Ecology of Fishes on Coral Reefs

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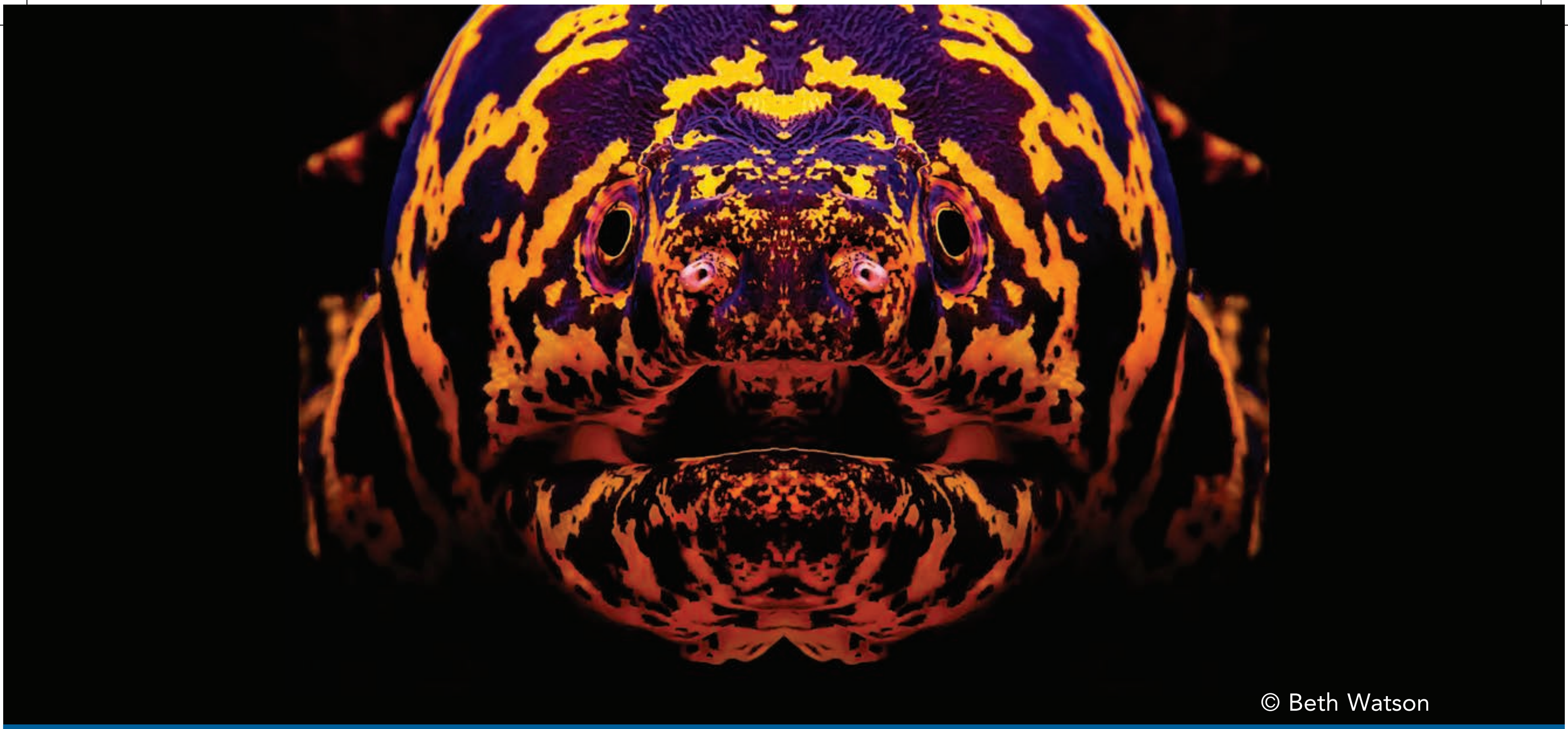
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5 Predation: piscivory and the ecology of coral reef fishes

Mark A. Hixon

Coral reef fishes are typically subjected to intense predation, especially by mid-trophic-level piscivores (mesopredators) targeting new recruits. Reef fishes thus display a broad variety of morphologies and behaviors associated with both capture and evasion. Different predators can interact with each other while foraging, cooperatively or negatively, and different prey species can interact in ways that increase or decrease the risk of predation. Short-term predator responses to changes in prey density, including functional and aggregative responses, have been quantified in only a few cases. Nonetheless, predation has often been found to be a source of direct density-dependent mortality in reef fishes, which in several studies has been further shown to regulate local populations. Such density dependence may involve interactions among different species of predator (synergistic predation), as well as predators forcing prey to compete for spatial refuges in the reef structure. In affecting the relative abundance of prey species, piscivores also structure reef fish communities. Differential colonization of reefs by predators affects subsequent relative recruitment rates of prey species (priority effects). Intense predation can extirpate relatively rare prey species via either differential consumption of those species or non-selective consumption. Coral reef fishes also provide examples of multiple piscivores consuming the same prey as well as each other (intraguild predation) and changes in the abundance of top predators, typically caused by overfishing, affecting abundance at lower trophic levels via mesopredator release (trophic cascades). Additional studies are needed to clarify the mechanistic local-scale patterns of predator–prey interactions in terms of both lethal and nonlethal ecological effects, as well as the broader holistic scale of predator–prey metapopulation and metacommunity dynamics, especially in the context of continued overfishing and reef degradation.

> "Life feeds on life."
>
> *Joseph Campbell*

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Two imperatives in the lives of animals are to eat and avoid being eaten. Thus, predation is often considered to be the primary ecological interaction among animal species [e.g. 533]. Coral reef fishes are no exception, and indeed, they display a broad variety of morphologies and behaviors involved in capturing prey and escaping predators. It seems almost a truism, then, to assert that piscivory (predation on fish) plays a major role in driving population dynamics and structuring communities of fishes on coral reefs. Reviewing the relevant literature published through the 1980s, Hixon [1114] found that empirical evidence for this assertion was convincing yet largely circumstantial, based on several well-documented observations:

