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Coral Reef Fishes ☆

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Introduction: Diversity, Biogeography, and Conservation Concerns

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 truly amazing. Adult body sizes range from gobies (Gobiidae) <1 cm in length as adults to tiger sharks (Carcharhinidae) nearly 8 m long. It has been estimated that over a third of about 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 and wrasse/parrotfish families), gobioids (gobies and related families), and acanthuroids (surgeonfishes and related families). Modern hard corals and dominant coral-reef fishes diversified rapidly together during the Miocene, indicating a close ecological association. Genetic evidence suggests that parapatric speciation, where species diverge without a geographic barrier physically separating populations, is common in reef fishes.

The latitudinal distribution of reef fishes reflects 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 and origin of many taxa is the Coral Triangle of the Indo-Pacific region, roughly delineated by the Philippines to the north, the Solomon Islands to the east and Indonesia to the west. 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—up to 100% in some locations in the northwestern Hawaiian Islands—and many species (about 9%) have highly restricted geographical ranges. Both the Hawaiian and Red Sea hotspots of endemism have been shown to export novel species. There is also genetic evidence of sporadic dispersal around southern Africa as the primary avenue of colonization between the Indo-Pacific and Atlantic Ocean.

Reef fishes are threatened by three major human activities. First, overfishing is rampant, especially from destructive subsistence fishing practices (e.g., dynamite) in some developing nations ("Mathusian overfishing") and live collections for export to high-end restaurants in Asia. As an example of the latter, endangered Napoleon or humphead wrasse (*Cheilinus undulatus*) wholesaled in Beijing for US$250/kg in 2010. Spawning aggregations of grouper (Serranidae) and snapper (Lutjanidae) are particularly vulnerable to extirpation. Overcollecting for the aquarium trade is also problematic for some species, especially seahorses (Syngnathidae, *Hippocampus* spp.). Second, local destruction of coastal reefs and associated nurseries near human population centers denies fishes of habitat via (a) eutrophication (from both sewage and fertilizer runoff) and sedimentation of reefs, and (b) dredging and burying of reefs, mangroves and seagrass beds, the latter two ecosystems providing nursery habitats for juvenile reef fishes. Third, and accelerating exponentially, coral reefs worldwide are dying from coral bleaching and inhibited by ocean acidification, both caused by carbon emissions from humans burning fossil fuels and clearing forests. To date, 8% of more than 1000 reef fish species that have been assessed by the International Union for the Conservation of Nature (IUCN) are considered threatened with extinction. The major solution for local conservation is fully protected marine reserves, which have proven

effective in replenishing depleted populations. For global conservation, human-caused carbon emissions must be reduced drastically, which is within the capabilities of current wind, solar, and other renewable energy technologies, yet is strongly resisted by fossil fuel interests.

Fisheries

Where unexploited by humans, coral reef fishes typically exhibit high standing stocks, the maximum documented on remote protected reefs being about 750 t/km^2. High standing crops reflect the high primary productivity of coral reefs, often exceeding 10^3 gC/m^2/year, which is mostly benthic in origin and consumed both directly and indirectly by fishes. Correspondingly, reported fishery yields have reached 44 t/km^2/year, with an estimated global potential of 6M t/year. These fisheries provide food and bait, as well as live fish for the restaurant and aquarium trades. However, the estimated maximum sustainable yield from shallow areas of actively growing coral reefs is only about 20–30 t/km^2/year, so many reefs are clearly overexploited. Indeed, overfishing of coral reefs occurs worldwide, due primarily to unregulated multispecies exploitation in developing nations using multiple gears. Reef fisheries are seldom managed. Few and inadequate stock assessments or other quantitative fishery analyses, susceptibility of fish at spawning aggregations (see above and 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. (Note that fishing of some teleost piscivores is naturally inhibited in some regions by ciguatera fish poisoning, caused by benthic dinoflagellate toxins concentrated in the tissues of some species.)

