aquat. Sci.* **55**, 1454–1465 https://doi.org/10.1139/f98-041
23 Bond, M.E., Valentin-Albanese, J., Babcock, E.A., Hussey, N.E., Heithaus, M.R. and Chapman, D.D. (2018) The trophic ecology of Caribbean reef sharks (*Carcharhinus perezi*) relative to other large teleost predators on an isolated coral atoll. *Mar. Biol.* **165**, 1–13 https://doi.org/10.1007/s00227-018-3322-2
24 Heupel, M.R., Knip, D.M., Simpfendorfer, C.A. and Dulvy, N.K. (2014) Sizing up the ecological role of sharks as predators. *Mar. Ecol. Prog. Ser.* **495**, 291–298 https://doi.org/10.3354/meps10597
25 Heithaus, M.R., Frid, A., Wirsing, A.J. and Worm, B. (2008) Predicting ecological consequences of marine top predator declines. *Trends Ecol. Evol.* **23**, 202–210 https://doi.org/10.1016/j.tree.2008.01.003

26 Bond, M., Valentin-Albanese, J., Babcock, E., Heithaus, M., Grubbs, R., Cerrato, R. et al. (2019) Top predators induce habitat shifts in prey within marine protected areas. *Oecologia* **190**, 375–385 https://doi.org/10.1007/s00442-019-04421-0

27 Rizzari, J.R., Frisch, A.J., Hoey, A.S. and McCormick, M.I. (2014) Not worth the risk: apex predators suppress herbivory on coral reefs. *Oikos* **123**, 829–836 https://doi.org/10.1111/oik.01318

28 Sherman, C.S., Heupel, M.R., Moore, S.K., Chin, A. and Simpfendorfer, C.A. (2020) When sharks are away, rays will play: effects of top predator removal in coral reef ecosystems. *Mar. Ecol. Prog. Ser.* **641**, 145–157 https://doi.org/10.3354/meps13307

29 Cinner, J.E., Maire, E., Huchery, C., MacNeil, M.A., Graham, N.A., Mora, C. et al. (2018) Gravity of human impacts mediates coral reef conservation gains. *Proc. Natl Acad. Sci. U.S.A.* **115**, E6116–E6E25 https://doi.org/10.1073/pnas.1708001115

30 DeMartini, E.E., Friedlander, A.M., Sandin, S.A. and Sala, E. (2008) Differences in fish-assemblage structure between fished and unfished atolls in the northern Line Islands, central Pacific. *Mar. Ecol. Prog. Ser.* **365**, 190–215 https://doi.org/10.3354/meps07501

31 Friedlander, A.M. and DeMartini, E.E. (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. *Mar. Ecol. Prog. Ser.* **230**, 253–264 https://doi.org/10.3354/meps230253

32 Graham, N.A., McClanahan, T.R., MacNeil, M.A., Wilson, S.K., Cinner, J.E., Huchery, C. et al. (2017) Human disruption of coral reef trophic structure. *Curr. Biol.* **27**, 231–236 https://doi.org/10.1016/j.cub.2016.10.062

33 McClanahan, T.R., Schroeder, R.E., Friedlander, A.M., Vigliola, L., Wantiez, L., Caselle, J.E. et al. (2019) Global baselines and benchmarks for fish biomass: comparing remote reefs and fisheries closures. *Mar. Ecol. Prog. Ser.* **612**, 167–192 https://doi.org/10.3354/meps12874

34 Newman, M.J.H., Paredes, G.A., Sala, E. and Jackson, J.B.C. (2006) Structure of Caribbean coral reef communities across a large gradient of fish biomass. *Ecol. Lett.* **9**, 1216–1227 https://doi.org/10.1111/j.1461-0248.2006.00976.x

35 Sandin, S.A., Smith, J.E., DeMartini, E.E., Dinsdale, E.A., Donner, S.D., Friedlander, A.M. et al. (2008) Baselines and degradation of coral reefs in the northern Line Islands. *PLoS ONE* **3**, e1548 https://doi.org/10.1371/journal.pone.0001548