- Piscivores are ubiquitous on coral reefs (Figure 5.1). At first glance, this finding seems to contradict the fact that large top predators, such as sharks and larger species of grouper (Serranidae), jack (Carangidae), snapper (Lutjanidae), and barracuda (Sphyraenidae), are now woefully overfished on many if not most reefs accessible to humans [652,656,867,2117,2257,2408,2422]. However, the vast majority of reef fishes settle as tiny post-larvae which are highly susceptible to a broad variety of small-gaped fishes, as well as predatory invertebrates, sea snakes, and seabirds. With the overfishing of larger piscivores that formerly limited the abundance and behavior of smaller predators, the ecological importance of mid-trophic-level carnivores among reef fishes is likely to have increased in recent decades, a phenomenon known as "mesopredator release" [reviews by 2039,2114, sensu 2384]. Of course, in regions where fishing is extremely intense (i.e. "Malthusian overfishing" of Pauly [1936]), even mesopredators can be depleted. Piscivorous mesopredators include several trophic levels distributed among over two dozen families, ranging from smaller groupers, jacks, and related families that also include large top carnivores, to various families typically considered to be mesopredators (such as lizardfishes, frogfishes, scoropionfishes, hawkfishes, etc.), to species not typically considered piscivorous, such as squirrelfishes and wrasses (Table 5.1). The feeding rates of these small piscivores on new recruits can be substantial [29,567,805,982,1167]. Recent studies of less documented sources of piscivory on reefs include egg predation [758], sharks consuming other sharks [431,1767], and sea snakes consuming schooling reef fish [1480].
- Early post-settlement mortality is high. This pattern is consistent with smaller fish being more susceptible to a broader range of predator sizes, as well as perhaps being more naïve to approaching predators. More recent documentation of this pattern includes compilations by Caley [404] and Almany and Webster [61]. Importantly, early post-settlement mortality caused by predation is now known to be a major source of locally regulating density dependence in reef fishes (see below).
- Fish abundance increases with reef structural complexity. This common (though not universal) finding is indicative of the importance of predation if reefs in fact provide effective spatial refuges for prey fish. Of course, more complex reefs also may provide more abundant food, so this pattern alone cannot separate causation from mere correlation. More recent studies have clarified the role of reef structure in predator–prey interactions among reef fishes (see below).
- The abundance of prey fish on patch reefs decreases with the abundance of resident predators. This common (though, again, not universal) pattern is consistent with the hypothesis that resident predators (e.g. small groupers) reduce the local abundance of their prey. However, among-reef movements, especially aggregative responses (sensu Hassell [1055]) by transient predators (e.g. jacks) following differential settlement of prey among reefs, may obfuscate this pattern. Indeed, on the Great Barrier Reef, Stewart and Jones [2425] found a consistently positive relationship between resident predator and prey abundances, whereas Connell [537] found a negative relationship between predator density and prey mortality at larger spatial scales yet not at smaller scales.

At the time Hixon's [1114] review, very few experimental studies of piscivory in reefs fishes had been published. Notable early field manipulations had demonstrated shelter limitation [864,1113,2334], as well as increases in the local abundance of some prey fishes following the removal of predators by caging [689]. During the intervening quarter of a century, understanding of the role of piscivory in reef fish ecology has increased tremendously (historical review by Hixon [1123]). This overview covers representative studies published from 1990 onwards, picking up where Hixon [1114] left off. This chapter focuses on predator–prey behavioral interactions, effects of piscivores on prey population dynamics, and top-down effects in reef fish communities, and concludes with a brief synthesis and directions for future research.

PREDATOR–PREY BEHAVIORAL INTERACTIONS

Predation can be a strong selective agent on prey escape mechanisms (review by Abrams [9]). New recruits of a variety of damselfish (Family Pomacentridae) learn to detect and avoid the odor of nearby piscivores, thereby enhancing early post-settlement survival [680,1166,1520,1654,2546]. In at least one case, prey fish can distinguish between predators that have been consuming fish versus those that have not [680]. Damselfish can also detect visual cues of predators [1166] as well as chemical alarm cues produced by injured conspecifics [1166,1520]. The goby *Asterropteryx semipunctatus* can both detect predators visually as well as react to chemical alarm cues of conspecifics [1656]. Settling anemonefish detect the odors of piscivores as well as both host and non-host anemones in selecting suitable habitat [679].

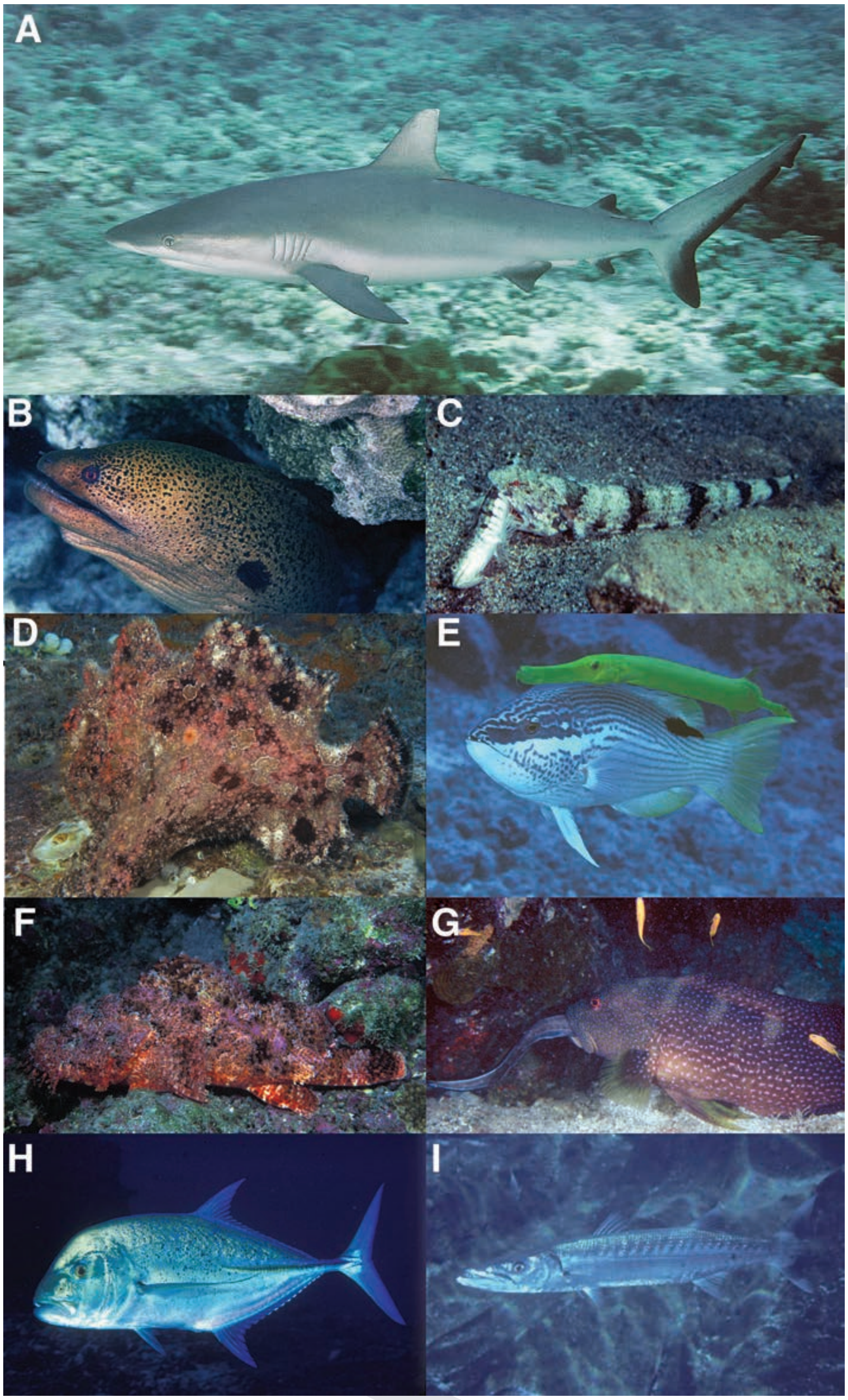


Figure 5.1 Some of the major families of piscivorous coral reef fishes (see also Table 5.1). (A) Reef shark (Carcharhinidae, *Carcharhinus amblyrhynchos*). (B) Moray eel (Muraenidae, *Gymnothorax javanicus*). (C) Lizardfish (Synodontidae, *Synodus dematogenys*) consuming a lizardfish. (D) Frogfish (Antennariidae, *Antennarius commersoni*) – note cryptic mimicry match of nearby coral. (E) Trumpetfish (Aulostomidae, *Aulostomus chinensis*) apparently using a hogfish as a mobile hunting blind. (F) Scorpionfish (Scorpaenidae, *Scorpaenopsis cacopsis*) – note cryptic coloration. (G) Grouper (Serranidae, *Varioloa louti*) consuming a conger eel. (H) Jack or trevally (Carangidae, *Caranx melampygus*). (I) Barracuda (Sphyraenidae, *Sphyraena barracuda*). All photos shot in Hawai'i, except *Varioloa louti* photographed in Red Sea, all courtesy of J.E. Randall.

