To Sally Lyons Brown
for her vision
and support

Slow down. . . .
You may be going the wrong way!

Hixon, M.A. 2004. How do so many species of coral-reef fishes coexist? Pages 216-217 in G.C. Ray and J. McCormick-Ray. Coastal-Marine Conservation: Science and Policy. Blackwell Science Limited; Malden, Massachusetts.

Coastal-Marine Conservation:

Science and Policy

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indicates a region-wide cause, although for reasons that remain unclear. Nationally, the degradation of coral reefs and reduction of reef inhabitants lessens attractions for tourists, reduces habitat quality for commercially important fishes, and exposes adjacent islands to forces of erosion. Locally, reefs are susceptible to pollution, sedimentation, anchoring of boats, excessive use by divers, and coastal development. Additionally, commercial and sport fisheries and tourists have removed significant segments of the reef community, especially fishes, corals, and shells. These effects, taken together, may increase stress on corals, which some scientists suggest might lead to loss of zooxanthellae and increased susceptibility to disease. Furthermore, removal by fishing of herbivorous fishes that feed on algae may result in seaweed overgrowth, which prevents coral recruitment. Thus, changes in the fish community can cascade to the coral community.

Caribbean coral reefs have waxed and waned for many thousands of years, surviving the vicissitudes of climate and sea level, and have recovered each time. High species diversity suggests that species, both animals and plants, provide fundamental roles in reef ecology, and helps explain reef resiliency. Fishes, for example, exhibit a spectacular variety of sizes, colors, shapes, life histories, and ecology. Many fishes depend solely (are obligate) on reef environments, and others are transients. Some form extensive schools, and some are solitary and territorial. Many are conspicuous, but as many are reclusive, particularly small gobies and blennies that hide in the nooks and crannies of the reef's rough and uneven habitat. However, explanations for reef diversity remain hypothetical (Box 7.4).

Reefs and their biota are most valuable to the Bahamas economy as an attractor for tourism. Reef fishes are especially sought for food and pleasure; reef-inhabiting species (e.g., lobsters and groupers) and seagrass dwellers (e.g., conch) supply a large portion of food for the Bahamas, as well as income from tourism. Nevertheless, knowledge of functional relationships among the biota and interdependencies with surrounding seascapes is poor. Presently, coral reefs are globally recognized as a research priority, and many nations, including the Bahamas, have established protected areas for them. The Bahamas forbids collecting of live coral, yet has no overall coral-reef conservation strategy. Further, protected areas that include coral reefs, but fail to include surrounding environments, are insufficient for conservation.

7.3.2 Nassau grouper, *Epinephelus striatus*

The Nassau grouper is the Bahamas' most valuable fish and typifies issues of fisheries and reef conservation. This species is listed as endangered by the International Union for the Conservation of Nature and Natural Resources (IUCN), but has not yet been listed under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). As a top

Box 7.4 How do so many kinds of coral-reef fishes co-exist?

Mark A. Hixon

Coral-reef fishes compose the most speciose assemblages of vertebrates on Earth. The variety of shapes, sizes, colors, behavior, and ecology exhibited by reef fishes is truly amazing. Reef fishes are dominated by about 30 families, mostly the perciform chaetodontoids (butterflyfish and angelfish families), labroids (damselfish, wrasse, and parrotfish families), gobioids (gobies), and acanthuroids (surgeonfishes). Worldwide, about 30% of the roughly 15 000 described species of marine fishes inhabit coral reefs at some stage of their life cycle. Hundreds of species may coexist on the same reef at one time or another.

A key question for the conservation of coral-reef fishes is: How do so many species coexist? This question is important because conservation requires the identification and protection of natural mechanisms that maintain high species diversity. It is best answered at the level of the ecological guild, which is defined as a group of species that use the same general suite of resources (food, space, etc.) in the same general habitat, such as butterflyfishes that feed on coral polyps inhabiting a reef slope. The central issue is that, as population sizes of species within a community grow to levels where resources are in short supply, one or a few species within each guild should outcompete other species, thereby reducing local species diversity. What prevents such competitive exclusions?

Four hypotheses provide clues to the question of coexistence of reef fishes (Fig. 1). Present information both corroborates and refutes each hypothesis at different reefs, suggesting that all four hypotheses may be valid at some time and place.

A review of the bipartite life cycle of reef fishes is necessary before examining these hypotheses. Many reef fishes (exceptions are gobies, blennies, pipefishes, and a few others) are broadcast spawners, whose gametes and larvae undergo pelagic dispersal, with varying degrees of local retention. Typically, after about a month, late-stage larvae settle in reef or near-reef habitats. Recruitment is the measure of settlement, estimated by counts of newly settled fish. The accuracy by which recruitment actually measures settlement is a major issue in distinguishing among these hypotheses.