36 Williams, I.D., Baum, J.K., Heenan, A., Hanson, K.M., Nadon, M.O. and Brainard, R.E. (2015) Human, oceanographic and habitat drivers of central and western Pacific coral reef fish assemblages. *PLoS ONE* **10**, e0120516 https://doi.org/10.1371/journal.pone.0120516

37 Zgliczynski, B.J. and Sandin, S.A. (2017) Size-structural shifts reveal intensity of exploitation in coral reef fisheries. *Ecol. Indicators* **73**, 411–421 https://doi.org/10.1016/j.ecolind.2016.09.045

38 Petit, I.J., Gaymer, C.F., Friedlander, A.M. and Gusmao, J.B. (2021) Humans at the top of the food web: are coastal benthic communities at Rapa Nui affected by fishing? *Environ. Biol. Fishes* **104**, 1433–1451 https://doi.org/10.1007/s10641-021-01182-9

39 Vermeij, M.J., Latijnhouwers, K.R., Dilrosun, F., Chamberland, V.F., Dubé, C.E., Van Buurt, G. et al. (2019) Historical changes (1905-present) in catch size and composition reflect altering fisheries practices on a small Caribbean island. *PLoS ONE* **14**, e0217589 https://doi.org/10.1371/journal.pone.0217589

40 Stallings, C.D. (2009) Fishery-independent data reveal negative effect of human population density on Caribbean predatory fish communities. *PLoS ONE* **4**, e5333 https://doi.org/10.1371/journal.pone.0005333

41 Sandin, S.A., Walsh, S.M. and Jackson, J.B.C. (2010) Prey release, trophic cascades, and phase shifts in tropical nearshore marine ecosystems. In *Trophic Cascades: Predators, Prey, and the Changing Dynamics of Nature* (Terborgh, J and Estes, J.A., eds), pp. 71–90, Island Press

42 Ruppert, J.L., Travers, M.J., Smith, L.L., Fortin, M.-J. and Meekan, M.G. (2013) Caught in the middle: combined impacts of shark removal and coral loss on the fish communities of coral reefs. *PLoS ONE* **8**, e74648 https://doi.org/10.1371/journal.pone.0074648

43 Graham, N.A.J., Evans, R.D. and Russ, G.R. (2003) The effects of marine reserve protection on the trophic relationships of reef fishes on the great barrier reef. *Environ. Conserv.* **30**, 200–208 https://doi.org/10.1017/S0376892903000195

44 Boaden, A. and Kingsford, M.J. (2015) Predators drive community structure in coral reef fish assemblages. *Ecosphere* **6**, 1–33 https://doi.org/10.1890/ES14-00292.1

45 Casey, J.M., Baird, A.H., Brandl, S.J., Hoogenboom, M.O., Rizzari, J.R., Frisch, A.J. et al. (2017) A test of trophic cascade theory: fish and benthic assemblages across a predator density gradient on coral reefs. *Oecologia* **183**, 161–175 https://doi.org/10.1007/s00442-016-3753-8

46 Desbiens, A.A., Roff, G., Robbins, W.D., Taylor, B.M., Castro-Sanguino, C., Dempsey, A. et al. (2021) Revisiting the paradigm of shark-driven trophic cascades in coral reef ecosystems. *Ecology* **102**, e03303 https://doi.org/10.1002/ecy.3303

47 Barley, S.C., Meekan, M.G. and Meeuwig, J.J. (2017) Diet and condition of mesopredators on coral reefs in relation to shark abundance. *PLoS ONE* **12**, e0165113 https://doi.org/10.1371/journal.pone.0165113

48 Barley, S.C., Meekan, M.G. and Meeuwig, J.J. (2017) Species diversity, abundance, biomass, size and trophic structure of fish on coral reefs in relation to shark abundance. *Mar. Ecol. Prog. Ser.* **565**, 163–179 https://doi.org/10.3354/meps11981