Table 5.1 Some common families of bony fish which include species that at least occasionally are piscivorous mesopredators on coral reefs. These and other mesopredators consume not only smaller adult fish but also recruits and juveniles of larger species. They are in turn prey for top predators, including sharks and larger species of grouper, jack, snapper, and barracuda, as well as passing pelagic predators (e.g. larger tunas). Distribution: A, Atlantic; I/P, Indian/Pacific; (A), family occurs in Atlantic, yet there are no piscivores in that family reported there. Sources: Allen and Robertson [38] for the tropical eastern Pacific, Allen and Steene [37] for Indian Ocean, Lieske and Myers [1493] for reefs worldwide, Myers [1818] for Micronesia, Randall [2069] for the Red Sea, Randall [2068] for the Caribbean Atlantic, Randall [2073] for the Tropical South Pacific, Randall [2076] for Hawai'i, Randall *et al*. [2071] for the Great Barrier Reef.

Family	Common Name	Distribution
Muraenidae	Moray Eels	A, I/P
Ophicththidae	Snake Eels	A, I/P
Congridae	Conger Eels	I/P
Synodontidae	Lizardfishes	A, I/P
Antennariidae	Frogfishes	A, I/P
Holocentridae	Squirrelfishes	A, I/P
Aulostomidae	Trumpetfishes	A, I/P
Fistulariidae	Cornetfishes	A, I/P
Scorpaenidae	Scorpionfishes	A, I/P
Serrandiae	Groupers	A, I/P
Pseudochromidae	Dottybacks	I/P
Plesiopidae	Longfins	I/P
Apogonidae	Cardinalfishes	(A), I/P
Carangidae	Jacks / Trevallies	A, I/P
Lutjanidae	Snappers	A, I/P
Lethrinidae	Emperors	I/P
Mullidae	Goatfishes	(A), I/P
Cirrhitidae	Hawkfishes	A, I/P
Sphyraenidae	Barracudas	A, I/P
Labridae	Wrasses	A, I/P
Uranoscopidae	Stargazers	A, I/P
Pinguipedidae	Sandperches	I/P
Bothidae	Left-eye Flounders	A, I/P
Pleuronectidae	Right-eye Flounders	A, I/P
Soleidae	Soles	(A), I/P

The physiological condition and behavior of both predator and prey interact with the local environment to determine prey susceptibility. Lab and field studies of planktivorous damselfishes illustrate some of the many variables that determine the outcome of predator–prey behavioral interactions. On the Great Barrier Reef, larger juvenile *Pomacentrus amboinensis* survived better than smaller juveniles, but only on reefs with stronger currents and more predators, circumstances that provided larger prey an advantage in evading predators while smaller prey were consumed [1164]. However, in the Bahamas, faster-growing juvenile *Stegastes partitus* suffered greater mortality rates than slower-growing fish, likely due to risk-prone behavior as faster-growing fish foraged further from reef refuges in obtaining more planktonic food [1272]. In this system, smaller adults suffered higher mortality rates than larger fish, resulting in a balancing ontogenetic reversal in the direction of viability selection on size-at-age over the life span [1272]. Typically, recruits and juveniles that are larger and/or more physically fit (usually measured as lipid content) survive better than smaller and/or thinner individuals [e.g. 295,1271,2296,2581,2700] (Review by Sogard [2378]; but see Walsh *et al*. [2602]). Vigliola *et al*. [2581] provided evidence that differences in survival between individual damselfish have a genetic basis.

Synergistic and indirect effects add to the complexity of predator–prey behavioral interactions. Considering predator–predator effects, multiple piscivores can attack prey simultaneously, such as jacks attacking from above while groupers attack from below [1117,2409]. Predators can also hunt cooperatively, such as moray eel and grouper attacking in concert [371], or compete with or otherwise inhibit each other [2406,2407]. Considering prey–prey effects, Webster and Almany [2633] showed experimentally that high survival of recruiting damselfishes was correlated with high abundance of cardinalfishes, which were differentially attacked by predators. Within species, adult damselfish (*Dascyllus marginatus*) can detect and avoid approaching predators better than juveniles, which follow adults when they occur together, a case of social facilitation of predator recognition and avoidance [1316]. This phenomenon may partially explain the well-documented preference by settling fish for coral heads already occupied by larger conspecifics [e.g. 291,2449]. Considering combined predator–competitor effects, aggression by territorial damselfish (interference competition) may increase the susceptibility of chased and unwary prey fish to lurking predators [56,423,846,1155]. Madin and Madin [1557] hypothesized that the presence of predatory snapper (known to consume surgeonfish) inhibits attacks by territorial damselfish on grazing surgeonfish while they invade and consume the defended algal mats of the damselfish. If so, then this is an example of a predator indirectly benefiting a prey species by inhibiting an interference competitor of that prey.

In summary, prey fish avoid predation in a variety of ways, just as piscivores display various means of successfully capturing prey. Different predators can interact with each other while foraging, cooperatively or competitively, and different prey can interact in ways that increase or decrease the risk of predation. Hixon [1114] reviewed other predator–prey behavioral interactions not summarized here, such as shoaling and schooling. Recent explorations indicate that multispecies aggregations of prey reef fishes may increase the mortality rate per species compared to single-species groups, perhaps due to increasing predator aggregation and/or decreasing prey vigilance [2427]. Behavioral interactions are the mechanisms underlying the effects of predation on prey population dynamics and community structure.

PREDATION AND PREY POPULATION DYNAMICS

It is a truism that, unless swamped by prey reproduction, predators typically affect the abundance of their prey (review by Taylor [2465]). This direct effect was well documented in coral reef fishes during the 1990s via predator removal/exclusion experiments showing that prey density increased when predation was reduced [399,422,538,742,1117]. Predation was subsequently found to have especially strong effects on the densities of recruit and juvenile fishes [e.g. 61,683,1156,1987,2412,2632]. For example, over 25% of bridled goby (*Coryphopterus glaucofraenum*) on Bahamian reefs can be consumed within a day of settlement [2412]. The Pacific red lionfish (*Pterois volitans*), an invasive piscivore on Atlantic reefs, has unusually strong effects on a broad variety of native reef fishes up to half the predator's body length [29,567,982,984,1758], sometimes causing reductions in native prey fish populations of over 90% in a matter of weeks [30,570].

