Review

The Ecological Role of Sharks on Coral Reefs

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Sharks are considered the apex predator of coral reefs, but the consequences of their global depletion are uncertain. Here we explore the ecological roles of sharks on coral reefs and, conversely, the importance of reefs for sharks. We find that most reef-associated shark species do not act as apex predators but instead function as mesopredators along with a diverse group of reef fish. While sharks perform important direct and indirect ecological roles, the evidence to support hypothesised shark-driven trophic cascades that benefit corals is weak and equivocal. Coral reefs provide some functional benefits to sharks, but sharks do not appear to favour healthier reef environments. Restoring populations of sharks is important and can yet deliver ecological surprise.

Sharks as Apex Predators on Coral Reefs

Apex predators (see Glossary) are usually large-bodied animals that occupy the highest **trophic level** [1] and are capable of structuring **food webs** both directly by regulating prey dynamics through predation and indirectly by modifying prey behaviour [2]. Widespread declines of apex predators have been observed across all marine and terrestrial ecosystems [3] and such 'trophic downgrading' [4] can have cascading effects on lower trophic levels resulting in **mesopredator** release, altered ecosystem functioning, and shifted food web dynamics [1].

The strength of predation and consequences of a loss of apex predators will vary among ecosystems, particularly in terms of species diversity and functional redundancy [5,6]. In ecosystems with the highest biodiversity, such as rainforests or coral reefs, the effects of predators on ecosystem functioning can be obscure [7] because trophic complexity allows compensatory processes to resist change in community structure by adjusting the interaction strengths among trophic levels [8].

In marine environments, sharks are considered to be some of the most diverse and abundant apex predators [2,9]. Over the past century, widespread exploitation of sharks has resulted in substantial declines in shark populations (Box 1), yet the broader ecological consequences of these losses are often unclear [2,9,10]. Here we explore the ecological role of sharks on coral reefs, one of the world's most diverse ecosystems [11], and discuss the ecological consequences of shark declines on ecosystem functioning.

The Trophic Position of Sharks on Coral Reefs

The potential for sharks (or a loss thereof) to impact reef ecosystem dynamics is largely driven by their interaction strength with prey [12], which is dependent on a range of factors including population abundance, body size, trophic level, and diet specialisation [13]. By synthesising the

Trends

Stable isotopes reveal that sharks span an extended range of trophic levels with true apex species being higher than most common reef sharks.

Dietary analysis reveals that most common reef sharks are mesopredators occupying a similar trophic level to large piscivorous fishes.

Evidence for shark-induced trophic cascades that benefit herbivorous fishes is weak or equivocal on coral reefs.

Sharks can exert non-consumptive or 'fear' effects that disrupt the foraging of potential prey.

While coral reefs provide a range of ecological benefits for sharks, the link between healthy reefs and shark abundance is unclear.

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predatory traits of 26 key species (Table S1 in the supplemental information online), we show that sharks occupy a diverse range of trophic roles in coral reef ecosystems (Figure 1A).

The largest-bodied species, such as the tiger shark (*Galeocerdo cuvier*) and the great hammerhead shark (*Sphyrna mokkaran*), with a maximum total length (TL_{max}) exceeding 3 m [10,14], have large home ranges encompassing 100 km to >1000 km, albeit with some exceptions [15]. These species migrate among coastal, pelagic, and coral reef ecosystems and their trophic role varies among habitats [16]. They occupy the highest trophic level on coral reefs (Box 2) and exhibit a high degree of omnivory (Figure 1A), consuming other large prey including other sharks [16,17], mammals [15], and turtles [18]. While transient in nature, these sharks fit the definition of apex predators in coral reef ecosystems [1,10] in that they are large bodied, occupy the highest trophic level (Box 2), have few natural predators, and might exert a strong influence on the structure and diversity of communities through direct [17] and indirect [18] interactions.

Below the apex sharks are mid-ranking sharks, or mesopredators [10,19]. These are of intermediate body size [$TL_{max} \sim$ 150–300 cm; e.g., grey reef shark (*Carcharhinus amblyrhynchos*)] and occupy high trophic levels (Box 2). Owing to their smaller body size, mesopredatory sharks are vulnerable to predation by apex sharks (e.g., [17]). Mesopredatory sharks tend to be reef associated (home range < 50 km; Figure 1A) and in many cases exhibit high fidelity to individual reefs (<10 km; Table S1). The remaining smaller mesopredatory sharks [TL_{max} < 100 cm; e.g. epaulette shark (*Hemiscyllium ocellatum*)] are also reef associated, yet occupy lower trophic levels (<4.0), and exhibit lower levels of omnivory (Figure 1A).

Theoretical definitions of apex predators as 'species that occupy the top trophic levels in a community' (e.g., [19]) can be limited when applied to sharks because trophic positions vary substantially among species, size class, habitat use, behaviour, and ontogeny (see the extensive review in [10]). Where historical fishing has truly eliminated large-bodied sharks from an ecosystem (Box 1), smaller, reef-associated mesopredator sharks fit the definition of apex predators. However, our analysis of trophic levels reveals that many of these mesopredatory species occupy the same trophic level as larger piscivorous fishes (Box 2) and therefore the term apex predator cannot be reserved exclusively for mesopredatory sharks (e.g., [20–23]).

The Role of Sharks in Driving Trophic Cascades on Coral Reefs

Sharks have the potential to modify the community structure of marine food webs through direct or indirect interactions resulting from the consumption of prey or the alteration of their behaviours [9,12]. The loss of large apex sharks has caused **trophic cascades** in temperate marine ecosystems [9,24] yet the effects of shark removal on coral reef food webs are largely unclear, largely due to the absence of historical data (Box 1).

Models of coral reef food webs would ordinarily be a good place to seek evidence of shark-driven trophic cascades (Figure 2A). However, an analysis of food webs finds that most models, including our own [25], were created before extensive dietary information on sharks became available, leading authors to aggregate sharks into a single apex class (Box 3), implicitly combining small-bodied sharks (<100 cm TL_{max}) that can feed on crustaceans [26] to large-bodied tiger sharks (>500 cm TL_{max}) that can feed on marine mammals [14] (Figure 2B). In other words, while these models remain available for use, they overestimate the true biomass of apex predators, which would tend to confound the importance of top-down controls on the food web. Furthermore, most earlier modelling studies did not explicitly test for trophic cascades. An important exception quantified the frequency and nature of tritrophic interactions in a Caribbean reef food web [12]. Trophic cascades are most likely to occur if consecutive pairs of interactions, such as apex predator to mesopredator and then mesopredator to primary resource, are both relatively strong. However, the study found that strong interactions were rarely found together in

Glossary

Apex predators: usually defined in terms of trophic position and commonly described as species that occupy the top trophic position in a community with no natural predators of their own [10,19].

Concentrated predation: occurs when one predator species determines patterns of community structure in a food web through direct (i.e., regulating prey dynamics through predation) or indirect (i.e., modifying prey behaviour) interactions [10].

Diffuse predation: occurs when several predators utilise the same prey species but no single predator can suppresses the resource population. Due to high functional redundancy, individual predators might have little measurable effect on community structure [10].

Food web: a framework comprising discrete functional groups within which individual species are measured on a continuous scale of trophic position [67].

Mesopredators: species that occupy a high trophic position but are below apex predators and are themselves vulnerable to predation [10,19].

Omnivory index: a measure of how prey consumption is distributed across trophic levels in food webs for each consumer [68]. When the value of the omnivory index is zero, the consumer is specialised (i.e., feeds on a single trophic level), whereas larger values indicate generalist feeding on many trophic levels.

Trophic cascades: indirect interactions in ecosystems whereby predators directly suppress the abundance or alter the behaviour of their prey thereby indirectly releasing the next lower trophic level from predation (or herbivory if the intermediate trophic level is a herbivore) [69].

