Hixon, M.A. 2001. Coral-reef fishes. Pages 538-542 in J.H. Steele, K.K. Turekian, & S.A. Thorpe (eds.) Encyclopedia of Ocean Sciences. Academic Press; London, U.K.

FISH

Coral-Reef Fish

M. A. Hixon, Department of Zoology, Oregon State University, Corvallis, OR 97331-2914, USA

doi:10.1006/rwos.2001.0015

Diversity, Distribution, and Conservation

0001 Coral-reef fishes comprise the most speciose assemblages of vertebrates on the Earth. The variety of shapes, sizes, colors, behavior, and ecology exhibited by reef fishes is amazing. Adult body sizes range from gobies (Gobiidae) less than 1 cm in length to tiger sharks (Carcharhinidae) reportedly over 9 m long. It has been estimated that about 30% of the some 15 000 described species of marine fishes inhabit coral reefs worldwide, and hundreds of species can coexist on the same reef. Taxonomically, 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).

0002 The latitudinal distribution of reef fishes follows that of reef-building corals, which are usually limited to shallow tropical waters bounded by the 20°C isotherms (roughly between the latitudes of 30°N and S). The longitudinal center of diversity is the Indo-Australasian archipelago of the Indo-Pacific region. Local patterns of diversity are correlated with those of corals, which provide shelter and harbor prey. There is a high degree of endemism in reef fishes, especially on more isolated reefs, and many species (about 9%) have highly restricted geographical ranges.

0003 The major human activities that threaten reef fishes include overfishing, especially by destructive fishing practices, and habitat destruction, including both local effects near human population centers and the ongoing global decline of reefs due to coral bleaching. Worldwide, about 31% of coral-reef fishes are now considered critically endangered and 24% threatened. The major solution for local conservation is 'no-take' marine protected areas, which have proven effective in replenishing depleted populations.

Fisheries

Where unexploited by humans, coral-reef fishes typically exhibit high standing stocks, the maximum being about $240\,t\,km^{-2}$ (about $24\,t\,C\,km^{-2}$). High standing crops reflect the high primary productivity of coral reefs, often exceeding $10^3\,gC\,m^{-2}\,y^{-1}$, much of which is consumed directly or indirectly by fishes. Correspondingly, reported fishery yields have reached $44\,t\,km^{-2}\,y^{-1}$, with an estimated global potential of $6M\,t\,y^{-1}$. These fisheries provide food, bait, and live fish for the aquarium and restaurant trades. However, the estimated maximum sustainable yield from shallow areas of actively growing coral reefs is around $20–30\,t\,km^{-2}\,y^{-1}$, so many reefs are clearly overexploited. Indeed, overfishing of coral reefs occurs worldwide, due primarily to unregulated multispecies and multigear exploitation in developing nations. Few and inadequate stock assessments and other quantitative fishery analyses, susceptibility of fish at spawning aggregations (see below), and destructive fishing practices (including the use of dynamite, cyanide, and bleach) are contributing factors. In the Pacific, some 200–300 reef-fish species are taken by fisheries, about 20 of which comprise some 75% of the catch by weight. As fishing intensifies in a given locality, large fishes, especially piscivores (see below), are typically depleted first, followed by less preferred, smaller, and more productive planktivores and benthivores. (Fishing is naturally inhibited in some regions by ciguatera fish poisoning, caused by dinoflagellate toxins concentrated in the tissues of some reef fish.) The indirect effects of overfishing include the demise of piscivores perhaps enhancing local populations of prey species, and the demise of urchin-eating species (such as triggerfishes, Balistidae) and various herbivorous fishes providing predatory and competitive release, respectively, of sea urchins, which then overgraze and bioerode reefs. 0004