Besides prey morphological defenses (review by Hixon [1114]) and evasive behavior per se (see above), the primary mechanism by which the effects of predation on prey abundance are moderated is via spatial prey refuges provided by the structural complexity of the habitat [179]. To demonstrate this mechanism, one would preferably show that increasing habitat complexity per se actually reduces predation rates beyond generating any confounding effect, such as providing additional food sources for prey fishes. Prey refuges may be absolute, where prey are safe from all predators, or partial, where predation is inhibited yet not eliminated [1115]. Absolute refuges include small reef holes into which prey fish barely fit and which are simultaneously too small for access by predators, such as abandoned tubeworm holes inhabited by the tubeblenny *Acanthemblemaria spinosa* [373]. Partial refuges include branching coral thickets through which predators have difficulty detecting and/or capturing prey [e.g. 402]. In some cases, increased habitat complexity may facilitate rather than inhibit predators, such as the limited visual field in gorgonian fields increasing the risk of predation for the demersal damselfish *Stegastes partitus* [2111].

There are a variety of recent studies indicating that habitat complexity provides prey refuges in reef fishes. The distribution and abundance of the corallivorous filefish *Oxymonacanthus longirostris* was correlated more with the availability of prey refuges provided by highly branching corals than with the availability of prey corals [350]. The planktivorous damselfish *Chromis margaritifer* foraged farther from the reef structure where piscivores had been excluded by cages [1599]. Field experiments that manipulated the abundance of shelter holes on artificial reefs showed that increasing prey refuge space enhanced recruitment and/or survival of prey fishes [373,402,1116]. On the Great Barrier Reef, Beukers and Jones [262] used lab and field experiments to demonstrate that survival of the planktivorous damselfish *Pomacentrus molluccensis* was clearly enhanced by prey refuges provided by highly branching corals. In French Polynesia, Shima *et al*. [2328] experimentally demonstrated a similar pattern for the wrasse *Thalassoma hardwicke*, yet with a twist: more complex corals not only provided more prey refuges, but also were inhabited by more predators [2329]. In this case, the benefits of additional partial prey refuges were balanced by the costs of more predators, resulting in nearly equal prey survival among treatments.

In terms of prey population dynamics, the key question is not so much whether predators reduce (or "limit", in ecological jargon) the abundance of their prey, as reviewed above, but rather, whether predation regulates local prey abundance. Regulation requires predators to cause direct density-dependent mortality of their prey, i.e. all predator responses (sensu Hassell [1055]) combined cause the per capita mortality rate of the prey to increase as prey density increases. This topic is covered in detail both in this volume [2511] and elsewhere [1119–1121,2666], so is only summarized here. Over the short (within-generation) time span of most ecological studies, predators can cause density-dependent mortality of their prey by some combination of a type 3 functional response and/or an aggregative response (review by Murdoch [1809]).

A "functional response" is the quantitative relationship describing the per capita feeding rate of an individual predator as a function of prey density [1160]. Only a type 3 functional response, which is sigmoid in shape, causes density-dependent mortality of the prey (up to the saturating inflection point of the curve). Functional responses have proven difficult to quantify in fishes (review by Hunsicker [1203]). As expected, feeding rates have been seen to increase with prey density in the field [261], yet most attempts to document the precise shape of the functional response curve have proven equivocal, especially in laboratory settings [1034]. However, Stier and White [2429] recently employed a somewhat assumption laden approach to suggest that the functional response of coney grouper (*Cephalopholis* *fulva*) feeding on bluehead wrasse (*Thalassoma bifasciatum*) in the Virgin Islands was a decelerating curve that declines as predator density increases (the predator-dependent Hassell–Varley model [1056]). Similarly, Stier *et al*. [2426] found a decelerating functional response in the hawkfish *Paracirrhites arcatus* attacking the wrasse *Thalassoma amblycephalum* in French Polynesia. Such decelerating functional responses in and of themselves (basically, type 2 in general shape, sensu Holling [1160]) cannot cause density-dependent mortality in prey [1809], as may often be the case if there is interference among predators [560].

An "aggregative response" occurs when predators congregate where prey are abundant, and spend less time where prey are rare, which can possibly cause density dependence in prey mortality even if each predator feeds at a constant rate [1057]. A variety of transient reef fish piscivores congregate at high concentrations of prey [e.g. 261,1117,1118,2634]. Because aggregative responses are readily observed compared to functional responses, the presence of density-dependent prey mortality in the absence of an aggregative response can indicate the presence of a type 3 functional response [839,1892].

Whether prey mortality is directly density dependent or not can depend on interactions among refuge space, competition, and predation (Figure 5.2, [1121]), relative spatial patterns of predator and prey recruitment [2661], and relative spatial scaling of predator–prey interactions [1890,1892,2256,2663]. As detailed by White *et al*. [2666], when "density" is more realistically considered in terms of group size comprising a patch of prey a large reef or collection of patch reefs, as can be the case in shoaling and schooling prey species, a safety-in-numbers benefit of larger group sizes is likely to result in inverse density dependence (Figure 5.3).

Regardless of the precise environmental factors and behavioral mechanisms involved, there is ample observational and experimental evidence that predation causes direct density-dependent mortality in a broad variety of coral reef fishes, as well as density-independent and occasional inversely density-dependent mortality [reviews by 1120,1121,2511,2666, see also 1886]. The details of particular case studies reveal the rich variety of factors involved in predator–prey interactions among reef fishes. In the Bahamas, Hixon and Carr [1117] experimentally documented that density-dependent mortality in new recruits of the planktivorous damselfish *Chromis cyanea* occurred only when both resident and transient predators were present, not when only one or the other kind of predator was present (Figure 5.4). The behavioral mechanism was that an aggregative response by transient predators (schooling jacks) forced these midwater prey to dive for cover in the reef, where survivors suffered increased susceptibility to resident predators (including small groupers and moray eels). In the absence of transient predators, these prey spend the day in midwater, relatively safe from resident predators (which may be benthic ambush predators or themselves forced to stay near shelter by the presence of still larger predators, such as barracuda and sharks). In the absence of resident predators, these prey find safety in the reef structure when transient predators approach. Thus, when both are present, transient and resident predators combined reciprocally remove two different partial prey refuges – midwater and reef, respectively – a case of "synergistic predation" [1117, see also 2409]. The direct density dependence detected by Hixon and Carr [1117] on patch reefs was later confirmed to occur on continuous reefs in the Bahamas [76], in contrast to the findings of Sandin and Pacala [2256] working in the Netherlands Antilles, who detected inverse density dependence.

Also in the Bahamas, Carr *et al*. [423] detected another synergy that caused density-dependent mortality in new recruits of the demersal damselfish *Stegastes partitus*. This synergy involved predators and interference competitors (territorial damselfish). Small *S. partitus* are normally sufficiently vigilant to avoid predation, yet when chased by larger aggressive damselfish, they are often picked off by predators that aggregate at high prey densities. This density dependence was also documented on both patch reefs and continuous reefs [423], and scaled up to populations inhabiting entire large reefs [1124].

In the same system, predation was clearly involved in causing density-dependent mortality of the goby *Coryphopterus glaucofraenum*. Despite an earlier field experiment that detected density dependence regardless of the presence or absence of resident predators [838], when Forrester and Steele [839] cross-factored goby density and refuge availability, density dependence occurred only where prey refuges were scarce, indicating predation as the underlying mechanism. In later experiments, Steele and Forrester [2413] demonstrated that density dependence detected on patch reefs scaled up to entire large reefs.

