

MARINE CONSERVATION

SCIENCE, POLICY, AND MANAGEMENT

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Box 5.2 How do so many kinds of coral-reef fishes coexist?

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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 8,000 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. B5.2.1). 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.

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

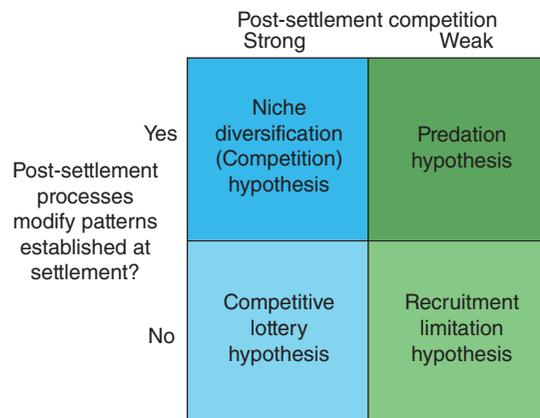


Fig. B5.2.1 Four hypotheses explaining the coexistence of many species of coral-reef fishes. From Jones GP (1991). Postrecruitment processes in the ecology of coral reef fish populations: a multifactorial perspective. In *The Ecology of Fishes on Coral Reefs* (ed. Sale PF), pp. 294–328. Academic Press, San Diego, CA.

(Continued)

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.

Sources: Jones (1991); Polunin and Roberts (1996); Sale (1991, 2002)

during one lifetime (Fig. 5.2); each form displays unique traits in food preference, habitat, etc. (as is also true for most terrestrial invertebrates and fishes). Such life-cycle diversity indicates unique ways that marine life has evolved, suggesting a correspondingly diverse number of roles that each kind of organism plays within its community. Size is yet another measure of diversity, broadly represented in the ocean, where species are classified as: microfauna, 0.001–0.1 mm in length or breadth (bacteria are even smaller); benthic meiofauna, <0.5 mm; benthic macrofauna, >0.5 mm; and megafauna, very large organisms. Each size class fulfills different functions (see also Ch. 9, Section 9.3.2.2).

Biodiversity is also a characteristic of each environment. The benthos is higher in biodiversity than pelagic systems, and coastal areas are higher than the open ocean (Gray, 1997). A host of different species lives within the sediment (infauna), on sediment (epifauna), near the bottom (demersal), or on benthic structures. Near coasts, coral reefs have high biodiversity. However, equating different climatic zones to biodiversity can be misleading; the tropics have high coral and fish species diversity, but temperate and polar regions hold the most diversity of pinnipeds and penguins. Thus, each environment has a biodiversity "signature," both in kind (what species live there) and number (abundance).

5.3.2 Measuring biodiversity

A central problem for biodiversity conservation is assessment. Species assessment depends on indices, for which statistical generalizations are subject to considerable uncertainty. These include: (i) *richness*, the numbers of species within a sampling unit; (ii) *abundance*, the numbers of individuals within that unit; and (iii) *evenness*, a measure of the relative abundances of all species present. These three measures may be applied across three geographical scales: (a) *alpha* diversity for within-area diversity; (b) *beta* diversity for between-area diversity; and (c) *gamma* diversity for the relative numbers of species within and among large geographical regions (Roff and Zacharias, 2011). A serious drawback for applying these measures is sampling error; that is, diversity indices rarely include all or even most taxa within a specified unit, especially for marine systems, which are difficult to sample. New methods have recently become available that allow diversity indices to be drawn from data consisting simply of species lists, arising from unknown or uncontrolled sampling effort (Ch. 9, Section 9.3.2).

Two criteria commonly used in conservation are species richness and endemism, used to identify "hot spots" of diversity as candidates for protected areas. In this case, "richness"