Trophic level: a quantitative, continuous measure of the hierarchical role of a given species within a food web [67]. In the case of marine ecosystems, the trophic levels of most fish range between 2.0 and 5.0, with 2.0 reflecting primary consumers (herbivores and detritivores) and 5.0 reflecting tertiary consumers (apex predators) [70].
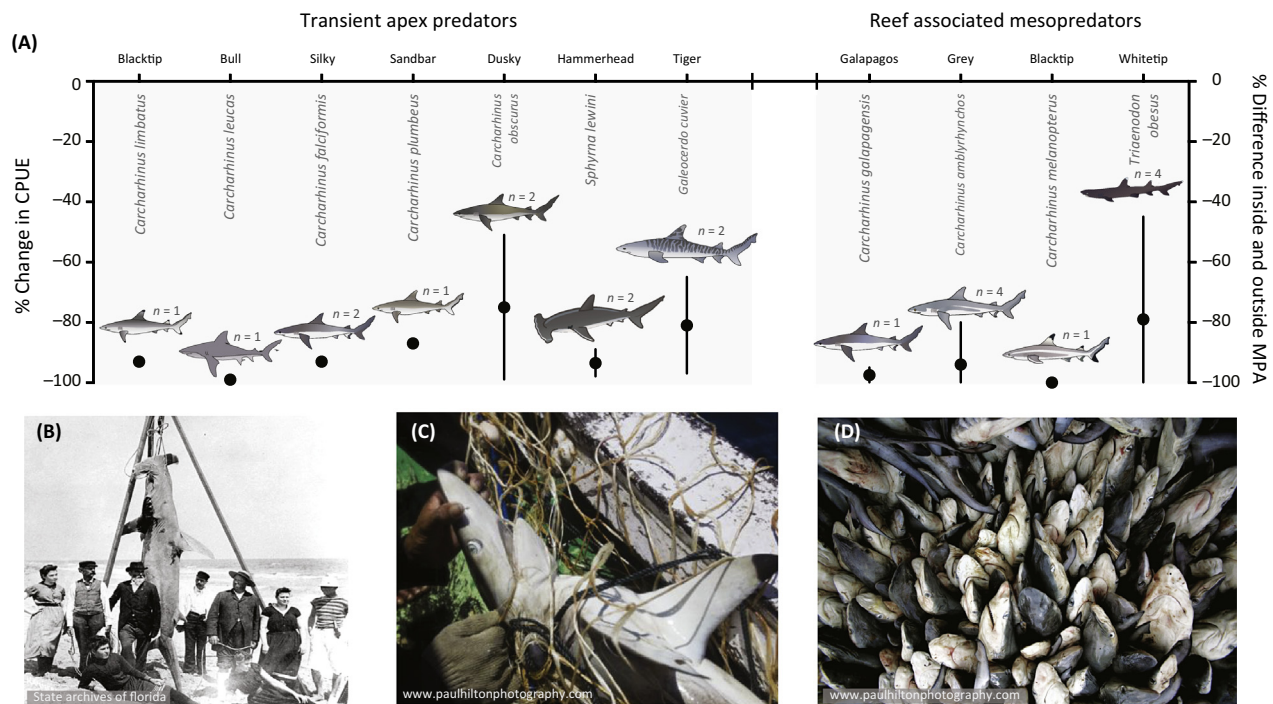
Box 1. Historical Declines in Coral Reef Shark Populations

The ongoing decline in shark populations throughout the past century has received considerable attention in the past few decades [24]. Through the industrialisation of fisheries, similar declines have occurred in shark populations in coral reef regions throughout the world. In the late 1940s, sharks were 'expected anywhere at anytime' in the West Indian Caribbean [71]. By contrast, a contemporary analysis of the greater Caribbean 50 years later concluded that sharks are 'expected anytime almost nowhere' [72]. The ongoing decline in shark populations raises important questions. How abundant were sharks on pristine coral reefs? How did the trophic and ecological roles of sharks differ on pristine reefs of the past?

Few historical baselines exist for transient apex sharks in coral reef ecosystems. However, following the onset of industrialised fisheries in the 1970s many species of apex sharks in adjacent coastal and oceanic ecosystems experienced substantial declines [9] (Figure I and Table S2 in the supplemental information online). Furthermore, reductions in the mean body mass and mean body length [24] of sharks caught over the past century indicate the loss of the largest individuals through increased fishing efforts. Such an impact in the higher trophic levels can result in changes in food web dynamics and altered prey behaviour that are not immediately obvious when considering contemporary ecosystems.

Reef-associated mesopredators have also declined substantially compared with historical baselines. One of the few available datasets on shark numbers from a remote atoll location (Chagos Archipelago) indicates that the sighting of sharks has declined over 90% between 1975 and 2006, with once common mesopredatory sharks rarely encountered in modern surveys [66]. Comparisons across marine park boundaries suggests that the abundance of reef-associated sharks is 75–99% lower in unprotected reefs than in protected areas (Figure 1) and model estimates suggest that the density of reef sharks has declined to 3–10% of pre-human baseline levels in many locations throughout the Pacific [73].

Such historical records provide a unique insight into the past structure of coral reef sharks before human exploitation and serial depletion and represent an important baseline for conservation and fisheries management to overcome the 'shifting baseline syndrome'. However, it is worth noting that estimates of declines based on mid-20th century data are likely to represent an already shifted baseline, as nearly all islands in the Caribbean were colonised by ~2000 years ago, and indigenous fishing began at least 35 000–40 000 years ago in the Western Pacific [31].

Figure I. Human Exploitation of Coral Reef Shark Populations. (A) Historical declines in apex sharks from mid-20th century to present (for references see Table S2 in the supplemental information online; *n*, number of studies) and differences in the abundance of mesopredatory sharks inside and outside marine protected areas (Table S2). (B) Large hammerhead shark caught off the coast of Florida in 1893 (State Archives of Florida). (C) Shark targeted by gillnet fishery (credit: Paul Hilton). (D) Juvenile sharks off the coast of Yemen awaiting transport for shark finning (credit: Paul Hilton).

the same tritrophic cascade. Moreover, where strong interactions did co-occur, they tended to be accompanied by high levels of omnivory (e.g., the apex predator also consumes the primary resource directly). Collectively, the paucity of paired strong interactions and high levels of omnivory tend to stabilise food webs and reduce the likelihood of a trophic cascade. It is
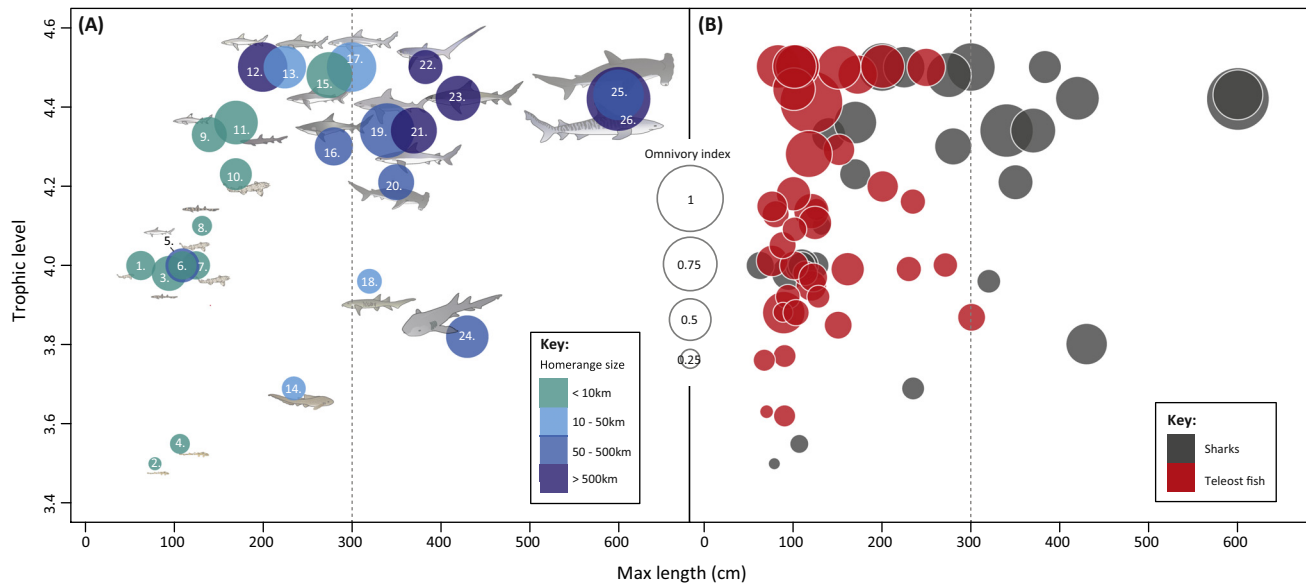
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Figure 1. Trophic Position of Sharks on Coral Reefs. (A) Synthesis of the key trophic characteristics [trophic position, maximum length (TL_{max}), home range size, and **omnivory index**] for 26 species of coral reef-associated sharks (see Table S1 in the supplemental information online for key) and (B) comparison of the trophic characteristics of reef sharks and 45 species of equivalently sized reef fish from the Caribbean and Indo-Pacific (Table S1). The significant overlap between mesopredator sharks ($TL_{max} < 300$ cm) and other reef predators allows functional redundancy and diffuse predation on species at lower trophic levels but there is a distinct lack of large-bodied ($TL_{max} > 300$ cm) fish capable of fulfilling an apex predator role and consuming other large-bodied species.

important to note, however, that of the few tritrophic cascades that had the potential to elicit cascades (strong interactions without omnivory), many involved sharks as the apex predator, therefore raising the possibility of some specific cascades.