The indirect effects of overfishing include the decline of piscivores causing both increases in and destabilization of prey fish populations. In extreme cases, a trophic cascade may occur, where overfishing top piscivores causes an increase in prey fish (e.g., mesopredators), which in turn causes a decline in the food of those prey fish (i.e., still smaller fish). Overfishing of both urchin-eating species (such as triggerfishes, Balistidae) and various herbivorous fishes may provide sea urchins release from both predation and competition, respectively. Although urchin grazing may help maintain benthic dominance by corals by removing macroalgae, overabundant urchins may overgraze and bioerode reefs. The best hope for enhancing both the sustainability and productivity of reef fisheries is to revive traditional, community-based management practices that focus on subsistence rather than export, combined with effective marine reserves that protect ecosystem function.

Morphology

A typical perciform reef fish 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 fishes have a greater proportion of musculature devoted to both locomotion and feeding. Their jaws and pharyngeal apparatus are complex and typically well developed for suction feeding of smaller invertebrate prey, with tremendous variation reflecting a wide variety of diets. For example, many butterflyfishes (Chaetodontidae) have small protrusible jaws that extract individual polyps from corals, many damselfishes (Pomacentridae, e.g., genus *Chromis*) have highly protrusible jaws that facilitate pipette-like suction feeding of zooplankton, and parrotfishes (Labridae) have fused beak-like jaw teeth and molar-like pharyngeal teeth enabling some species to excavate endolithic algae that grow within 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 perhaps 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.

Diurnal reef fishes are primarily visual predators. Visual acuity is high and retinal structure indicates color vision. At least some planktivorous damselfishes have ultraviolet-sensitive cones, which may assist in detecting zooplankton by enhancing contrast against background light. Coloration is highly variable (including ultraviolet reflectance), ranging from cryptic to dazzling. Bright "poster" colors are hypothesized to serve as visual signals in aggression, courtship, and other social interactions. Mimicry is common. 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). Many nocturnal species are reddish in color, which becomes virtually invisible under low-light conditions. Consistent with their myriad sensory and swimming capabilities, coral reef fishes generally have larger brains than those of other seafloor-oriented fishes.

Behavior

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

Mutualism

Three of the best-documented cases of marine mutualism occur in reef fishes (Fig. 1). "Cleaning symbiosis" occurs when small microcarnivorous fish consume ectoparasites or necrotic tissue off larger client fish, which often allow cleaners to feed within their mouths and gill cavities. The major cleaners are various gobies (Gobiidae) and wrasses (Labridae). Some cleaners are specialists that maintain fixed cleaning stations regularly visited by clients, 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 client 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 host from butterflyfishes (Chaetodontidae) and other predators that attack anemones. However, some host anemones survive well without anemonefish, in which case the relationship may be commensal rather than mutualistic. Finally, a variety of gobies cohabit the burrows of various burrowing alpheid shrimps. The shrimp provides shared shelter and the goby alerts the shrimp to the presence of predators.
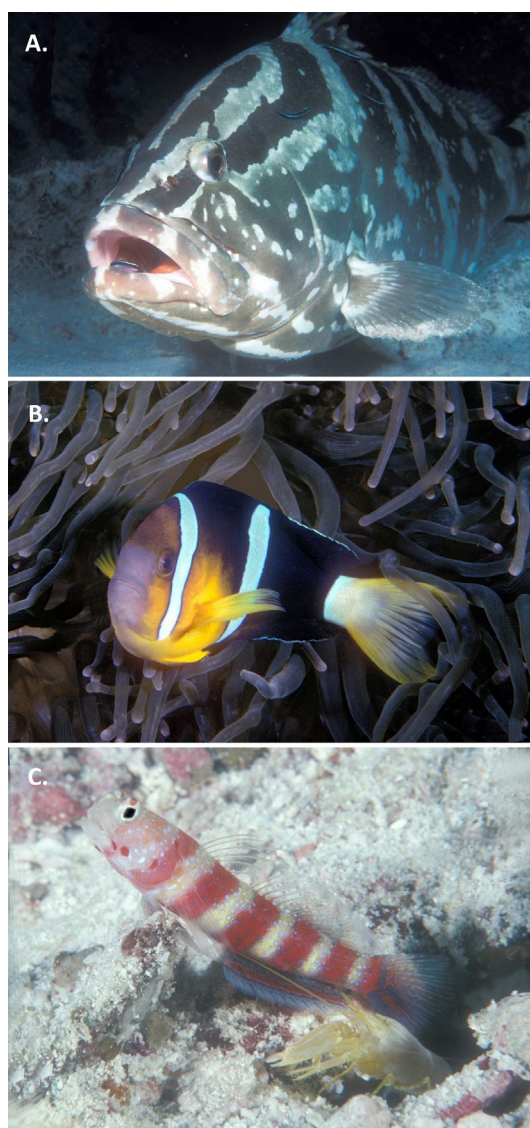
Fig. 1   Examples of mutualisms involving coral-reef fishes. (A) Cleaning symbiosis (goby *Gobiosoma lobeli* cleaning grouper *Epinephelus striatus*, Belize). (B) Anemonefish and anemone (*Amphiprion clarkii* inhabiting *Entacmaea quadricolor*, Japan). (C) Goby with burrowing shrimp (*Amblyeleotris wheeleri* with *Alpheus ochrostriatus*, Maldive Archipelago). All photos courtesy of John E. Randall.