In French Polynesia, Schmitt and Holbrook [2275] found that mortality in three species of planktivorous *Dascyllus* damselfish was density dependent for only a short time (about 2 weeks) following settlement. Subsequent field experiments showed that this density dependence was caused ultimately by various small resident predators and proximally by competition for limited prey refuges in coral heads [1155,1156,2281].

Ultimately, direct density dependence is necessary but not sufficient for population regulation. For density-dependent predation to be truly regulating, prey population dynamics must as a consequence of predation exhibit three closely related criteria over multiple generations – persistence (avoiding extirpation), boundedness (varying within non-zero limits), and return tendency (increasing when below a certain size and vice versa) – that is, long-term temporal density dependence [1119,1811,2526]. To date, these phenomena have been documented for only two coral reef fishes, both in the Bahamas. First, Webster [2634] demonstrated experimentally that spatial density-dependent mortality (i.e. density dependence among local populations) in the fairy basslet *Gramma loreto* was caused by

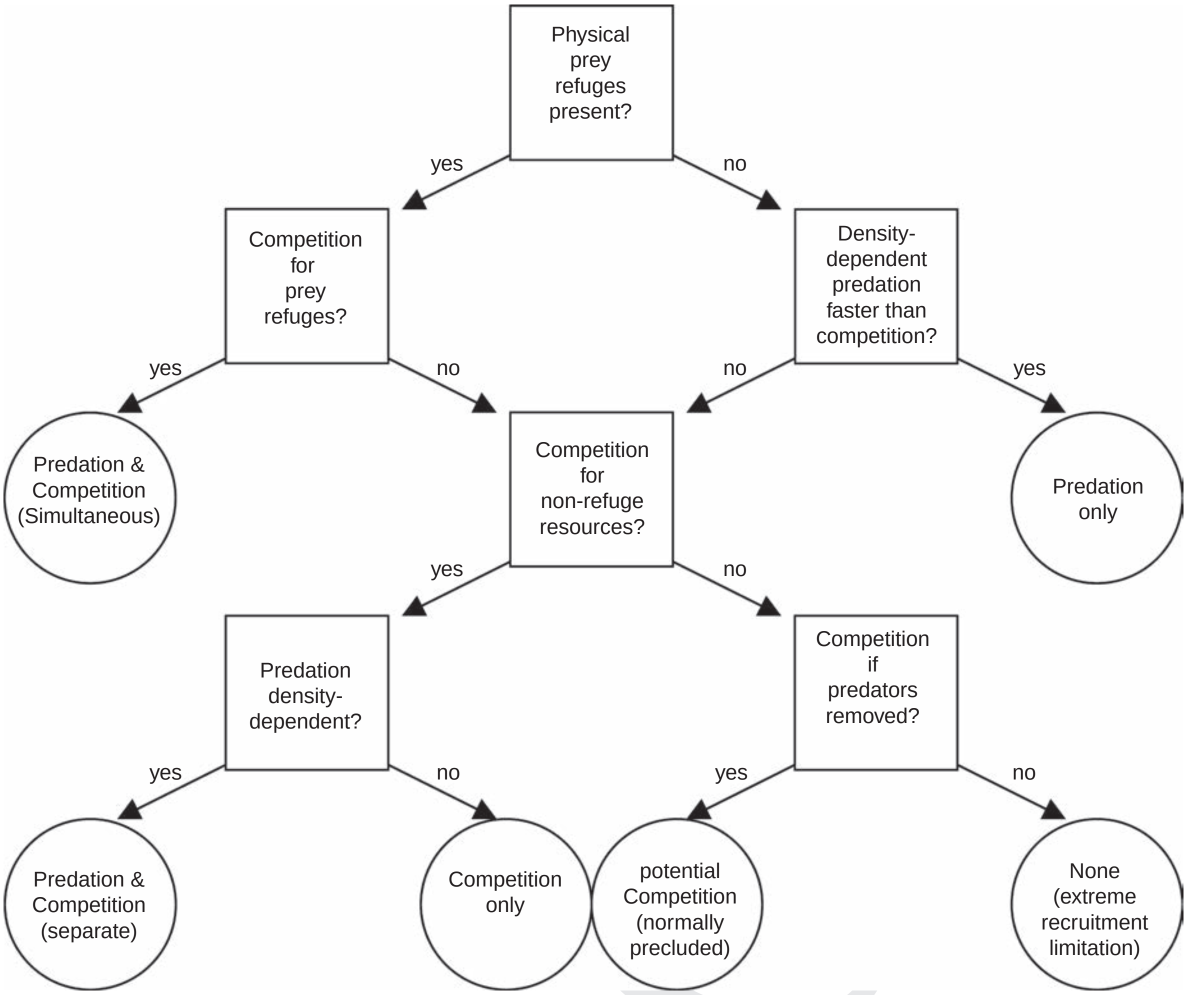


Figure 5.2 Flowchart of causation showing that predation, spatial prey refuges, and competition may or may not interact in determining whether or not mortality in reef fishes is density dependent. Squares enclose empirical questions and circles enclose conclusions. For example, predation and competition simultaneously cause density dependence when predation forces prey to compete for spatial refuges. Modified from Hixon and Jones [1121].

aggregative responses of piscivores and led to between-generation, regulating, temporal density dependence (i.e. density dependence within populations over roughly two generations). Mechanistically, on reef ledges occupied by social groups of this species, larger individuals forced smaller individuals away from preferred plankton-feeding positions and toward the backs of ledges [2631], where small resident predators aggregated at higher prey densities [2634]. Second, Hixon *et al*. [1124] monitored multiple generations of bicolor damselfish (*Stegastes partitus*) over 8 years, including manipulations of recruitment over half that period. Regulating density dependence caused largely by predation (see above) was evident only on reefs that were structurally complex, providing sufficient prey refuges that ensured high survival at low densities (i.e. persistence). On these reefs, the coefficient of variation of population size (N) was less than expected if interannual dynamics were density independent (i.e. boundedness), and the correlation between $\ln(N_t)$ and $\ln(N_{t+1}/N_t)$ was also less than expected if dynamics were density independent (i.e. return tendency).

In summary, recent studies have demonstrated that coral reef piscivores greatly affect the abundance of their prey, and often cause density-dependent mortality in those prey, which may regulate local prey populations. Short-term direct density dependence may occur via predator aggregative responses and type 3 functional responses, and the risk of predation may cause competition for spatial prey refuges in the reef framework.