In the absence of suitable long-term empirical studies, comparisons of the trophic structure between protected and fished sites can provide insight into the effects of shark removal on coral reefs. Theoretically, the loss of sharks would result in an increase in mesopredators, with cascading effects towards multiple prey at lower trophic levels. However, a critical evaluation of the available empirical studies (Table 1) finds weak evidence for shark-driven cascades. Nearly all studies reported simultaneous declines across all trophic levels (Table 1) driven primarily by high levels of fishing pressure in populated and heavily fished locations [22,27]. Most studies focused on links between sharks and fish species at the base of the food chain: herbivores. This interest stems from the key ecological role herbivores provide on coral reefs, enhancing coral resilience by consuming fleshy macroalgae that outcompete corals for space [28]. Theoretically, high shark abundance might lead to reduced mesopredator abundance and allow herbivorous fish to escape predation and become more abundant [12] (Figure 2A). However, empirical demonstration of trophic cascades involving sharks, mesopredators, and herbivores has proved elusive [27,29] and nearly all studies find that reductions in shark densities occur in conjunction with reductions in mesopredators and herbivores (Table 1A–H). Further, in regions where herbivores are not targeted for fisheries, higher densities of sharks inside marine reserves had no effect on the density or biomass of herbivorous fish (Table 1C,E,H). While a recent study purports to show evidence of a shark-driven trophic cascade following catastrophic reef disturbance (Table 1I), no differences were found in the abundance of lower trophic groups (herbivores, corallivores, or planktivores) among fished and unfished atolls before disturbance, despite mesopredators being more abundant in areas where sharks were depleted by fishing [23]. Increases in herbivore abundance in the area protected from shark fishing were observed only following cyclone disturbance, but the consequences of habitat damage confound

Box 2. Trophic Roles of Sharks on Coral Reefs

Identifying the trophic positions of sharks in food webs can be difficult due to practical constraints, as large sharks can feed infrequently or in adjacent habitats. While stomach content analysis can provide insight into the relative proportions of prey types and their trophic level, stable isotope analysis of nitrogen (δ^{15}N) and carbon (δ^{13}C) from tissues provides estimates of assimilated prey sources [74]. Consequently, stable isotopes are increasingly being applied in ecological research to pinpoint the trophic positions of large sharks [75] and quantify carbon flow to consumers in coral reef food webs [76]. While trophic positions based on stomach content analysis suggest that a broad range of apex and mesopredatory sharks occupy similar trophic levels (trophic position $\sim$ 4.5; Figure 1A), isotope data collected from a diverse and intact Pacific coral reef ecosystem (Figure I) indicates that large apex tiger sharks (*Galeocerdo cuvier*) feed at higher trophic levels than other mesopredator fish and sharks (e.g., *Carcharhinus amblyrhynchos*) [76].

Rescaled food webs based on δ^{15}N estimates indicate that the trophic positions of apex predators have been substantially underestimated by previous models, suggesting that higher trophic levels have been truncated (Figure 1A) and species interactions oversimplified [67]. Such expanded trophic complexity among sharks indicates that diverse shark assemblages can exhibit a lower degree of functional equivalence than previously realised [75] and might in part explain the lack of cascading effects observed in diverse ecosystems such as coral reefs.

Stable isotope analysis can also reveal novel insights into resource use and habitat partitioning of sharks in coral reef ecosystems. For example, while grey reef sharks (*C. amblyrhynchos*) are dominant predators observed in reef slope environments in many Pacific reefs [56,73], isotope analysis indicates that they derive most of their prey from adjacent pelagic habitats adjacent to the reef slope [41].
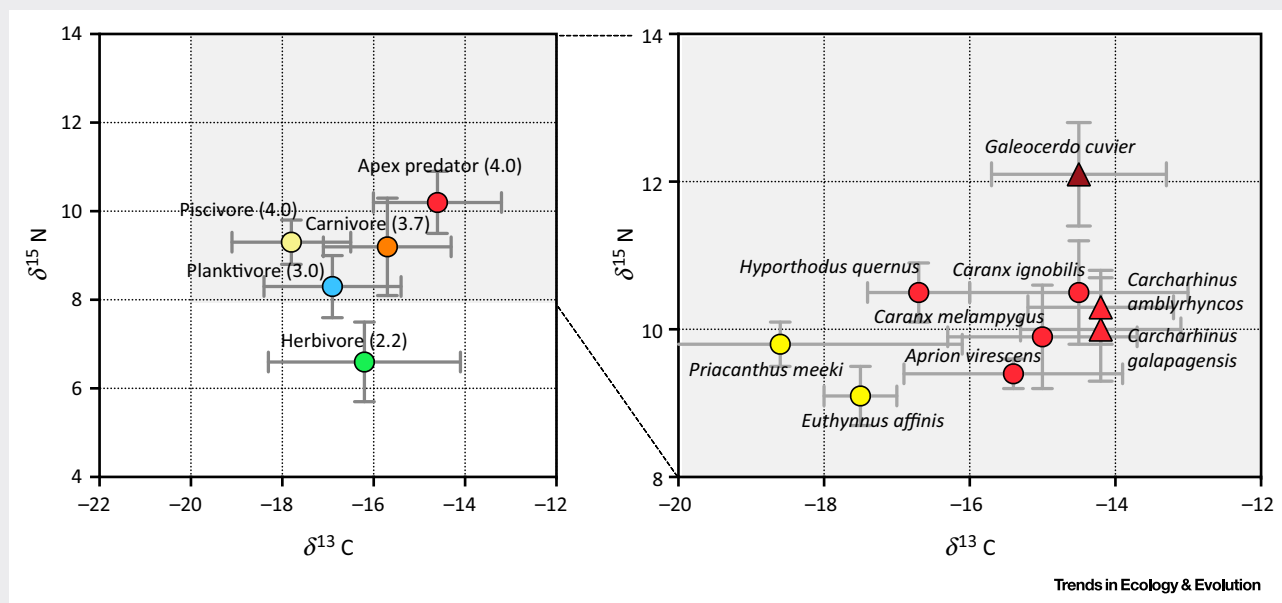

Figure I. Stable Isotope Values for Consumer Groups Derived from Coral Reef Fish Collected from the Hawaiian Archipelago [76]. Inset: Stable isotope values from piscivores and apex predators (trophic position > 4.0; circles, fish; triangles, sharks) showing the lack of overlap between the large apex tiger shark (*Galeocerdo cuvier*) and other 'apex' predators such as the grey reef shark (*Carcharhinus amblyrhynchos*) [76].

interpretation. Because the cyclone caused loss of coral and a concomitant increase in algal resources [23], food limitation provides an alternative, and perhaps parsimonious, explanation for the positive response of herbivores rather than a shark-driven trophic cascade.

While the lack of a clear relationship between sharks and lower trophic levels implies weak top-down control, many empirical studies are limited in their ability to distinguish shark-driven trophic cascades. In most studies (Table 1A–F), sharks were merged with other predatory fish into a single 'apex' or 'top predator' category (Figure 2B), often because sharks were entirely absent at fished sites [22,30]. Where studies separated sharks from other predators (Table 1G–I), they were invariably classified into a single 'apex' shark group, ignoring the broad trophic roles of sharks in coral reefs (Box 2 and Figure 2C). Finally, while several studies surveyed large spatial scales including remote locations, there was a notable absence of large-bodied apex shark species (Table 1) that were historically abundant on coral reefs (Box 1), implying that most trophic studies are predicated on a shifted baseline [31].
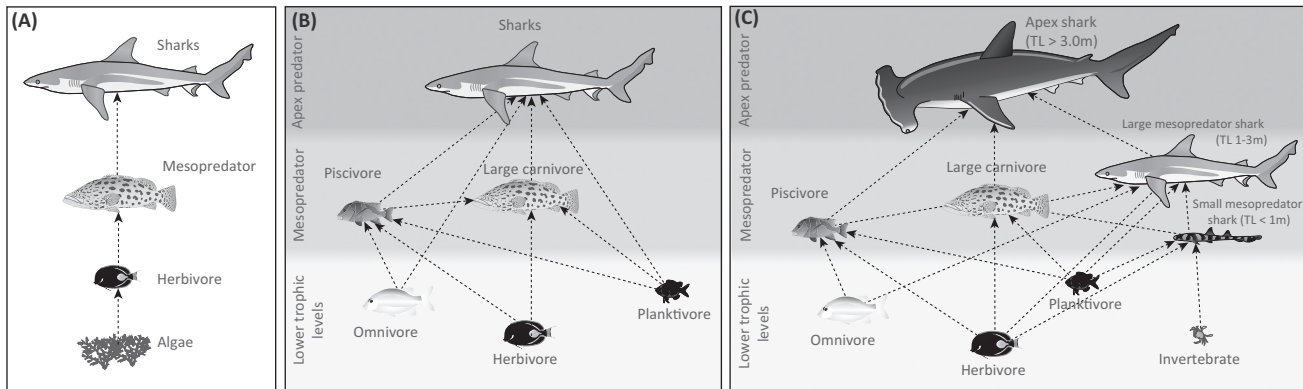
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Figure 2. Food Web Models of Coral Reefs. (A) Simplified food web illustrating hypothesised trophic cascades. (B) Representative food web from an Ecopath model (simplified from [25]) where herbivores experience greater levels of diffuse predation from higher trophic levels. (C) Food web model including the differing trophic roles of sharks as apex predators and mesopredators, highlighting the increasing complexity of trophic links and greater functional redundancy among mesopredators.