Territoriality

The most overt form of competition involves territoriality or defense of all or part of an individual's home range. Many reef fishes behave aggressively toward members of both the same and other species, yet 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 benthic algae. These algal mats serve as a food source for the damselfish as well as refuges from predation for small juvenile fish of various species that manage to avoid eviction. Juvenile corals may escape predation in damselfish territories or be smothered by the algal mats. At a local spatial scale, the algal mats can maintain high species diversity of algae and associated invertebrates. By forming dense schools, nonterritorial herbivores (especially parrotfishes (Labridae) and surgeonfishes (Acanthuridae)) can successfully invade damselfish territories.

Piscivory and Defense

Predation is a major factor affecting the behavior and ecology of reef fishes. There are three main 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 (Fig. 2). The vision of piscivores is often suited for crepuscular twilight, when the vision of their prey is least acute (the latter 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 (Labridae) may 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/or 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, often during new moons, is also an apparent anti-predatory adaptation.

Reproduction

Social Systems and Sex Reversal

The best-studied examples of highly structured social systems in reef fishes are the harems of wrasses and parrotfishes (Labridae). 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 (Pomacentridae) have monogamous social systems in which the largest individual is female, the second largest is male, and the remaining fish are immature. 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 (Sparidae) and serranine sea basses (Serranidae). 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 and reproductive modes found in reef fishes, individuals have been documented to behave in a way that tends to maximize lifetime reproductive success.