TOP-DOWN EFFECTS ON COMMUNITY STRUCTURE

Because coral reef piscivores clearly affect the abundance of their prey, and are often involved in regulating prey population

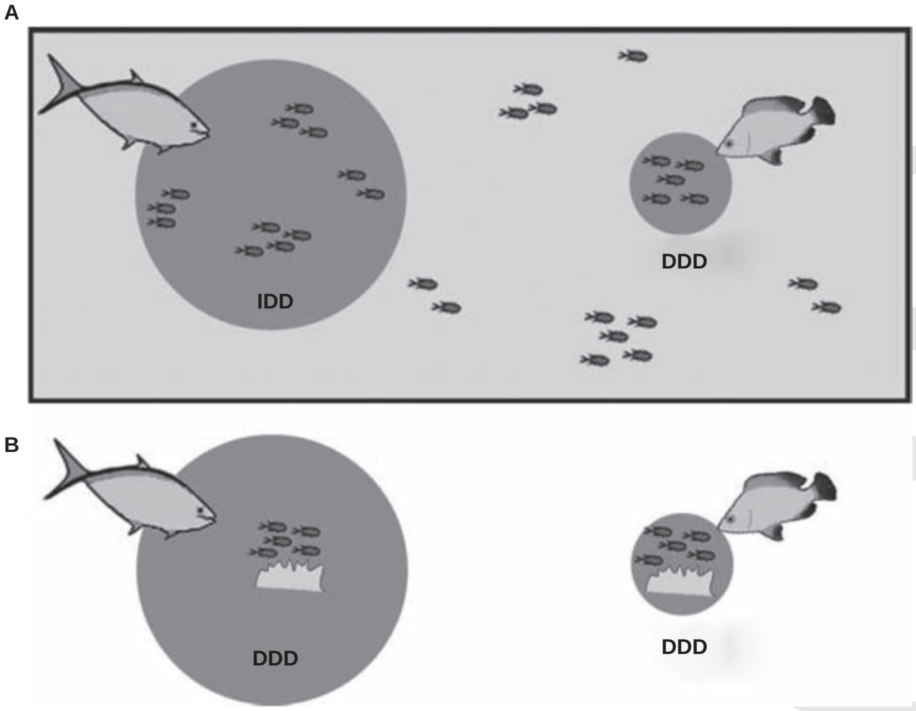
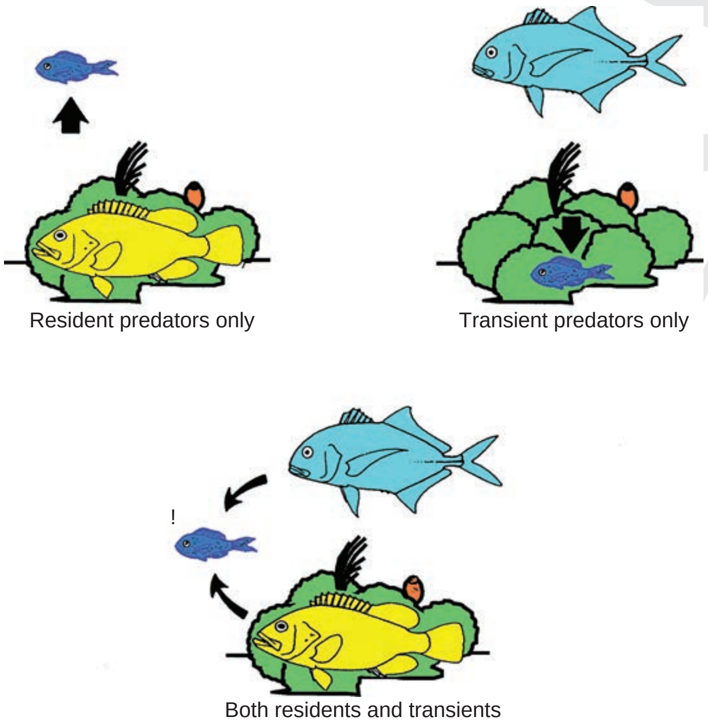


Figure 5.3 Effects of the spatial scale of predator foraging on density dependence of prey mortality. Two predator species have different characteristic foraging scales; each defines a patch of prey at the spatial scale indicated by the shaded circle (left large, right small). The predator distributes foraging effort randomly within that patch. (A) On a continuous reef (shaded rectangle), the larger foraging scale (left) tends to overlap multiple prey shoals, leading to inverse density-dependent (IDD) prey mortality at the shoal scale. The smaller foraging scale (right) coincides with the spatial scale of prey aggregation, leading to direct density-dependent (DDD) prey mortality at the shoal scale. A similar pattern occurs on closely spaced patch reefs. (B) When reef spacing is wider, the foraging scale of all predators is constrained to the scale of a single prey aggregation, producing DDD mortality in all cases, given sufficient time and the appropriate type of predator functional response. Modified from White *et al.* [2666].



Resident predators only

Transient predators only

Both residents and transients

Figure 5.4 Synergistic predation. When only one kind of predator is present on a reef, planktivorous fishes have two alternative spatial refuges: midwater when only resident piscivores are present (upper left) and in the reef structure when only transient piscivores are nearby (upper right). In either case, predation is typically sporadic and density independent, depending on the vicissitudes of predator stealth and prey vigilance. However, when both kinds of predator are present, both refuges are reciprocally removed, increasing the prey mortality rate. Synergistic predation occurs when only the combined effect of multiple predators causes density-dependent mortality in their shared prey.

dynamics, it follows that piscivory likely is a process structuring communities of coral reef fishes. Community-level effects of predation are evident in a variety of studies. "Priority effects" occur when the species composition and density of residents on a reef inhibit or enhance subsequent recruitment of other species, thereby affecting community structure [2333,2340]. Field experiments in the Bahamas showed that resident predators (groupers and moray eels) inhibited subsequent recruitment of a damselfish and a surgeonfish, and enhanced recruitment of a wrasse [56]. Further experiments showed that these effects were caused by differential mortality rather than differential settlement [56]. Conducting the same experiment on the Great Barrier Reef, Almany [57] found that predators inhibited recruitment of damselfishes, surgeonfishes, butterflyfishes, and rabbitfishes. In French Polynesia, Stier *et al*. [2427] found that the timing of colonization of coral heads by the predatory hawkfish *Paracirrhites arcatus* did not affect within-patch species richness of prey fishes, yet did cause detectable shifts in the relative abundance of resident species.

Depending on which prey species are attacked, the intensity of predation, and other factors, piscivores may increase or decrease the local species diversity (richness and/or evenness) of their prey (review by Hixon [1112]). In studies of artificial reefs in the Great Barrier Reef [399] and the Virgin Islands [1116], the number of prey species per reef decreased as the abundance of resident piscivores increased. In the Virgin Islands study, the local population sizes of both common and rare prey species were negatively correlated with the abundance of resident predators, suggesting generalized predation [1116]. Non-selective predation was also evident in a field experiment showing negative effects of predators on prey richness in French Polynesia [1079]. In contrast, in the Bahamas and the Great Barrier Reef [60], as well as French Polynesia [2428], generalist predators disproportionately reduced the abundance of relatively rare prey species in decreasing local prey richness, including both beta diversity (among patches) and gamma diversity (among reefs) in the latter study. Laboratory experiments indicated that the dottyback *Pseudochromis fuscus* preferred relatively rare prey, perhaps because those prey were individually more conspicuous [63]. Albins [30] demonstrated experimentally that, unlike the native grouper *Cephalopholis fulva*, the invasive Pacific lionfish *Pterois volitans* extirpated native prey fishes on patch reefs in the Bahamas. All these studies concur with theory predicting that either selective predation on rare species or intense non-selective predation can reduce local prey diversity (review by Hixon [1112]). The importance of counting all species on a reef in demonstrating such patterns cannot be overemphasized. Statistically, one would expect fewer species to be present where fewer individuals occur (rarefaction), and given that predation reduces prey abundance, mere correlation may not demonstrate causation due to predation [e.g. 2429]. Despite earlier hypotheses that predation may prevent competitive exclusions among reef fishes [e.g. 2459], there are presently no published studies indicating that predation increases the local diversity of fishes on coral reefs beyond being a source of regulating density dependence for some species.