Importantly, an absence of evidence for shark-driven trophic cascades is not necessarily evidence that trophic cascades do not follow shark extirpation, but might reflect the fact that detecting top-down effects of sharks in coral reefs ecosystems is challenging. We suggest four potential hypotheses for the lack of clear trophic impacts of sharks on coral reefs. (i) Historical fishing: Trophic cascades might have occurred after the larger apex sharks were depleted by fishing, but this occurred so long ago that it cannot be evaluated (Box 1). Compared with historical baselines, differences in shark density between fished and even relatively pristine modern environments is so limited that trophic cascades either fail to exist or are undetectable. (ii) Predator–prey interaction strength: Even at historical baselines, sharks might not exert strong predatory control on food web dynamics owing to quantitatively low impacts *per capita*. High levels of omnivory and considerable trophic overlap between teleost predators and

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Box 3. Using Food Web Models to Assess the Trophic Role of Reef-Associated Sharks

In general, food web models provide a useful framework for evaluating trophic cascades. One popular approach is the Ecopath with Ecosim (EwE) tool [68], which assumes mass balance of trophic interactions among species or trophic groups. Provided that stock size, diet, production, and consumption rates are accurately defined for every group, EwE models allow the characterisation of food web dynamics in terms of biomass flows and trophic controls. So far, relatively few EwE models have been developed for coral reefs (16 models; see Table S3 in the supplemental information online).

Diet information for sharks used to parameterise EwE coral reef models is generally sparse and largely unreported (Table S3). While this reflects limited data on shark feeding pre-2000, incomplete parameterisation has been propagated in later EwE applications. Another common shortcoming of many published models is that shark consumption is non-specialised and is instead distributed across all potential prey groups, thus making the implicit assumption of opportunistic feeding. Critically, only seven models provided a clear definition of the shark species represented. In the remaining models, sharks were grouped with rays (n = 6) or predatory fish such as jacks and scombrids (n = 7), so the relevance of model outcomes for assessing trophic cascades or functional redundancies among apex predators is questionable. Finally, most EwE applications on coral reefs have been static (i.e., Ecopath without Ecosim, but see Table S3 for exceptions), while robust evaluations of prey responses to changing predator abundance requires dynamic interactions that consider both prey shifting and predator-induced behavioural responses.

In light of the multiple trophic roles occupied by a range of shark species on coral reefs (Figure 1A), most EwE models to date are limited in their capacity to address the trophic importance of sharks on coral reefs (Figure 2). Adequately evaluating the trophic role of reef sharks in the future will require: (i) better estimates of shark biomass (e.g., [73]); (ii) incorporating measures of trophic position based on stable isotope values that expand the complexity of food webs among higher trophic levels [67]; (iii) evaluating the importance of scavenging in sharks; (iv) dedicated trophic groups for each shark species and competitor (e.g., [12]); (v) consideration of changes in trophic position with ontogenetic shifts; and (vi) the inclusion of dynamic prey–predator responses.

Table 1. Empirical Studies of Trophic Cascades Comparing Differences in the Abundance and Biomass of Trophic Groups between Control (Undisturbed) and Impacted Reefs (Arrows Represent Differences Relative to Impacted Reefs)

#	Location	Comparison	Metric	Trophic Group						Benthic		Shark Species[c]
				Sharks[a]	*Apex*[b]	*Mesopredator*	*Corallivore*	*Planktivore*	*Herbivore*	*Coral*	*Algae*	
A	Micronesia [33]	Remote vs populated atolls	Abundance	–	27× ↑	0.7× ↑	–	2.4× ↑	0.8× ↑	NS	0.7× ↓	Not reported
			Biomass	–	20× ↑	7.6× ↑	–	5.9× ↑	1.6× ↑			
B	Hawaii [22]	Remote vs populated islands	Abundance	–	10× ↑	0.6× ↑	–	–	0.2× ↑	–	–	11, 13, 21
			Biomass	–	70× ↑	0.5× ↑	–	–	0.8× ↑			
C	Northern Line Islands [23]	Remote vs populated islands	Biomass	–	17× ↑	0.6× ↓	–	NS	NS	2.9× ↑	4.5× ↓	Not reported
D	Line Islands [36]	Remote vs populated islands	Biomass	–	4.2× ↑	2× ↑	–	–	3.3× ↑	–	–	9, 11, 13
E	Easter Island [37]	No-take marine reserve vs fished reefs	Biomass	–	47× ↑	NS	–	NS	6.6× ↑	NS	3.0× ↓	21
F	Caribbean [31]	Lightly fished vs heavily fished	Biomass		110× ↑	17× ↑	–	0.3× ↓	2.8× ↑	2.6× ↓	4.4× ↓	17
G	Hawaiian Archipelago [35]	Remote vs populated islands	Biomass	50.9× ↑	–	22.1× ↑	–	2.6× ↑	3× ↑	–	–	13, 15, 16, 18, 21, 23, 24
	Mariana Archipelago [35]			4.1× ↑	–	6.8× ↑	–	6.8× ↑	2.1× ↑	–	–	
	American Samoa [35]			NS	–	2.0× ↑	–	2.2× ↑	0.7× ↓	–	–	
H	Great Barrier Reef [34]	No-take marine reserve vs fished reefs	Abundance	1.2× ↑	–	NS	–	–	NS	NS	–	9, 11, 13
		No-entry marine reserve vs fished reefs	Abundance	3× ↑	–	NS	–	–	NS	NS	–	
I	Northwest Australia [24]	Protected vs fished atolls (pre-disturbance)	Abundance	~3× ↑	–	1.4× ↓	NS	NS	NS	NS	NS	13, 15
		Protected vs fished atolls (post-disturbance)	Abundance	~3× ↑	–	1.3× ↓	NS	NS	~1.3× ↑	NS	NS	

Trophic groups are assigned by the studies where reported.
NS, no significant difference between control and impacted reefs.
[a]Where sharks have been isolated as a separate group, predatory fish are categorised as mesopredators.
[b]'Apex' group incorporating sharks and other large predatory fish.
[c]Shark species identified following Figure 1A.

mesopredatory sharks (Figure 1B) means that predation pressure on coral reefs tends to be **diffuse** rather than **concentrated** [7], which might weaken interaction strengths in food webs [7]. (iii) Predator diversity: Linear views of trophic relationships (Figure 2A) can oversimplify the dynamics of complex systems like coral reefs (Box 3). High functional redundancy among mesopredator sharks and other reef predators (Figure 1B) might promote food web stability [32,33] and dampen the effects of trophic cascades [34]. This might in part explain why shark-driven trophic cascades appear to be absent on coral reefs yet are observed in other coastal ecosystems with lower diversity [9]. (iv) Knowledge gaps: Alternatively, there might simply be insufficient case studies on coral reefs to test unequivocally for trophic cascades. Evaluating the impacts of sharks across their home range is logistically problematic and many studies aggregate sharks with other teleost predators (Table 1 and Box 2).

Differentiating among these hypotheses is important, as the first implies that sharks could once have caused trophic cascades whereas the second and third imply that sharks have always

played a relatively weak ecological role on coral reefs. One of the key questions to answer on coral reefs is the role of non-consumptive effects of sharks on their prey. For example, mesopredator sharks can alter herbivore foraging rate and fish distribution through behavioural modification [20,35,36]. However, as shark–herbivore interactions occur relatively infrequently on most present-day reefs, it is unclear how this would influence ecosystem functioning, and the cessation of foraging is likely to be temporary or merely displaced out of the path of the shark. Occupying the top trophic positions in coral reef food webs (Figure 1A), large apex sharks are unique in that they can exert fear over multiple trophic levels [17,37]. The consequences of non-consumptive effects can be as important as consumptive effects [2], yet the potential cascading effects of the loss of apex sharks on lower trophic levels is largely unknown. In short, while the evidence for shark-driven trophic cascades remains equivocal, the combined effects of the direct and non-consumptive impacts of a recovery of large-bodied sharks remain a tantalising enigma that could alter this paradigm.