### Life Cycle: Spawning, Larval Dispersal, and Settlement

The typical bony reef fish has a bipartite life cycle: a pelagic egg and larval stage followed by a demersal (seafloor-oriented) juvenile and adult stage (Fig. 3). Most bony reef fishes (with a variety of exceptions) broadcast spawn, releasing gametes directly into the water column where they are swept to the open ocean (Fig. 4). 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 rush" followed by rapid return to the seafloor. Exceptions to broadcast spawning include demersal spawners that brood eggs until they hatch, either externally (e.g., benthic egg masses defended by damselfishes, Pomacentridae) 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 often not strongly related to any particular annual variable. In contrast, lunar, semilunar, and tidal spawning cycles are common. These are presumably adaptations that transport larvae offshore away from reef-based predation, maximize the number of settlement-stage larvae returning during favorable conditions that vary on lunar cycles, and/or directly benefit spawning adults in some way.
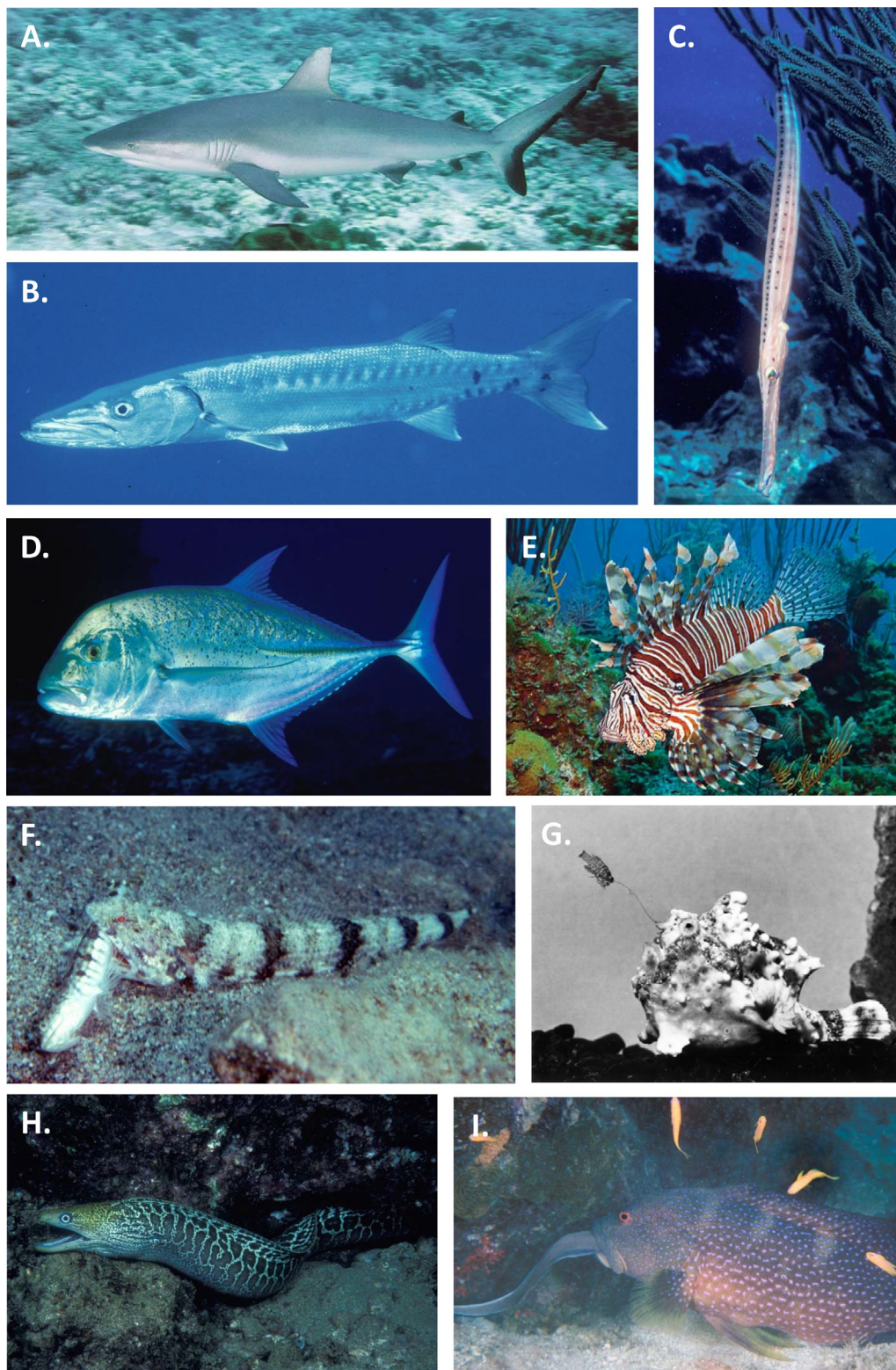
Fig. 2   The piscivore feeding guild of coral-reef fishes. (A) Large elasmobranch piscivore, a top predator (reef shark *Carcharhinus amblyrhynchos*, Tuamotu Archipelago). (B) Large solitary teleost piscivore (barracuda *Sphyraena barracuda*, Virgin Islands). (C) Stalking mesocarnivore (trumpetfish *Aulostomus maculatus*, Puerto Rico). (D) Large