Morphology

A typical perciform reef fish (virtually an oxymoron) is laterally compressed, with a closed swimbladder and fins positioned in a way that facilitates highly maneuverable slow-speed swimming. Compared to more generalized relatives, reef fish have a greater proportion of musculature devoted to both locomotion and feeding. Their jaws and pharyngeal apparatus are complex and typically well developed for 0005 suction feeding of smaller invertebrate prey, with tremendous variation reflecting a wide variety of diets. For example, most butterflyfish (Chaetodontidae) have forceps-like jaws that extract individual polyps from corals, many damselfish (Pomacentridae, e.g., genus *Chromis*) have highly protrusible jaws that facilitate pipette-like suction feeding of zooplankton, and parrotfishes (Scaridae) have fused beak-like jaw teeth and molar-like pharyngeal teeth enabling some species to excavate algae from dead reef surfaces. (This excavation and subsequent defecation of coral sand can bioerode up to 9 kg of calcium carbonate per square meter annually.) Tetraodontiform reef fishes typically swim relatively slowly with their dorsal and anal fins, and consequently are morphologically well defended from predation by large dorsal–ventral spines (triggerfishes, Balistidae), toxins (puffers, Tetraodontidae), or quill-like scales (porucupinefishes, Diodontidae). The latter two families have fused dentition which is well adapted for consuming hard-shelled invertebrates.

0006 Diurnal reef fishes are primarily visual predators. Visual acuity is high and retinal structure indicates color vision. Coloration is highly variable, ranging from cryptic to dazzling. Bright 'poster' colors are hypothesized to serve as visual signals in aggression, courtship, and other social interactions. Sexually dimorphic coloration is associated with haremic social systems (see below). Nocturnal reef fishes are either visually oriented, having relatively large eyes (e.g., squirrelfishes, Holocentridae), or rely on olfaction (e.g., moray eels, Muraenidae).

Behavior

0007 Overt behavioral interactions between coral-reef fishes include mutualism (when both species benefit), interference competition (often manifested as territoriality), and predator–prey relationships.

Mutualism

0008 Three of the best-documented cases of mutualism occur in reef fishes. 'Cleaning symbiosis' occurs when small microcarnivorous fish consume ectoparasites or necrotic tissue off larger host fish, which often allow cleaners to feed within their mouths and gill cavities. The major cleaners are various gobies (Gobiidae) and wrasses (Labridae). Some of the cleaner wrasses are specialists that maintain fixed cleaning stations regularly visited by hosts, which assume solicitous postures. The interaction is not always mutualistic in that cleaners occasionally bite their hosts, and some saber-tooth blennies (Blenniidae) mimic cleaner wrasse and thereby parasitize host fish. Anemonefishes (Pomacentridae, especially the genus *Amphiprion*) live in a mutualistic association with several genera of large anemones. By circumventing discharge of the cnidarian's nematocysts, the fish gain protection from predators by hiding in the stinging tentacles of the anemone. In turn, the fish defend their home from butterflyfishes and other predators that attack anemones. However, some host anemones survive well without anemonefish, in which case the relationship is commensal rather than mutualistic. Finally, some gobies cohabit the burrows of digging shrimp. The shrimp provides shared shelter and the goby alerts the shrimp to the presence of predators.

Territoriality

The most overt form of competition involves terri- 0009
toriality or defense of all or part of an individual's home range. Many reef fishes behave aggressively toward members of both their own and other species, but the most obviously territorial species are benthic-feeding damselfishes (Pomacentridae, e.g., genus *Stegastes*). By pugnaciously defending areas about a meter square from herbivorous fishes, damselfish prevent overgrazing and can thus maintain dense patches of seaweeds. These algal mats serve as a food source for the damselfish as well as habitat for small juvenile fish of various species that manage to avoid eviction. At a local spatial scale, the algal mats can both smother corals as well as maintain high species diversity of seaweeds. By forming dense schools, nonterritorial herbivores (parrotfishes and surgeonfishes) can successfully invade damselfish territories.