Other Ecological Functions of Sharks on Coral Reefs

While many studies have explored the trophic roles of sharks [9,24], few have considered the impacts of shark removal on other ecosystem processes. We identify a broad range of potential ecological functions of sharks on coral reefs, including nutrient cycling [38], scavenging [39], habitat disturbance [40], and the removal of invasive species [1]. Within coral reef ecosystems, the small-scale movement of reef-associated mesopredatory sharks (home range < 50 km; Figure 1A) provides nutrient cycling between adjacent pelagic and reef habitats [41,42], while the large-scale migrations of apex sharks (>1000 km) results in nutrient flux among coastal and oceanic ecosystems [15,41]. Through opportunistic feeding, apex and mesopredatory sharks remove weak and diseased individuals [16,43], potentially reducing the incidence of disease by maintaining low densities of prey populations [44]. Apex sharks might play an important role as facultative scavengers consuming dead carcasses [45], which can promote stability in food webs [39]. Mesopredatory sharks might have the potential to exert top-down control of invasive species such as lionfish [46], although the severe depletion of sharks on Caribbean reefs (Box 1) means that their ability to regulate lionfish abundance is likely to be severely limited [47]. Finally, although minor, mesopredatory sharks can cause habitat disturbance by damaging individual corals while foraging for prey in reef frameworks [48]. While many of these ecosystem processes are critical to the structure and function of ecosystems [3,4], they are poorly quantified in coral reef ecosystems. As with trophic roles, these ecological functions are species specific and vary with body size, diet specialisation, and home range (Figure 1A). Importantly, some ecological functions identified here are unique to apex sharks, such as the removal of larger weak and diseased turtles, rays, and marine mammals. Thus, the loss of transient large apex sharks that move among coastal ecosystems (e.g., [15,49]) is likely to have a greater impact on nutrient transfer among ecosystems than that of reef-associated sharks, which show a high degree of fidelity and mainly move among habitats within reefs (e.g., [42,50]).

## The Ecological Benefits of Coral Reefs for Sharks

At large spatial and temporal scales, coral reef habitats have significantly influenced the diversification, distribution, and behaviour of sharks. Following the emergence of coral reefs ~45 million years ago, carcharhinid sharks underwent rapid diversification in response to prey and habitat diversity associated with this habitat [51]. Subsequently, many mesopredatory sharks have evolved behavioural adaptations to coral reef habitats and prey sources. To date, few studies have explicitly examined the ecological benefits of coral reefs for shark populations. We identify a series of unique functional roles that coral reefs might serve for sharks, including prey sources, nursery habitats, refugia from predation, and parasite removal (Box 4).

In the past few decades, reefs have undergone substantial declines in coral cover, reduced structural complexity, increasing algal dominance, and novel community dynamics [11,52]. The

Box 4. The Functional Role of Coral Reefs for Sharks

Coral reefs convey numerous important ecological functions for shark populations. As residents on coral reefs with limited home ranges (Figure 1A), mesopredatory sharks are dependent on coral reefs for prey. Stomach content analysis of a small mesopredatory shark (*Hemiscyllium ocellatum*) indicates a broad reliance on reef-associated cephalopods, invertebrates, and crustaceans [26], while the stomach contents of a large mesopredator shark (*Carcharhinus amblyrhynchos*) reveal a broad range of coral reef fish as prey items [77] (Figure I). By contrast, the stomach contents of a large apex shark (*Galeocerdo cuvier*) included birds, turtles, and other sharks and rays [78] (Figure I), highlighting a high degree of omnivory in apex sharks and extensive foraging in adjacent coastal and pelagic ecosystems [15,18].

Coral reef ecosystems also have an important function as nursery habitats for reef-associated sharks. Habitats such as shallow sand flats [79], mangrove habitats [80], lagoons [80], and tidal pools [81] function to reduce predation risk and provide resources for juveniles before they undertake ontogenetic shifts towards deeper reef slope environments [56]. The 3D structure of coral reefs can influence the behaviour and distribution of sharks across and within habitats. Smaller sharks, such as whitetip reef sharks, are most often encountered around coral heads and ledges with high vertical relief, resting in caves, or under coral ledges during the day [82] to avoid predation from larger sharks and groupers [83]. By contrast, smaller blacktip reef sharks prefer shallow sand flats and might actively avoid habitats with high structural complexity, such as reef ledges and lagoons, that larger predators (e.g., tiger sharks) often frequent [79]. In some species (e.g., epaulette sharks), medium scale (1–10 m) structural complexity can also provide refuge from strong currents [84]. At larger spatial scales, reef-associated sharks (e.g., grey reef sharks) aggregate at forereef locations where topographic features concentrate currents and allow sharks to maximise water ventilation for minimal energetic cost [85]. Finally, the mutualistic removal of ectoparasites by 'cleaner fish' (e.g., cleaner wrasse, *Labroides dimidiatus*) on coral reefs might play an important role in controlling shark parasite loads, reducing the incidence of skin disease and compromised respiratory efficiency associated with parasite loading [86,87].
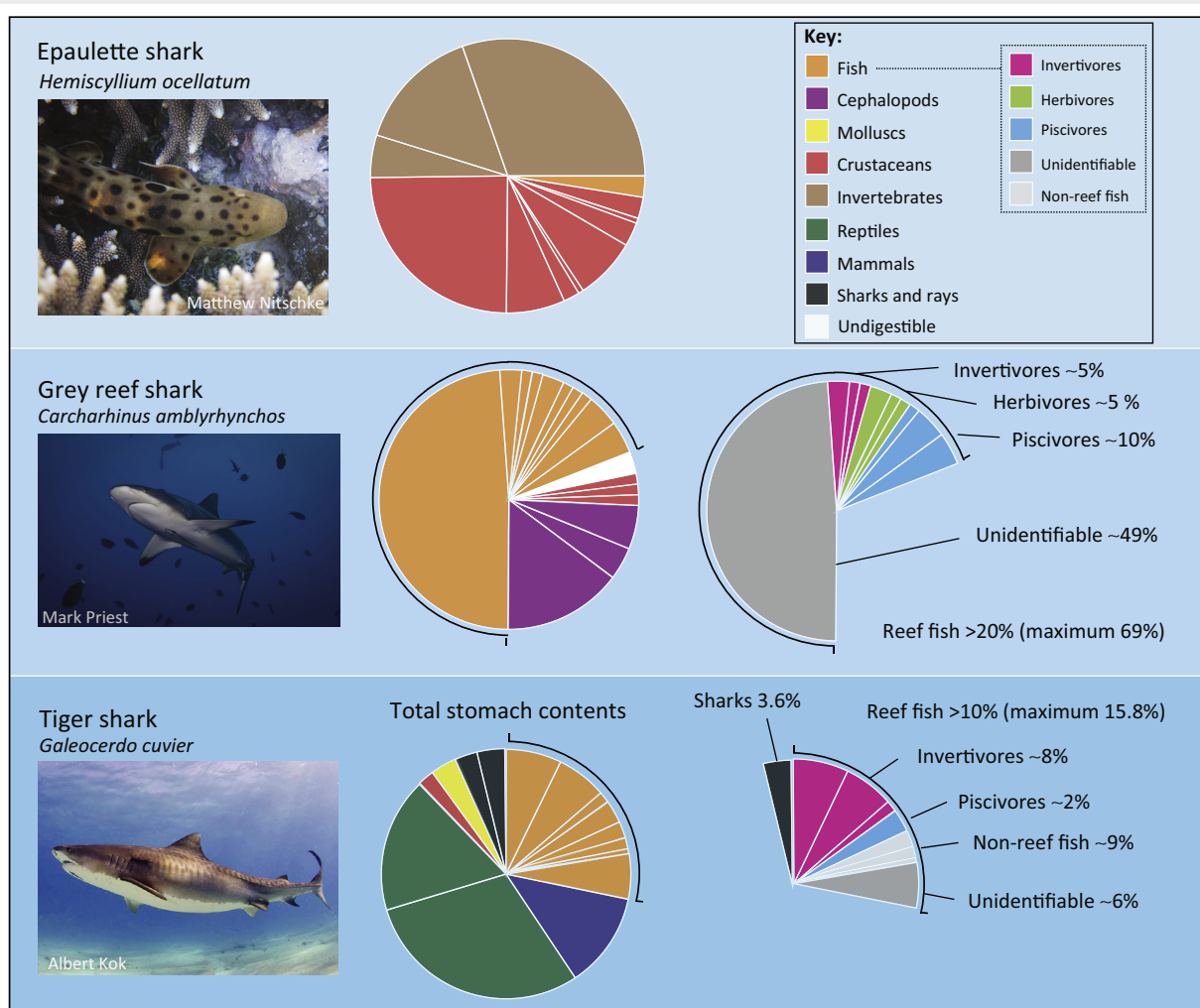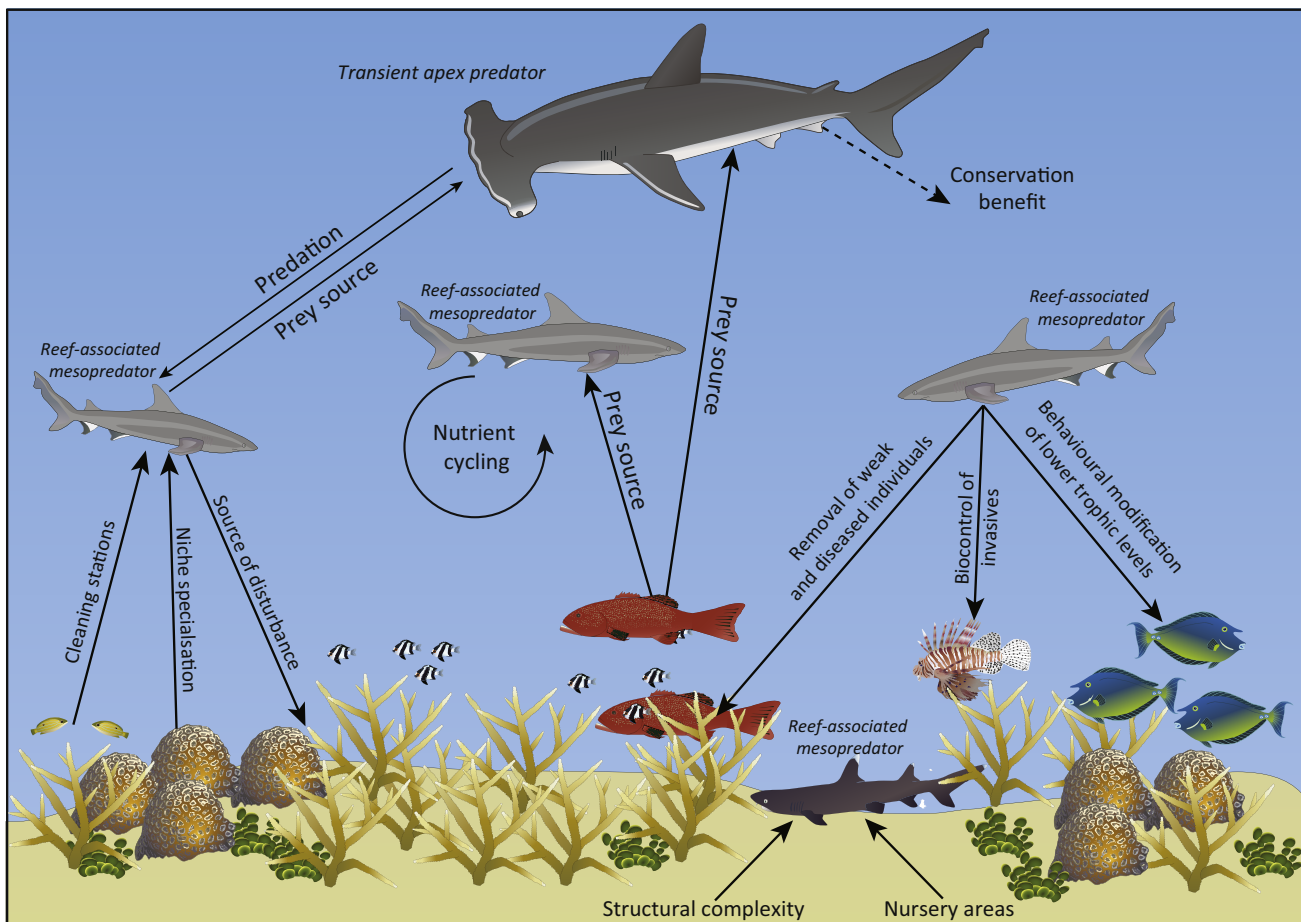