schooling teleost piscivore (jack *Caranx melampygus*, Hawai'i). (E) Stalking mesocarnivore (lionfish *Pterois volitans*, invasive in Bahamas). (F) Ambushing small piscivore on sand (lizardfish *Synodus dermatogenys* cannibalizing juvenile, Red Sea). (G) Ambushing small piscivore on reef (frogfish *Antennarius maculatus*, note fishlike lure, Philippines). (H) Nocturnal mesocarnivore (moray eel *Gymnothorax undulatus*, Hawai'i). (I) Diurnal mesocarnivore (grouper *Variola louti* consuming conger eel *Conger cinereus*, Red Sea). All photos courtesy of John E. Randall, except those courtesy of (E) Paul Humann, and (G) Theodore W. Pietsch.
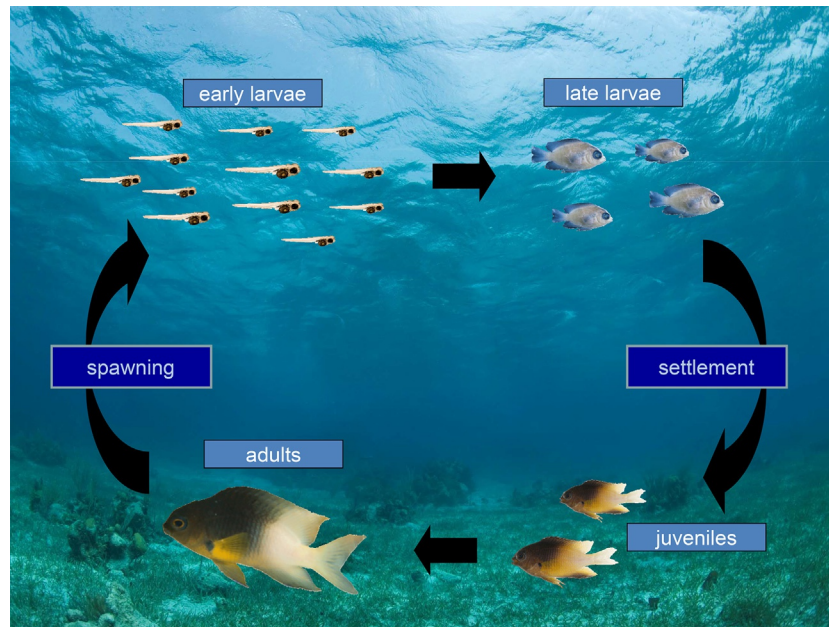
Fig. 3 Life cycle of a typical teleost coral-reef fish. Note that the Caribbean damselfish species shown here (*Stegastes partitus*) lays demersal eggs that are guarded until hatching into larvae, whereas most reef fishes release their eggs and sperm directly into the water column (see Fig. 4). The differences in numbers represent the tremendous mortality suffered between the larval stage and adulthood. Modified from unpublished design courtesy of Darren W. Johnson.
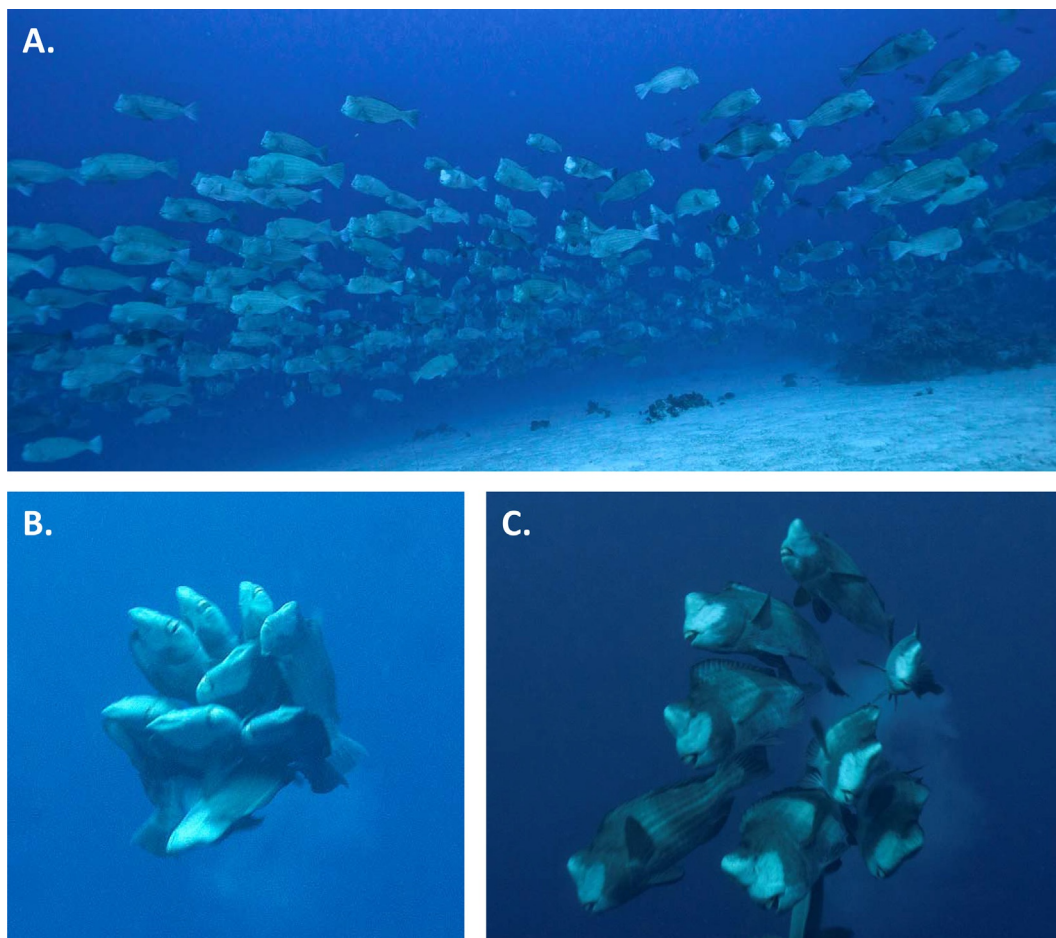
Fig. 4 Broadcast spawning by endangered bumphead parrotfish (*Bolbometopon muricatum*). (A) A spawning aggregation in Palau. (B) Upward spawning rush of males (white faces) with a female. (C) Release of a cloud of gametes just before a rapid return to the seafloor. All photos courtesy of Mandy T. Etpison.