49 Roff, G., Doropoulos, C., Rogers, A., Bozec, Y.-M., Krueck, N.C., Aurellado, E. et al. (2016) Reassessing shark-driven trophic cascades on coral reefs: a reply to ruppert et al. *Trends Ecol. Evol.* **31**, 587–589 https://doi.org/10.1016/j.tree.2016.05.005

50 Ruppert, J.L., Fortin, M.-J. and Meekan, M.G. (2016) The ecological role of sharks on coral reefs: response to Roff et al. *Trends Ecol. Evol.* **31**, 586–587 https://doi.org/10.1016/j.tree.2016.05.003

51 Hammerschlag, N. (2019) Quantifying shark predation effects on prey: dietary data limitations and study approaches. *Endanger. Species Res.* **38**, 147–151 https://doi.org/10.3354/esr00950

52 Rogers, A., Blanchard, J.L., Newman, S.P., Dryden, C.S. and Mumby, P.J. (2018) High refuge availability on coral reefs increases the vulnerability of reef-associated predators to overexploitation. *Ecology* **99**, 450–463 https://doi.org/10.1002/ecy.2103

53 Burkepile, D.E. and Hay, M.E. (2010) Impact of herbivore identity on algal succession and coral growth on a Caribbean reef. *PLoS ONE* **5**, e8963 https://doi.org/10.1371/journal.pone.0008963

54 Hempson, T.N., Graham, N.A.J., MacNeil, M.A., Hoey, A.S. and Wilson, S.K. (2018) Ecosystem regime shifts disrupt trophic structure. *Ecol. Appl.* **28**, 191–200 https://doi.org/10.1002/eap.1639

55 Hughes, T.P., Bellwood, D.R., Folke, C.S., McCook, L.J. and Pandolfi, J.M. (2007) No-take areas, herbivory and coral reef resilience. *Trends Ecol. Evol.* **22**, 1–3 https://doi.org/10.1016/j.tree.2006.10.009

56 Smith, J.E., Hunter, C.L. and Smith, C.M. (2010) The effects of top-down versus bottom-up control on benthic coral reef community structure. *Oecologia* **163**, 497–507 https://doi.org/10.1007/s00442-009-1546-z

57 Vermeij, M.J.A., Smith, J.E., Smith, C.M., Vega Thurber, R. and Sandin, S.A. (2009) Survival and settlement success of coral planulae: independent and synergistic effects of macroalgae and microbes. *Oecologia* **159**, 325–336 https://doi.org/10.1007/s00442-008-1223-7

58 Mumby, P.J., Dahlgren, C.P., Harborne, A.R., Kappel, C.V., Micheli, F., Brumbaugh, D.R. et al. (2006) Fishing, trophic cascades, and the process of grazing on coral reefs. *Science* **311**, 98–101 https://doi.org/10.1126/science.1121129

59 Vermeij, M.J.A., DeBey, H., Grimsditch, G., Brown, J., Obura, D., DeLeon, R. et al. (2015) Negative effects of gardening damselfish *Stegastes planifrons* on coral health depend on predator abundance. *Mar. Ecol. Prog. Ser.* **528**, 289–296 https://doi.org/10.3354/meps11243

60 Feeney, W.E., Bertucci, F., Gairin, E., Siu, G., Waqalevu, W., Antoine, M. et al. (2021) Long term relationship between farming damselfish, predators, competitors and benthic habitat on coral reefs of Moorea Island. *Sci. Rep.* **11**, 14548 https://doi.org/10.1038/s41598-021-94010-0

61 Edwards, C.B., Friedlander, A.M., Green, A.G., Hardt, M.J., Sala, E., Sweatman, H.P.A. et al. (2014) Global assessment of the status of coral reef herbivorous fishes: evidence for fishing effects. *Proc. R. Soc. B Biol. Sci.* **281**, 20131835 https://doi.org/10.1098/rspb.2013.1835

62 Ceccarelli, D.M., Jones, G.P. and McCook, L.J. (2001) Territorial damselfishes as determinants of the structure of benthic communities on coral reefs. *Oceanogr. Mar. Biol. Annu. Rev.* **39**, 355–389