Piscivory and Defense

Predation is a major factor affecting the behavior 0010
and ecology of reef fishes. There are three major modes of piscivory. Open-water pursuers, such as reef sharks (Carcharhinidae) and jacks (Carangidae), simply overtake their prey with bursts of speed. Bottom-oriented stalkers, such as grouper (Serranidae) and trumpetfishes (Aulostomidae), slowly approach their prey before a sudden attack. Bottom-sitting ambushers, such as lizardfishes (Synodontidae) and anglerfishes (Antennariidae), sit-and-wait cryptically for prey to approach them. The vision of piscivores is often suited for crepuscular twilight, when the vision of their prey is least acute (being adapted for either diurnal or nocturnal foraging). Hence, many prey species are inactive during dawn and dusk, resulting in crepuscular 'quiet periods' when both diurnal and nocturnal

species shelter in the reef framework. (Parrotfishes may further secrete mucous cocoons around themselves at night, and small wrasses may bury in the sand.) Otherwise, prey defensive behavior when foraging or resting typically involves remaining warily near structural shelter and shoaling either within or among species. Associated with day–night shifts in activity are daily migrations between safe resting areas and relatively exposed feeding areas. Caribbean grunts (Haemulidae) spend the day schooling inactively on reefs, and after dusk migrate to nearby seagrass beds and feed. Reproducing reef fishes may avoid predation by spawning (in some combination) offshore, in midwater, or at night. Spawning during ebbing spring tides that carry eggs offshore or guarding broods of demersal eggs further defends propagules from reef-based predators. Subsequent settlement of larvae back to the reef which occurs mostly at night, is also an apparent antipredatory adaptation.

Reproduction

Social Systems and Sex Reversal

0011 The best-studied examples of highly structured social systems in reef fishes are the harems of wrasses and parrotfishes. Typically, these fish are born as females that defend individual territories or occupy a shared home range. A larger male defends a group of females from other males, thereby sequestering matings. When the male dies, the dominant (typically largest) female changes sex (protogyny) and becomes the new harem master. At high population sizes, some fish may be born as males, develop huge testes, resemble females, infiltrate harems, and sneak spawnings with the resident females. Spatially isolated at their home anemones, anemonefishes have social systems in which the largest individual is female, the second largest is male, and the remaining fish are immature (i.e., monogamy). Upon the death of the female, the male changes sex (protandry) and the behaviorally dominant juvenile fish matures into a male. Simultaneous hermaphroditism occurs among a few sparids and serranine sea basses. These fish have elaborate courtship behaviors during which individuals switch male and female roles between successive pair spawnings. Regardless of the broad variety of mating systems found in reef fishes, each individual behaves in a way that maximizes lifetime reproductive success.

Life Cycle

0012 The typical bony reef fish has a bipartite life cycle: a pelagic egg and larval stage followed by a demersal (bottom-oriented) juvenile and adult stage. Most bony reef fishes broadcast spawn, releasing gametes directly into the water column where they are swept to the open ocean. Smaller species spawn at their home reefs and some larger species, such as some grouper (Serranidae) and snapper (Lutjanidae), migrate to traditional sites and form massive spawning aggregations. Gametes are released during a paired or group 'spawning ascent' followed by rapid return to the seafloor. Exceptions to broadcast spawning include demersal spawners that brood eggs until they hatch, either externally (e.g., egg masses defended by damselfishes) or internally (e.g., mouthbrooding cardinalfishes, Apogonidae), and a few ovoviviparous or viviparous species that give birth to well-developed juveniles (including reef sharks and rays). Annual fecundity of broadcast spawners ranges from about 10 000 to over a million eggs per female. Spawning is weakly seasonal compared to temperate species, typically peaking during summer months but not strongly related to any particular environmental variable. Lunar and semilunar spawning cycles are common. These are presumably adaptations to transport larvae offshore away from reef-based predation, to maximize the number of settlement-stage larvae returning during favorable conditions that vary on lunar cycles, or to benefit spawning adults in some way.

Little is known about the behavior and ecology of 0013
reef-fish larvae. Duration of the pelagic larval stage ranges from about 9 to well over 100 days, averaging about a month. Larval prey include a variety of small zooplankters. Comparisons of fecundity at spawning to subsequent larval settlement back to the reef suggest that larval mortality is both extremely high and extremely variable, apparently due mostly to predation. Patterns of endemism, settlement to isolated islands, and limited data tracking larvae directly suggest that there is considerable larval retention at the scale of entire islands. Later-stage larvae are active swimmers and may control their dispersal by selecting currents among depths. The overall reproductive strategy is apparently to disperse the larvae offshore from reef-based predators, but then to retain them close enough to shore for subsequent settlement.