Predation does not occur in isolation of other interactions, such as mutualism and competition, as well as the modifying effects of prey refuges, the combination of which structures prey communities [1115]. Working in French Polynesia, Holbrook *et al*. [1159] studied interactions between predation and mutualism involving reef fishes. Here, excretions by resident fishes fertilize pocilloporid corals, which in turn provide prey refuges for those fishes, a mutualism. Larger coral heads support a greater abundance of fish and number of species. However, when smaller coral heads are occupied by the predatory hawkfish *Paracirrhites arcatus*, recruitment by smaller fishes declines, thereby inhibiting the fish–coral mutualism and reducing coral growth.

Predation can also interact with competition in structuring ecological communities [reviews by 1009,2352]. The most common form of this interaction in coral reef fishes is predation causing competition for limited spatial prey refuges, as reviewed above [e.g. 846,1116,1155]. The key question is whether such interactions among reef fishes at the population level (reviewed by Hixon [1121]) have community-level consequences. To date, the factorial predator × competitor experiments of Almany [56,57,58,59, reviewed above] are the closest we have to the required experimental design. These studies documented interactive, species-specific effects of resident predators and competitors, such that experimental communities (residents plus subsequent recruits) eventually differed detectably among treatments. Because mortality is greatest in the few weeks following settlement [61,404], these differences would likely persist through time, yet multiyear experiments are required to test this conclusion. Predation-competition interactions were also examined in a study of "intraguild predation", which occurs when multiple predators that consume the same prey also consume each other [1998]. In French Polynesia, *P. arcatus*, a trapezid crab, and the planktivorous damselfish *Dascyllus flavicaudus* inhabit colonies of pocilloporid corals together. The hawkfish, the crab (anecdotally), and various transient mesopredators (e.g. groupers, jacks, emperors) consume the damselfish, and the transient predators consume all three species inhabiting the coral heads. In a series of field experiments, Schmitt *et al*. [2282] found that, although the species inhabiting the coral competed for spatial refuges from the transient predators, the predators inhabiting the corals were stronger competitors for space with the damselfish than they were competitors for food with transient predators. Overall, habitat complexity was sufficient to prevent substantial indirect community-level effects, such as trophic cascades, in this assemblage.

"Trophic cascades" occur when high abundance or efficiency of top predators results in reduced abundance at the next lower

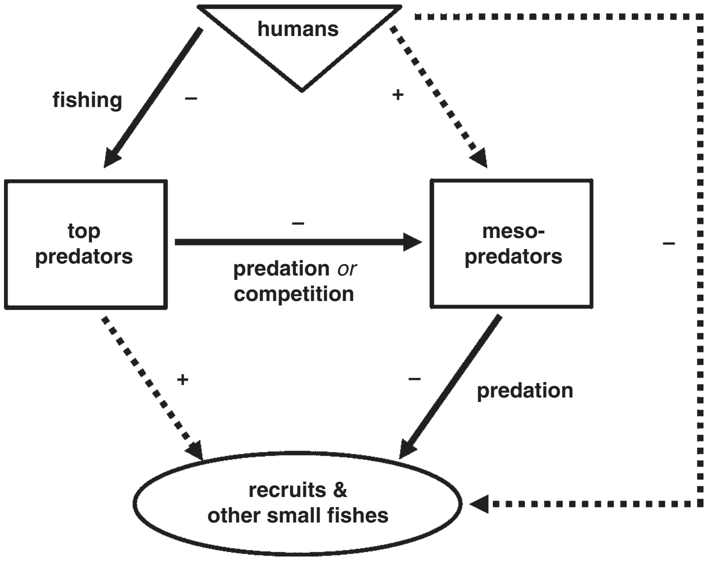


Figure 5.5 Trophic cascade. Top predators (large piscivores) negatively affect piscivorous mesopredators, which consume recruits and other small fishes, such that top predators indirectly benefit small prey fishes (lower left dashed arrow). Overfishing of top predators allows mesopredators to proliferate, a positive indirect effect known as "mesopredator release". In doing so, humans indirectly benefit mesopredators (upper right dashed arrow) yet indirectly reduce recruitment (rightmost dashed arrow). Modified from Stallings [2407].

trophic level, which in turn causes increased abundance in the next lower trophic level, and so forth (review by Terborgh and Ester [2472]). Such cascades are typically detected when the abundance of top predators is reduced by fishing (i.e. predation by humans), which allows their mesopredator prey to proliferate (i.e. mesopredator release), resulting in subsequent indirect effects that cascade from level to level down the food web (review by Baum and Worm [153]). In a large and effective marine reserve in the Bahamas (Exuma Cays Land and Sea Park), Lamb and Johnson [1412] found evidence for a cascade involving three trophic levels of fishes: sharks and large groupers, mesopredators, and planktivores. In an experimental study elsewhere in the Bahamas, Stallings [2406,2407] also found that the large grouper *Epinephelus striatus* negatively affected foraging by smaller mesopredatory groupers (*Cephalopholis cruentata* and *C. fulva*), which in turn enhanced recruitment of the fish prey of the smaller groupers (Figure 5.5). The interactions between the large grouper and the smaller groupers were largely nonlethal, so this cascade was mostly behaviorally mediated, as hypothesized for Pacific reefs by Madin *et al.* [1558,1559]. A similar trophic cascade was revealed by overfishing of large groupers in Belize [1782]. However, in the same marine reserve studied by Lamb and Johnson [1412], Mumby *et al.* [1775,1776] concluded that overfishing of grouper outside the reserve did not initiate a trophic cascade that benefited parrotfish prey because parrotfishes were also overfished. Instead, both groupers and parrotfishes were more abundant inside the reserve, apparently resulting in less seaweed (prey of parrotfishes) and more coral cover (competitors of seaweeds) there (see also [722,1632,1861,1862]). Clearly, if overfishing of all trophic levels occurs, then trophic cascades cannot occur.