The duration of the pelagic larval stage, typically measured by counting ear-stone (otolith) rings, ranges from about 9 to well over 100 days, averaging about a month. The prey of larval reef fish include a variety of small zooplankters, especially copepods. Comparisons of fecundity at spawning to subsequent larval settlement back to the reef suggest that larval mortality is extremely high and variable, apparently due mostly to predation. Patterns of endemism, settlement to isolated islands, and increasing data tracking larvae directly via genetics and other methods all suggest that there is considerable larval retention at the scale of particular islands (facilitated by oceanic gyres), yet substantial larval dispersal nonetheless. The collective evidence suggests that populations of coral reef fishes tend to be semi-closed (or semi-open, depending on one's perspective). Later-stage larvae are well-endowed with a variety of senses, are active swimmers, and may control their dispersal by selecting horizontal currents among depths. The overall reproductive strategy apparently disperses the larvae offshore from reef-based predators, but then retains offspring close enough to shore for subsequent settlement in suitable habitat.

Settlement, the transition from pelagic larva to life on the reef (or nearby nursery habitat), occurs at a total length of ~8 to ~200 mm, often at night during new moons. Larger larvae are either morphologically distinct (e.g., the acronurus of surgeon-fishes, Acanthuridae) or essentially pelagic juveniles (e.g., squirrelfishes (Holocentridae) and porcupinefishes (Diodontidae)). There is increasing evidence that transitioning reef fishes use a variety of sensory cues to detect and select where to settle. Whereas many species settle directly onto reefs, 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. Empirical estimates of settlement are generally called "recruitment" and are based on counts of the smallest juveniles that can be found by divers 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 and some small surgeonfish live at least 40 years.

Ecology

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. These characteristics make studies of reef fishes conceptually relevant to both demersal fisheries biology and marine ecology in general.

Population Dynamics

Coral reefs are patchy at all spatial scales, ranging from isolated coral heads surrounded by sand to long stretches of continuous reef separated by broad tidal channels. Combined with the fact that fishes inhabiting reefs are largely sedentary, coral reef fishes typically form marine metapopulations: groups of local populations linked by larval dispersal. Local populations tend to be at least partially open demographically, such that reproductive output drifts away and is thus often unrelated to subsequent larval settlement originating from elsewhere. Ultimately, the degree of openness depends on the spatial scale examined. For example, populations of anemonefish (genus *Amphiprion*, Pomacentridae) 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 a small archipelago. It is clear that variability in population size is driven by variation in recruitment due to larval mortality (and perhaps spawning success). Input to local populations via recruitment varies considerably at virtually every spatial and temporal scale examined. Increasing evidence indicates that two mechanisms predominate in regulating reef fish populations. 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 post-settlement mortality is often density-dependent, and has been demonstrated experimentally in a variety of species to be caused by predation, which may result in competition for prey refugia. There is also evidence that different species compete with each other for food and/or shelter.