Settlement, the transition from pelagic larva to 0014
life on the reef (or nearby nursery habitat), occurs at a total length of about 8 mm to about 200 mm. Larger larvae are either morphologically distinct (e.g., the acronurus of surgeonfishes) or essentially pelagic juveniles (e.g., squirrelfishes and porcupinefishes). Choice of settlement habitat is apparent in some species, and both seagrass beds and mangroves can serve as nursery habitats. Some wrasses

larvae bury in the sand for several days before emerging as new juveniles. There is typically weak metamorphosis during settlement involving the growth of scales and onset of pigmentation. Estimates of settlement are generally called 'recruitment' and are based on counts of the smallest juveniles that can be found some time after settlement. Once settled, most reef fish are thought to live less than a decade, although some small damselfish live at least 15 years.

Ecology

0015 Coral-reef fishes are superb model systems for studying population dynamics and community structure of demersal marine fishes because they are eminently observable and experimentally manipulable *in situ*.

Population Dynamics

0016 Because reefs are patchy at all spatial scales and reef fish are largely sedentary, coral-reef fishes form metapopulations: groups of local populations linked by larval dispersal. Many local populations are demographically open, such that reproductive output drifts away and is thus unrelated to subsequent larval settlement originating from elsewhere. Ultimately, the degree of openness depends on the spatial scale examined. For example, anemonefish populations are completely open at the scale of each anemone, may be partially closed at the scale of an oceanic island, and mostly closed at the scale of an archipelago. It is clear that variability in population size is driven by variation in recruitment due to larval mortality (and perhaps spawning success). Recruitment varies considerably at virtually every spatial and temporal scale examined. The mechanisms naturally regulating populations are less clear, but are probably twofold. First, given that density-dependent growth is common and that there is a general exponential relationship between body size and egg production in fish, density-dependent fecundity is likely. Second, early postsettlement mortality is often density-dependent, and has been demonstrated experimentally to be caused by predation.

Community Structure

0017 Due to high local species diversity, reef-fish communities are complex. There are about five major feeding guilds, each containing dozens of species locally (with approximate percentage of total fish biomass): zooplanktivores (up to 70%), herbivores (up to 25%), and piscivores (up to 55%), with the remainder being benthic invertebrate eaters or detritivores. The benthivores can be further subdivided based on prey taxa (e.g., corallivores) or other categories (e.g., consumers of hard-shelled invertebrates). Grunts that migrate from reefs at night and feed in surrounding seagrass beds subsequently return nutrients to the reef as feces. There is also considerable consumption of fish feces by other fish on the reef. Fishes thus contribute substantially to nutrient trapping (via planktivory and nocturnal migration) and recycling (via coprophagy and detritivory) on coral reefs. Within each feeding guild, there is typically resource partitioning: each species consumes a particular subset of the available prey or forages in a distinct microhabitat. Communities are also structured temporally, with a diurnal assemblage being replaced by a nocturnal assemblage (the resting assemblage sheltering in the reef framework). The diurnal assemblage is dominated by perciform and tetraodontiform fishes, whereas the nocturnal assemblage is dominated by beryciform fishes (evolutionary relicts apparently relegated to the night by more recently evolved fishes).