Coral reef fishes are often subjected to intensive fishing [652,656,867,2117,2257,2408,2422]. As uncontrolled manipulations, overfishing piscivores can potentially reveal the role of predation in marine communities [1081], including on coral reefs [2118,2548], yet it is important to keep in mind that correlation does not necessarily reveal causation. Comparisons of reefs near and far from human habitation, thus providing a geographical gradient of fishing intensity, have shown contrasting patterns. In Fiji, Jennings and Polunin [1244] found that, although there was a clear gradient in fishing intensity, inversely correlated with the abundance of large piscivores (groupers and snappers), no gradient was evident in the biomass or diversity of potential prey fishes that were not targeted by fishing (invertivores and herbivores). The authors concluded that predation did not play an important role in structuring these reef fish communities. In both the Hawai‘ian Archipelago [867] and the mid-Pacific Line Islands [652,2257,2422], fish communities on isolated reefs where fishing is minimal are dominated by large top-level piscivores, whereas those on reefs near concentrations of humans and subject to intensive fishing and other sources of reef degradation are dominated by smaller invertivorous and herbivorous fishes. In extreme cases, the pyramid of biomass can be inverted on relatively pristine reefs [2261]. As in Fiji, patterns in the Line Islands suggest no evidence of trophic cascades; even though prey fishes were smaller where top predators were abundant, there was no consistent trend in prey abundance [2199]. However, body mass adjusted for length and liver mass (measures of physiological condition) of several prey species were consistently lower at reefs with higher predator abundance [2602]. These patterns were attributed to the increased risk of predation on unfished reefs inhibiting foraging by prey-sized fishes. On the Great Barrier Reef, comparisons inside versus outside marine reserves showed that the biomass of the grouper *Plectropomus leopardus* was 3–4 times higher inside, whereas the density of known prey fishes inside reserves was only half that outside, suggesting a substantial effect of predation on prey abundance and perhaps community structure [957].

In summary, where severe overfishing does not occur, piscivores have strong top-down effects on reef fish community structure. Documented patterns include priority effects, where the presence of piscivores affects subsequent recruitment and assemblage composition, and diversity effects, where intensive predation may reduce local diversity and even extirpate rare species. Predation occurring simultaneously with other interactions, especially competition and mutualism, can have unpredictable indirect effects on community structure. High abundance of top predators can cause trophic cascades, as well as reduce the physiological condition of prey fishes via the risk of predation reducing prey foraging opportunities.

SYNTHESIS AND FUTURE DIRECTIONS

Combining Hixon's [1114] previous review with this updated overview, the generalities listed at the beginning of this chapter can now be expanded:

1. Coral reef piscivores and their prey display a broad variety of morphologies and behaviors associated with both capture and evasion.
2. Despite widespread overfishing of coral reefs, piscivory is nonetheless ubiquitous because there is a broad diversity of mesopredators, many of which are not targeted by most fisheries (except in extreme cases of Malthusian overfishing).
3. The intensity of predation, especially on new recruits, is substantial and may often regulate local population sizes.
4. High levels of piscivory may reduce local species diversity of prey fishes and extirpate locally rare species.
5. Piscivory interacts in complex ways with prey refuge space, competition, mutualism, and other processes in structuring communities of coral reef fishes.
6. Overfishing – either directly by humans or indirectly by introduced piscivores – can cause mesopredator release and reveal trophic cascades.

The third and fourth generalities may appear to contradict each other, yet do not. Due to the typically high diversity of both predator and prey species on any particular reef, predation is "diffuse", i.e. many predator species consume each prey species [1114]. Therefore, all piscivore species combined may simultaneously regulate local populations of some species and extirpate other species. A hypothesis worthy of further exploration is that high concentrations of common and rare prey species combined stimulate an aggregative (and possibly type 3 functional) response by schooling piscivores that results in local population regulation of the more abundant prey species, yet occasional extirpation of locally rare species that may incidentally become disproportionately targeted. Global persistence of those rare species may be ensured on other reefs with few predators, sufficient prey refuges, or other mechanisms fostering locally high abundance.

The fifth and sixth generalities above are likely to be a fertile ground for future studies relevant to both fisheries management and conservation biology. Consider two examples. First, as reefs continue to degrade due to coral bleaching, ocean acidification, and other human-generated assaults, predator–prey interactions are likely to change as habitat quality and structure shift [514]. Second, the evidence for trophic cascades among reef fishes is thus far inconsistent (see above). It is important to understand the factors that both facilitate and inhibit trophic cascades because this phenomenon can be indicative of phase shifts that are deleterious from a human perspective and often difficult for management to reverse [e.g. 420,855,856,857]. High predator diversity is predicted to decrease the likelihood of trophic cascades [2344], so it is important to understand whether and how food-web simplification caused by overfishing coral reef piscivores can lead to trophic cascades and phase shifts.

Regarding behavioral ecology, we have much more to learn about short-term behavioral responses of different predators to prey of different densities and relative mobilities, including both functional and aggregative responses. At the same time, even the basic natural history of most reef fish mesopredators remains glaringly undocumented and worthy of study. Additionally, most studies of reef fishes occur during midday, even though most predatory behavior occurs at dawn and dusk, so further study during crepuscular hours is warranted.

Regarding population ecology, the current frontier is at the scale of marine metapopulations: linking rates of larval retention and connectivity with demographic rates of both predators and prey among isolated reefs [86,2664]. Only then can long-term linkages between predator and prey population dynamics – reciprocal numerical responses [1055] – be adequately addressed. Additionally, the ecological effects of parasites as micropredators of reef fishes remain an understudied topic [but see 841,999].

Regarding community ecology, we have only begun to explore how suites of piscivore species interact with suites of prey species, as mediated by the abiotic environment, habitat structural complexity, and non-predatory interactions within and between species. Especially fascinating are potential positive (synergistic, cooperative) and negative (competitive, amensal) interactions among different types of piscivores – schooling transients (such as jacks), stalkers (such as groupers), and ambushers (such as frogfishes) – and how they collectively affect prey species diversity at various scales (alpha, beta, and gamma). Combined with studies of larval dispersal, such multifactorial studies will ultimately provide understanding of the metacommunity ecology of reef fishes [2668].

At the intersection of behavioral, population, and community ecology, the nonlethal effects of predators – how the risk of predation alters prey foraging and reproduction, and consequently, prey population dynamics and predator–prey community structure – is ripe for additional studies in reef fishes. Indeed, such effects are the focus of much current research in terrestrial and freshwater predator–prey systems, be they called nonlethal effects [1495], the ecology of fear [359], trait-mediated interactions [2033], risk effects [589], or nonconsumptive effects [1941]. Currently in vogue are studies of spatio-temporal variation in the habitat distribution of predators and prey, known as the "landscape of fear" [1424], as well as the ecological effects of protracted physiological stress on prey ecology [506]. Examples of studies of risk of predation in reef fishes include effects of habitat structure

[2111] and water clarity [1431], behaviorally mediated trophic cascades [1558,1559,2406,2407], and prey flight initiation distances [1235].

Another question for future research regards the circumstances under which introduced piscivores become invasive, i.e. negatively affect native prey [see 2112]. The severity of the invasion of Atlantic coral reefs by Pacific lionfish caught the scientific community off guard [reviews by 29,568,570]. Beyond intentional introductions in the past [2070], the aquarium trade is now perhaps the most efficient vector for introducing alien coral reef fishes [2213,2303]. With the rate of marine species invasions increasing dramatically, are other invasions by coral reef piscivores imminent and can they be prevented, or at least moderated? Presently, the question of whether native coral reef piscivores will provide biotic resistance to the lionfish invasion is unresolved [220,1012,1781].

Ultimately, native coral reef predators are prized by fisheries, just as they simultaneously play important roles in regulating populations and structuring communities of coral reef fishes. The key question is whether humans will learn to enhance the ecological resilience of coral reef ecosystems by conserving coral reef piscivores across trophic levels [1637,2244]. Recent history indicates that the only realistic choice regarding larger reef piscivores is between severe overexploitation [656,2117,2408] or effective networks of large marine reserves, which are at present woefully rare [1736].

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