63 Gauff, R.P., Bejarano, S., Madduppa, H.H., Subhan, B., Dugény, E.M., Perdana, Y.A. et al. (2018) Influence of predation risk on the sheltering behaviour of the coral-dwelling damselfish, *Pomacentrus moluccensis*. *Environ. Biol. Fishes* **101**, 639–651 https://doi.org/10.1007/s10641-018-0725-3

64 Helfman, G.S. and Winkelman, D.L. (1997) Threat sensitivity in bicolor damselfish: effects of sociality and body size. *Ethology* **103**, 369–383 https://doi.org/10.1111/j.1439-0310.1997.tb00153.x

65 Lafferty, K.D. and Morris, A.K. (1996) Altered behavior of parasitized killifish increases susceptibility to predation by bird final hosts. *Ecology* **77**, 1390–1397 https://doi.org/10.2307/2265536

66 Kuris, A.M., Hechinger, R.F., Shaw, J.C., Whitney, K.L., Aguirre-Macedo, L., Boch, C.A. et al. (2008) Ecosystem energetic implications of parasite and free-living biomass in three estuaries. *Nature* **454**, 515–518 https://doi.org/10.1038/nature06970

67 Grutter, A.S., Crean, A.J., Curtis, L.M., Kuris, A.M., Warner, R.R. and McCormick, M.I. (2011) Indirect effects of an ectoparasite reduce successful establishment of a damselfish at settlement. *Funct. Ecol.* **25**, 586–594 https://doi.org/10.1111/j.1365-2435.2010.01798.x

68 Binning, S.A., Barnes, J.I., Davies, J.N., Backwell, P.R., Keogh, J.S. and Roche, D.G. (2014) Ectoparasites modify escape behaviour, but not performance, in a coral reef fish. *Anim. Behav.* **93**, 1–7 https://doi.org/10.1016/j.anbehav.2014.04.010

69 Binning, S.A., Roche, D.G. and Layton, C. (2013) Ectoparasites increase swimming costs in a coral reef fish. *Biol. Lett.* **9**, 20120927 https://doi.org/10.1098/rsbl.2012.0927

70 Allan, B.J., Illing, B., Fakan, E.P., Narvaez, P., Grutter, A.S., Sikkel, P.C. et al. (2020) Parasite infection directly impacts escape response and stress levels in fish. *J. Exp. Biol.* **223**, jeb230904 https://doi.org/10.1242/jeb.230904

71 Packer, C., Holt, R.D., Hudson, P.J., Lafferty, K.D. and Dobson, A.P. (2003) Keeping the herds healthy and alert: implications of predator control for infectious disease. *Ecol Lett.* **6**, 797–802 https://doi.org/10.1046/j.1461-0248.2003.00500.x

72 Bernal, M.A., Floeter, S.R., Gaither, M.R., Longo, G.O., Morais, R., Ferreira, C.E.L. et al. (2016) High prevalence of dermal parasites among coral reef fishes of Curaçao. *Mar. Biodivers.* **46**, 67–74 https://doi.org/10.1007/s12526-015-0322-z

73 Lafferty, K.D., Shaw, J.C. and Kuris, A.M. (2008) Reef fishes have higher parasite richness at unfished Palmyra Atoll compared to fished Kiritimati Island. *EcoHealth* **5**, 338–345 https://doi.org/10.1007/s10393-008-0196-7

74 Wood, C.L., Sandin, S.A., Zgliczynski, B., Guerra, A.S. and Micheli, F. (2014) Fishing drives declines in fish parasite diversity and has variable effects on parasite abundance. *Ecology* **95**, 1929–1946 https://doi.org/10.1890/13-1270.1

75 Wood, C.L., Zgliczynski, B.J., Haupt, A.J., Guerra, A.S., Micheli, F. and Sandin, S.A. (2018) Human impacts decouple a fundamental ecological relationship: the positive association between host diversity and parasite diversity. *Glob. Change Biol.* **24**, 3666–3679 https://doi.org/10.1111/gcb.14159