Trends in Ecology & Evolution

Figure I. Analysis of Stomach Contents for Three Representative Species of Shark (Small Mesopredator, Large Mesopredator, Apex). Colours of pie charts represent major categories of prey derived from stomach contents.

impacts of such ecological shifts on shark populations are unclear. Are reefs with more diverse and abundant corals more important for sharks? Several studies have reported correlations between reduced shark abundance and more degraded reef states with higher macroalgal cover [22], lower herbivore densities [22],or more frequent outbreaks of crown-of-thorns starfish [53]. An implicit assumption in these studies is that a loss of sharks can have negative effects on coral reefs [54] or that degraded coral reefs can have negative implications for shark populations [55]. Yet, surprisingly few studies have established a clear link or mechanism between 'healthy' reefs (i.e., high coral cover, high structural complexity, low macroalgal cover) and shark abundance [55,56]. On the Great Barrier Reef, reef slope environments with high coral cover support more diverse and abundant shark assemblages than adjacent habitats such as back-reef and reef flat, which are typically characterised by low coral cover [56]. However, the degree of hard coral cover and structural complexity within reef slopes are not significant predictors of

Key Figure

Hypothesised Ecological Role of Sharks on Coral Reefs (Top-Down Arrows) and Ecological Role of Coral Reefs for Sharks (Bottom-Up Arrows)

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Figure 3. Symbols courtesy of the Integration and Application Network (http://ian.umces.edu/symbols/).

shark densities [56], indicating that sharks might exhibit a preference for reef slope habitats for a range of behavioural reasons that are independent of coral cover, such as utilising strong currents or seeking parasite removal at cleaning stations (Box 4). Testing the effect of coral cover on shark abundance is difficult, as human disturbance has both impacted coral reef structure and depleted shark populations. While sharks are reported to be more abundant in fisheries reserves and no-entry zones (e.g., [54]), it seems more likely that these increases relate directly to fishery closures that protect shark populations from exploitation or other forms of anthropogenic stress [54,57] rather than to any potential beneficial effects of protected reefs on shark populations. Despite limited evidence linking coral cover and shark abundance, there are some mechanistic reasons for expecting a positive association between coral habitat complexity and reef shark abundance. High-complexity habitats tend to support high densities of prey [58,59] and higher fish productivity [59], which could enhance food availability for species of sharks with a high dependence on reef fish in their diet (Box 3).

Conservation of Sharks and Coral Reefs

Increasingly, sharks play an important role in the conservation of coral reefs [60] by serving as 'flagship species' that facilitate the raising of awareness and financial support for conservation [61]. For example, the recent establishment of shark sanctuary in Palau, Micronesia has increased public awareness of coral reef conservation and the replacement of shark fishing with shark diving has brought measurable socioeconomic and community benefits [62]. Similarly, agreements between dive tourism operators seeking sharks and traditional stakeholders in Fiji have generated effective marine protected areas [63]. Such marine protected areas play an important role in reducing fishing pressure on reef-associated mesopredatory sharks, allowing recovery of local populations [54]. Yet, large transient apex predatory sharks that frequent multiple coastal and pelagic ecosystems are at continued risk from exploitation by pelagic long-line fisheries (e.g., [64]) and will require cross-jurisdictional management strategies [10].

In the past few decades, global increases in shark fishing and anthropogenic stress have led to a simultaneous decline of shark populations and reef state. While restoration of sharks to historical baselines might restore numerous ecosystem processes, the relatively weak evidence for shark-driven trophic cascades implies that conservation of shark populations is unlikely to reverse macroalga-dominated states or militate against the ongoing declines in coral cover. While local and global efforts to reverse the declines in reef state ultimately aim to increase ecosystem resilience [65] and enhance fisheries productivity [59], restoring reefs to high coral cover is unlikely to have a substantial impact on the recovery of shark populations unless combined with targeted regulation of shark fisheries. Conservation efforts might therefore focus on reducing fishing pressure on shark populations [66] while simultaneously reducing local and global stressors on coral reefs [11].

Concluding Remarks

Our review identifies a broad range of ecological roles for sharks on coral reefs, highlighting: (i) the unique functional role of large-bodied apex sharks; (ii) the overlap between mesopredatory sharks and other teleost predators; (iii) the evolutionary and behavioural adaptation of sharks to coral reefs; and (iv) the functional role of coral reefs for sharks (Figure 3, Key Figure). Characterising the roles of sharks is complicated, largely because of a history of exploitation and limited understanding of the trophic levels of many apex predators and mesopredators. In considering the ecological roles of sharks on coral reefs, our review raises numerous research questions and potential new directions for the field (see Outstanding Questions).