Community Structure

Due to high local species diversity, reef fish communities are the most complex assemblages of vertebrates in the world. There are at least five major feeding guilds, each containing dozens of species locally (with typical rough percentage of total fish biomass): planktivores (up to 70%), herbivores (up to 25%), and piscivores (up to 55%), with the remainder being benthic invertivores (aka benthivores) of several kinds and detritivores (Fig. 5). Piscivores attain higher biomass on relatively unexploited reefs. Benthivorous guilds include fishes consuming specific prey taxa (e.g., corallivores) or other prey categories (e.g., consumers of hard-shelled invertebrates). There is also considerable consumption of fish feces (coprophagy). 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. Guilds can also be subdivided into diurnal and nocturnal categories, each often consuming different prey that also follow diel cycles of activity. Indeed, the entire reef fish community is structured temporally, with a diurnal assemblage being replaced at night 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 anguilliform and beryciform fishes, ancestral groups apparently relegated to the night by more recently evolved fishes.
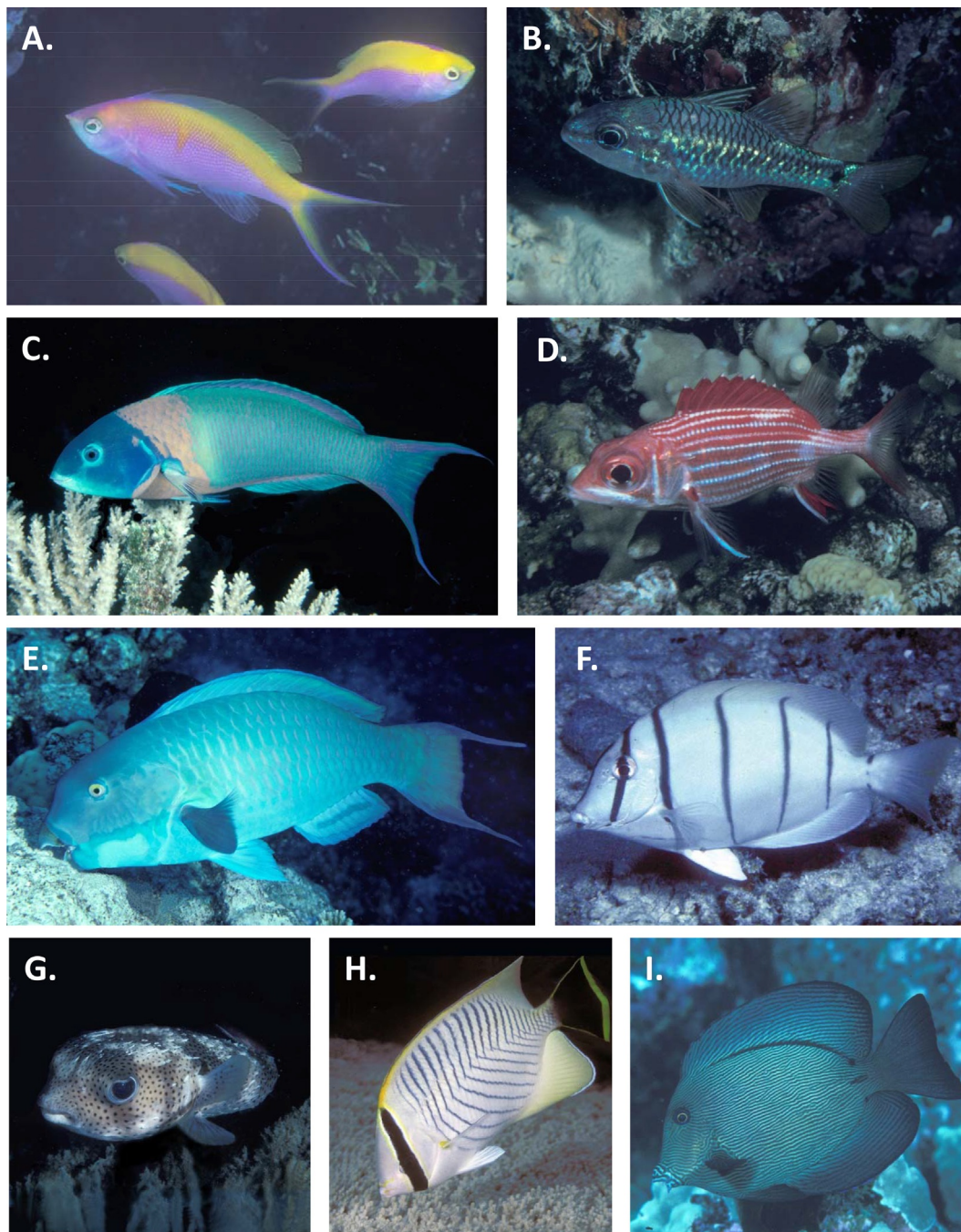
Fig. 5 Examples of feeding guilds of coral-reef fishes (see Fig. 2 for piscivore guild). (A) Diurnal planktivore (anthias *Pseudanthias bartlettorum*, Marshall Islands). (B) Nocturnal planktivore (cardinalfish *Pristiapogon kallopterus*, Philippines). (C) Diurnal benthic invertivore (wrasse *Thalassoma duperrey*, Hawai'i). (D) Nocturnal benthic invertivore (squirrelfish *Sargocentron xantherythrum*, Hawai'i). (E) Excavating herbivore (parrotfish *Chlorurus microrhinos*, Marshall Islands). (F) Grazing herbivore (surgeonfish *Acanthurus triostegus*, Easter Island). (G) Hard-shelled invertivore (porcupinefish *Diodon hystrix*, Midway Islands). (H) Corallivore (butterflyfish *Chaetodon trifascialis*, Johnston Atoll). (I) Detritivore (surgeonfish *Ctenochaetus hawaiiensis*, Hawai'i). All photos courtesy of John E. Randall.