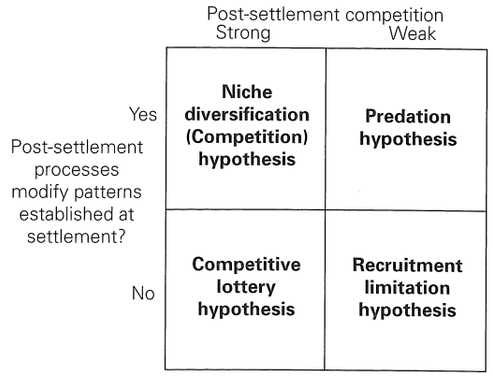

Fig. 1 Four hypotheses explaining the coexistence of many species of coral-reef fishes. Modified from G. Jones, in Sale (1991).

The niche diversification and competitive lottery hypotheses both assume that competition is strong among juveniles and adults on the reef, so that coexistence of species is maintained despite the risk of competitive exclusion. The basic idea for the former (sometimes called the "competition hypothesis") is that high overlap in resource use within a guild, combined with competition between the constituent species, selects for lower overlap or diversification of niches. This scenario results in resource partitioning, whereby species within a guild that overlap greatly in diet tend to forage in slightly different microhabitats; alternatively, species that forage in the same location may have slightly different diets. However, a description of resource partitioning provides only a pattern, not the process that caused that pattern.

Some guilds seem to coexist despite an apparent absence of resource partitioning. For example, territorial, herbivorous damselfishes are highly aggressive toward each other, and if all suitable habitat space is occupied by territories, how do such species coexist without niche diversification? The competitive lottery hypothesis (sometimes called the equal chance hypothesis) offers a relatively complex explanation, based on several restrictive assumptions. First, there has to be a strong prior residency effect, whereby a fish that finds a place to live on the reef can successfully defend its territory against all comers. Second, late-stage larvae of all species have to be available to settle in any space that opens on the reef, be it by the death of a territorial fish or by the creation of new habitat space by storms or other disturbances. These larvae are analogous to lottery tickets, in that whichever individual finds the open space first is the winner of that space. Under these conditions, it is proposed that no single species can gain the upper hand in the competition for living space, despite the lack of resource partitioning. In reality, the rate of competitive exclusion may only be slowed rather than prevented, since no two species are truly equal, by definition.

The remaining two hypotheses both assume that competitive exclusion of species is not an issue because some factor keeps population sizes below levels where resources become limiting. Some fish populations have low larval settlement rates, so that living space is not as limiting as the former hypotheses assume. The recruitment limitation hypothesis proposes that low larval supply prevents juvenile and adult populations from reaching levels where substantial competition occurs, in which case post-settlement mortality is density-independent – that is, occurs at a constant proportional rate. Unfortunately, the definition of recruitment limitation has changed through time, so that recruitment is sometimes measured up to months past settlement, and early post-settlement processes are thus ignored. In fact, shortly after settlement, many reef fishes undergo density-dependent mortality in which case mortality rate increases with local population size.

Finally, as an alternative to recruitment limitation, the predation hypothesis suggests that competitive exclusion is prevented by predation rather than low larval supply. In fact, both density-dependent and density-independent predation on newly settled reef fishes, which are typically less than 2 cm long, is usually severe. Many different species of generalized reef fishes and macroinvertebrates – mostly species not normally considered piscivorous – have been found to consume new settlers. There is mounting observational and experimental evidence that such intense predation keeps populations of many reef fishes in check, precludes competitive exclusions, and thereby maintains high local species diversity.

The picture that emerges from the past several decades of research on coral-reef fishes is that a variety of factors maintain high species diversity, and that the relative importance of these factors varies from system to system. This situation indicates the truth of John Muir's admonition that "when we try to pick out anything by itself, we find it hitched to everything else in the universe." Such complexity suggests that the conservation of coral-reef fishes can be best accomplished by preserving entire systems from direct human impact in fully protected marine reserves.

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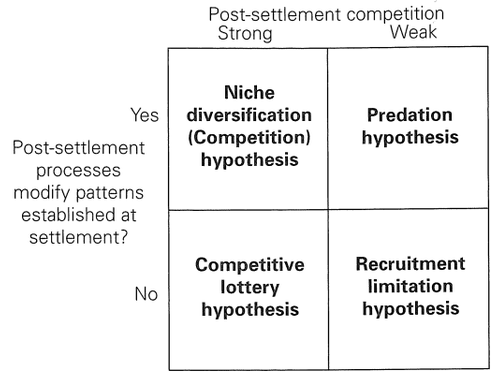

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