Despite considerable speculation over the ability of sharks to drive trophic cascades that benefit coral health, most empirical evidence finds no such pattern, and where such trends are evident they remain open to alternative interpretations. Perhaps the most likely circumstance

Outstanding Questions

How have declines in apex sharks affected coral reef food webs? Is the trophic role of most mesopredatory reef sharks greater today than in the past because their foraging is less frequently interrupted by the presence (and threat) of larger apex species?

To what extent do direct consumptive versus non-consumptive effects of sharks influence mesopredator and herbivore abundance on reefs? Small-scale observations of predator avoidance by prey need to be scaled up in time and space to consider the demographic consequences, if any.

What physical, biological, and ecological mechanisms drive the distribution of sharks on coral reefs? Disentangling multiple mechanisms is challenging. For example, reef sharks are frequently encountered in areas of high flow along the tops of reef promontories. Such areas typically attract many reef fish because of high benthic and pelagic productivity and often the siting of spawning aggregation sites. To what extent are sharks attracted by the bounty of potential prey or the ability to conserve energy by utilising the lift provided by strong currents?

How would a decline of reef habitat quality affect the abundance and productivity of sharks? A complex reef habitat provides refuge for high densities of prey and attracts high densities of mesopredators, potentially including reef sharks. To what extent would a reduction in reef fish influence the growth and survival of reef sharks? Conversely, many sharks themselves take shelter among corals. How great (if any) is the demographic benefit to sharks of avoiding predators while sheltering within a structurally complex reef?

In theory, high diversity and functional redundancy among predators will dampen the likelihood of predator-driven trophic cascades. Yet field evidence of trophic cascades is mixed and where trophic patterns do occur they tend to be strongest between mesopredatory bony fishes and smaller reef fish. Can improvements in theory account for the diverse and mixed evidence of trophic cascades and in doing so help resolve the feasibility of shark-driven cascades?

for a shark-driven trophic cascade would involve large-bodied sharks, which are true apex predators that can exert strong direct and indirect controls over their prey. Conservation efforts that aim to promote the recovery of these species towards historical baselines may one day allow ecologists to quantify their ecological and trophic roles on coral reefs.

Supplemental Information

Supplemental information associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.tree.2016.02.014.

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Letter
The Ecological Role of Sharks on Coral Reefs: Response to Roff *et al.*

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Marie-Josée Fortin,[2] and
Mark G. Meekan[3]

Recently, Roff *et al.* reviewed the ecological roles of sharks as predators on coral reefs [1], with a focus on evidence that the loss of reef sharks drives trophic cascades in these ecosystems. They concluded that there is little support for the idea that sharks have a major structuring influence on the abundance and biomass of fishes at lower trophic levels of food webs or that they have an indirect influence on the cover of live coral and, thus, measures of reef 'health'. However, a major issue with their approach is that it primarily reviews evidence from correlative, observational studies that compare trophic structures of fishes on reefs with and without sharks.

Roff *et al.* make the same error as many of the studies they criticize; they fail to acknowledge that the abundances of fishes on coral reefs are driven by both top-down (e.g., predation or competition) and bottom-up (e.g., recruitment or disturbance) processes, so that changes in trophic structure can only be attributed to one of these processes if both are quantified simultaneously [2]. This is a major problem for most observational studies,

because many are simple trophic snapshots of reefs with and without sharks, with limited temporal context [3,4]. Only rarely do studies monitor change over the decadal timescales that are sufficient to show the effects of recovery of benthic communities from disturbance or the impact of recruitment pulses on abundances of reef fishes. Given that we invested 15 years of long-term monitoring of coral reefs to achieve this goal, it is disappointing that our results reported in Ruppert *et al.* [5] were dismissed as equivocal evidence of a trophic cascade.

Briefly, we monitored changes in the abundance of all major trophic groups of reef fishes on two groups of isolated coral reefs, one of which had a long history of targeted shark fishing that severely reduced shark numbers, whereas the other group was protected from all forms of fishing [6]. During monitoring, both sets of reefs underwent disturbance (bleaching and cyclones) that removed most live coral and increased the cover of benthic algae [7] (Figure 1). During the recovery phase, the abundance of herbivorous fishes increased significantly on both fished and unfished reefs, but the magnitude of this increase was greater on reefs where sharks were still present. The abundances of piscivorous teleosts did not change with

these disturbances and were always higher on reefs without sharks, a pattern that we argued to be consistent with predictions of mesopredator release [8]. Roff *et al.* suggested that the contrasting abundances of herbivores on fished and unfished reefs were simply a result of differences in the amount of algal food available to this guild during the recovery from disturbance, an assertion that we refuted in the original study [5] and do so explicitly here again (Figure 1). Despite the difficulties in ascribing causality in natural experiments such as ours, we note that these offer the only means to examine processes at the scales of whole reefs, which are relevant to the movements of predatory sharks, and our results are consistent with predictions of the effects of predator removal in many other systems [8,9].

However, changes in abundance and biomass are just one line of evidence of the ecological role of sharks. In focusing on trophic cascades and diet, Roff *et al.* fail to take a balanced view of predator–prey relations. If sharks are important regulators of system function, then their impacts will be expressed in not only the abundances, but also the diet, genetics, movement (transient versus resident), condition, behavior, and morphology of
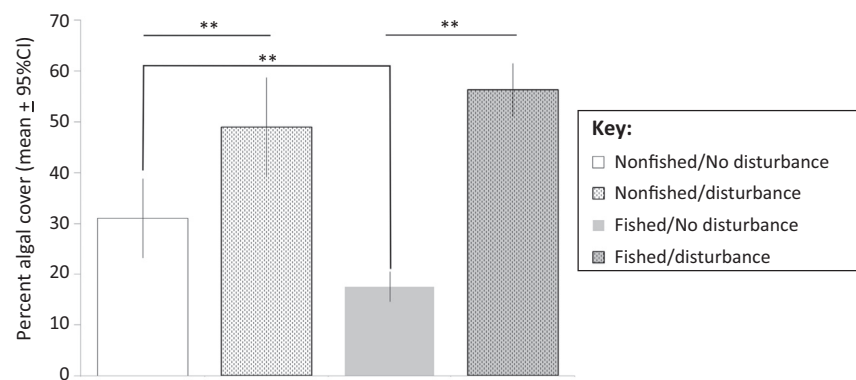
Figure 1. Comparison of Mean Algal Cover between Fished and Nonfished Reefs during Disturbance and No-Disturbance Phases. We tested for significance using a permuted *t*-test and showed significant differences in algal cover before and after disturbance events on fished and nonfished reefs. Furthermore, we observed significant differences between nondisturbed algal cover between reefs, but importantly not during disturbance phases. ** Denotes significance at *P* <0.01.

their prey [10,11]. At present, a key part of the puzzle that is missing in a coral-reef context is evidence for behavioral risk effects in prey [11], although some of these data are beginning to emerge [12]. An ecological focus on the behavioral effects of predators on prey is not only more tractable in experimental terms, but also provides evidence for the critical link between prey responses and trophic structure. Furthermore, it offers an introduction to the large literature of evolved behaviors of prey to predation threat (e.g., alarm cues, learning, etc.) that can then be examined in the context of coral reefs. These ideas received little attention from Roff *et al.* in their review [1]. A rebalancing of research effort to focus on predator–prey relations (rather than simply the ecology of the predator) is required to reflect the equal roles of sharks and their prey in the evolutionary arms race that is the process of predation. After all, from the perspective of the prey, it is largely irrelevant whether the reef shark that tries to consume them is an apex or mesopredator, because, in either case, the outcome is the same; they must evade the threat or be eaten.

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Letter

Reassessing Shark-Driven Trophic Cascades on Coral Reefs: A Reply to Ruppert *et al*.

George Roff,[1],*
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In our recent review of the ecological roles of sharks on coral reefs [1], we concluded that the evidence to support hypothesised shark-driven trophic cascades on coral reefs was weak and equivocal. In their response to our review, Ruppert *et al.* [2] assert that a major issue with our approach was that we primarily reviewed evidence from correlative observational studies to reach this conclusion. This is incorrect, because our conclusion is based upon multiple lines of evidence, including observational studies, food-web models, dietary and stable isotope analysis, trophic position, habitat use, and behavioural evidence [1]. While the authors are disappointed that we interpreted their long-term study of fished and unfished reefs [3] as equivocal evidence of a shark-driven trophic cascades [2], we identify key issues with their evidence and reasoning, as discussed below.

Fishing Effects on Shark Abundances

In their original study, Ruppert *et al.* reported that shark abundances were significantly higher at unfished versus fished reefs across a broad depth range (10–60 m, [3]). Yet, a survey of shark stocks using an identical survey technique across the same time period [4] found no significant differences in the mean numbers of sharks between fished and unfished sites at the shallow depths (5–30 m) surveyed by Ruppert *et al.* [3]; fishing effects on sharks were only evident at deeper sites (40–70 m) [4,5].