Maintenance of Species Diversity

Four major hypotheses have been proposed to explain how many species of ecologically similar coral reef fishes can coexist locally (Fig. 6). 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 densities where resources become limiting. First, the "competition hypothesis," borrowed from terrestrial
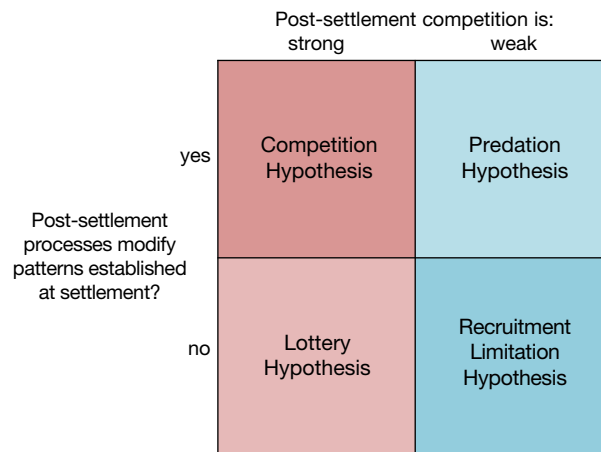
Fig. 6   The four major hypotheses proposed to explain the maintenance of high local species richness in coral-reef fishes. See text for details. Modified from Jones (in Sale 1991): Jones, G. P. (1991) Postrecruitment processes in the ecology of coral reef fish populations: A multifactorial perspective. In Sale, P. F. (ed) The ecology of fishes on coral reefs, pp. 294–328. San Diego, CA: Academic Press.

vertebrate ecology, suggests that coexistence is maintained despite ongoing interspecific competition by fine-scale resource partitioning ("niche diversification") among species. Second, the "lottery hypothesis," derived to explain coexistence among similar territorial damselfishes (Pomacentridae) 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 resource 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 multiyear life span of reef fishes and the fact that settlement varies through time. Even though a species may at times be an inferior competitor, as long as adults can persist until the next substantial settlement event, then that species can persist in the community indefinitely.

The other two hypotheses assume that some factor limits population sizes below levels where competition occurs. 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 post-settlement mortality is density-independent and coexistence among species is guaranteed (assuming a storage effect). Finally, the "predation hypothesis" predicts that early post-settlement predation, rather than limited larval supply, keeps populations from reaching levels where competition occurs, thereby ensuring coexistence. Implicit in this hypothesis is the assumption that predation is sufficiently density-dependent so as to ensure that species are not extirpated by piscivores.

Note that the mechanisms underlying these hypotheses are not mutually exclusive, in that predation is known to cause competition for prey refugia. All told, coral reef fishes comprise a cornucopia of vertebrate biodiversity that feeds and fascinates humanity. Their fate is linked with ours.

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