Maintenance of Species Diversity

Four major hypotheses have been proposed to explain how many species of ecologically similar coral-reef fishes can coexist locally. There are data that both corroborate and falsify each hypothesis in various systems, suggesting that no universal generalization is possible. The first two hypotheses are based on the assumption that local populations are not only saturated with settlement-stage larvae, but also regularly reach sizes where resources become limiting. First, the 'competition hypothesis,' borrowed from terrestrial vertebrate ecology, suggests that coexistence is maintained despite ongoing interspecific competition by fine-scale resource partitioning (or niche diversification) among species. Second, the 'lottery hypothesis,' derived to explain coexistence among similar territorial damselfishes that did not appear to partition resources, is based on the assumptions that, in the long run, competing species are approximately equal in larval supply, settlement rates, habitat and other resources requirements, and competitive ability. Thus, settling larvae are likened to lottery tickets, and it becomes unpredictable which species will replace which following the random appearance of open space due to the death of a territory holder or the creation of new habitat. The relatively restrictive assumptions of this hypothesis can be relaxed if one considers the 'storage effect,' which is based on the multi-year life span of reef fishes and the fact that settlement varies 0018 through time. Even though a species is at times an inferior competitor, as long as adults can persist until the next substantial settlement event, that species can persist in the community indefinitely. The third hypothesis, 'recruitment limitation,' assumes that larval supply is so low that populations seldom reach levels where competition for limiting resources occurs, so that postsettlement mortality is density independent and coexistence among species is guaranteed. Finally, the 'prediction hypothesis' predicts that early postsettlement predation, rather than limited larval supply, keeps populations from reaching levels where competition occurs, thereby ensuring coexistence.

Summary

0019 About 4500 fish species inhabit coral reefs globally, yet their fisheries are overexploited, their habitat is threatened, and there are indications that species are endangered. Coral-reef fishes are so diverse that there are many exceptions to virtually every generalization that can be made about them. The typical species is a distinctively colored, highly compressed perciform that readily maneuvers and picks small invertebrates from complex reef habitats. Regarding behavior, mutualism, territoriality, antipredatory mechanisms, and complex social systems (sometimes involving sex reversal) are common. Reproduction is typically via broadcast spawning, with pelagic larval duration averaging about a month, and life span less than a decade. Population dynamics are apparently driven by fluctuations in larval mortality, and populations are probably regulated in the absence of fishing by density-dependent fecundity and early postsettlement mortality via predation. Community structure is complex, involving numerous feeding guilds, and includes day–night transitions between diurnal and nocturnal assemblages. Communities are variously structured by recruitment, competition, and predation in a way that maintains high local species diversity.

See also

Climate: Corals and Climate Change. **Coastal Regimes:** Coral Reefs. **Diversity, Marine Species. Fish:** Feeding/Foraging (Behaviour, Food Chains, Feeding Mechanisms, Density Dependence); Predation/Mortality; Reproduction. **Fisheries:** Fisheries for Coral Reef/Tropical Species. 0020

Further Reading

Birkeland C (ed.) (1997) *Life and Death of Coral Reefs*. New York: Chapman and Hall.

Böhlke JE and Chaplin CCG (1993) *Fishes of the Bahamas and Adjacent Tropical Waters*. 2nd edn. Austin: University of Texas Press.

Caley MJ (ed.) (1998) Recruitment and population dynamics of coral-reef fishes. *Australian Journal of Ecology* 23(3).

Helfman GS (ed.) (1978) Patterns of community structure in fishes. *Environmental Biology of Fish* 3(1).

Longhurst AR and Pauly D (1987) *Ecology of Tropical Oceans*. San Diego: Academic Press.

Montgomery WL (1990) Zoogeography, ecology and behavior of coral reef fishes. In: Dubinskiz (ed.) *Coral Reefs*, pp. 329–364. Amsterdam: Elsevier.

Polunin NVC and Roberts CM (1996) *Reef Fisheries*. London: Chapman and Hall.

Randall JE, Allen GR and Steene RC (1997) *Fishes of the Great Barrier Reef and Coral Sea*. 2nd edn.Honolulu: University of Hawaii Press.

Sale PF (ed.) (1991) *The Ecology of Fishes on Coral Reefs*. San Diego: Academic Press.

Sale PF (ed.) (2001) *The Ecology of Fishes on Coral Reefs*. 2nd edn. San Diego: Academic Press.

Thresher RE (1984) *Reproduction in Reef Fishes*. Neptune City: T.F.H. Publishers.