Absence of Trophic Cascades

Perhaps the clearest opportunity to demonstrate a trophic cascade occurs before disturbance, when coral cover and habitat quality were comparable between protected reefs and those open to shark fishing [3]. However, no significant differences were found in herbivore densities in reefs with shark fisheries versus unfished reefs before disturbance, despite a higher density of carnivores on the reefs without sharks [3], which is at odds with the theory of trophic cascades [1].

Equivocal Evidence for Mesopredator Release

In their response [2], Ruppert *et al.* state that abundances of piscivorous teleosts were higher on reefs without sharks, and argue this to be consistent with predictions of mesopredator release. However, their original analysis [3] included a diverse range of species as so-called 'mesopredators' (carnivore trophic group), including butterflyfish (*Forcipiger* spp.), and Moorish idols (*Zanclus cornutus*). More than half of these 'mesopredator' species (54%) feed

their prey [10,11]. At present, a key part of the puzzle that is missing in a coral-reef context is evidence for behavioral risk effects in prey [11], although some of these data are beginning to emerge [12]. An ecological focus on the behavioral effects of predators on prey is not only more tractable in experimental terms, but also provides evidence for the critical link between prey responses and trophic structure. Furthermore, it offers an introduction to the large literature of evolved behaviors of prey to predation threat (e.g., alarm cues, learning, etc.) that can then be examined in the context of coral reefs. These ideas received little attention from Roff *et al.* in their review [1]. A rebalancing of research effort to focus on predator–prey relations (rather than simply the ecology of the predator) is required to reflect the equal roles of sharks and their prey in the evolutionary arms race that is the process of predation. After all, from the perspective of the prey, it is largely irrelevant whether the reef shark that tries to consume them is an apex or mesopredator, because, in either case, the outcome is the same; they must evade the threat or be eaten.

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Box 1. Trophic Cascades and Food Web Complexity on Coral Reefs

Coral reef food webs are highly diverse and often complex [11]. In their study, Ruppert et al. compared five broad trophic groupings [carnivores (intermittently termed 'mesopredators'), detritivores, planktivores, corallivores, and herbivores; Figure IA] between protected reefs and those open to shark fishing [3]. A closer examination of the trophic level, maximum size, and general diet for the 114 species of fish recorded in the study reveals expanded trophic complexity within their trophic groups, and substantial overlap among trophic groups (Figure IB; Table S1 in the supplemental information online), highlighting the diversity of reef fish assemblages and complexity of coral reef food webs. Notably, the 'herbivore' grouping encompasses a range of functional roles, from grazers to damselfish that cultivate algal gardens, zooplanktivores. and even clownfish (Table S1 in the supplemental information online), making it difficult to infer a functional response of herbivory. Considering the broad trophic groupings, absence of size or biomass data, and questionable predator–prey relations among trophic groups, comparisons between the structure of fish assemblages in fished and unfished sites in the study by Ruppert et al. [3] are difficult to interpret. As we highlighted in our review [1], high functional redundancy at every trophic level (Figure IB) is likely to promote stability in coral reef food webs by dampening the effects of trophic cascades.
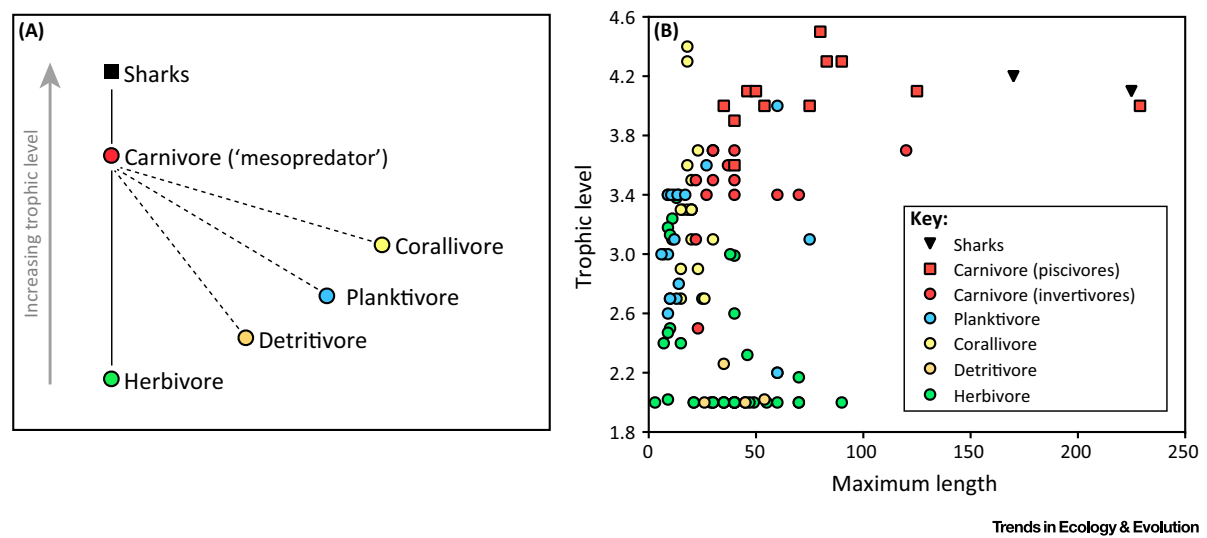

Figure I. Structure of Coral Reef Food Webs. (A) Trophic groups and inferred trophic cascade (shark–carnivore–herbivore) [3]. (B) Actual trophic complexity within trophic groups for 114 species of fish from [3] (expanded trophic level and maximum body length; Table S1 in the supplemental information online).

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on small invertebrates and are not piscivorous (Box 1 and Table S1 in the supplemental information online), and are unable to exert top-down control over herbivorous fishes. As such, the argument for mesopredator release resulting in lower abundances of primary consumers following shark removal [3] is weak.

Reassessing the Role of Reef Sharks as Mesopredators

Surveys of sharks at the fished and unfished sites (5–30 m depth) revealed that 97.6% of records were from two species of mesopredatory reef shark (*Carcharhinus amblyrhynchos* and *Triaenodon obesus* [4]) that occupy a trophic level similar to large piscivorous fishes [1,6] (Box 1). Ruppert et al. assume a simple trophic cascade of shark–mesopredator–herbivore [3], yet there is little direct evidence

that these reef shark species prey upon teleost mesopredators: stomach-content analysis indicates that reef sharks feed primarily on small or juvenile fishes, with few or no records of large piscivorous fish in reef shark diets ([6] and references therein). While mesopredatory reef sharks might have an important consumptive [6] and/or nonconsumptive [7] role in structuring herbivore assemblages at unfished sites, this was not explicitly tested [3] and does not constitute a trophic cascade.

Bottom-Up Drivers of Key Grazers

The authors provide new data on algal cover in their response, and state that algal cover did not differ significantly between fished and nonfished reefs following disturbance [2]. This assertion directly contradicts the original paper [3], which states

'fished reefs had more algae and less coral following bleaching than non-fished reefs after the cyclone event (Figure S1)'. We argue that the clearest insight into herbivore dynamics can be drawn from the 'detritivore' group, dominated by the surgeonfish *Ctenochaetus striatus* [3]. Although it derives nutrition from detritus, *C. striatus* is functionally an important grazer of algal turfs [8]. Importantly, the detritivore group only showed marked increases in abundance following disturbance where 'mesopredators' were most abundant, sharks scarce, and the availability of algal turf increased the most [3]. These trends show the opposite pattern to an expected trophic cascade and are consistent with food limitation.

In summary, while sharks clearly have an important and largely unexplored trophic

role on coral reefs [1], we maintain that the evidence for trophic cascades provided by Ruppert *et al*. [3] is weak and equivocal.

Finally, we are confused by the final paragraph of Ruppert *et al.*'s response, which asserts that we present an imbalanced view of predator–prey relations by focussing on consumptive effects. Our review clearly stated that sharks can exert nonconsumptive behavioural 'fear' effects that can influence lower trophic levels by disrupting their foraging activity [1]. While the study of behavioural risk effects represents an exciting emerging field of research (e.g., [9]), to date only two studies have quantified the indirect effects of mesopredatory reef sharks on lower trophic levels in coral reef ecosystems [7,10]. Importantly, from the perspective of the prey, it seems largely irrelevant whether the predator is a reef shark or a fish, because herbivores exhibit similar behavioural responses to reef sharks and to large coral groupers [7]. As

we identified in our review, quantifying the consumptive versus nonconsumptive effects of mesopredatory sharks on lower trophic levels in coral reefs at ecosystem scales represents an important future research direction (see Outstanding Questions in [1]).

Appendix A Supplementary Information

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