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TEN

The Amazing Yet Threatened World of Marine Fishes

MARK A. HIXON AND BRIAN W. BOWEN

Summary

Fishes are the original and most diverse group of vertebrates, including over 35,000 of the estimated 69,000 species with backbones. Most marine fishes have large geographic ranges that may provide some protection from extinction, but there are very important exceptions:

- *Fishes that move between freshwater and seawater*, including salmon, sturgeon and freshwater eels. The migration from coastal seas to rivers and streams makes these species very vulnerable to capture and habitat degradation.
- *Fishes with very small geographic ranges* can be wiped out by a single catastrophic disturbance or intense fishing. Aquarium fishes with high economic values but small ranges include the resplendent angelfish (*Centropyge resplendens*) that occurs on a single island, and the Banggai cardinalfish (*Pterapogon kauderni*), native to a few islands in eastern Indonesia.
- *Invasive species* can consume naïve native prey or otherwise disrupt ecosystems. The disastrous introduction of the Indo-Pacific lionfish (genus *Pterois*) to the western Atlantic has done both, consuming small-range fishes like the Mardi Gras wrasse (*Halichoeres burekae*) and altering coral reef ecosystems by reducing native fish biomass.
- *Fishes with low reproductive potential* may not be able to recover from overfishing or natural population declines. While many large bony fishes (teleosts) can produce millions of eggs and readily rebound from population depletion, fishes such as the sharks, rays and relatives (chondrichthyans) produce only a few progeny at a time.
- *Overfishing* has brought many species to the brink of extinction. Fishing has historically been the primary cause of declines in marine fishes, both directly in terms of catch and indirectly in terms of bycatch (incidental take of non-targeted species) and fishing gear that destroys seafloor habitat. The introduction of mechanised fishing in the 1880s began a century of severe population reductions, especially via the very destructive practice of bottom trawling.
- *Ocean warming and acidification* are the major threats to the future of marine fishes. These sea changes are expected to result in loss of fish habitat, reduced productivity, behavioural and physiological problems, and disruption of ecological processes that are the basis for healthy fish populations, healthy ocean ecosystems and, by extension, healthy humanity.

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10.1 Introduction

Fishes are the ancestors of all vertebrates. They were the wellspring of vertebrate evolution over 500 million years ago (Ma), the progenitors of all biodiversity with a backbone. Because of this high diversity, fishes are known as the insects of the subphylum Vertebrata, with over 35,000 described species (Fricke et al., 2022). Dozens of fish species are still being discovered every year, especially small species of unknown vulnerability. Marine fishes include about half of all known fish species. While freshwater fishes have been devastated by habitat alterations, especially diversion of water for human use (see Chapter 9), the threats to marine fishes are more diverse. Currently at the top of the list is overfishing, followed by seafloor habitat destruction, both possibly soon to be overtaken by the evil twins of ocean warming and acidification.

What is a fish? The most common definitions include vertebrates living in water and typically having gills, scales, jaws and fins. However, none of these traits apply to all fishes. The lungfishes (Subclass Dipnoi) live in stagnant freshwater and breathe air directly, the gills of African and South American species being too atrophied to function for respiration. The moray eels (Family Muraenidae) lack scales, relying instead on a coating of mucus for protection (Figure 10.2A). The ancient hagfishes (Figure 10.2B) and lampreys (Class Myxini) lack both jaws and fins, as well as scales. Faced with the fact that each fishy characteristic is lacking in some fish, we recall the famous words of US Supreme Court Justice Potter Stewart when attempting to define hard-core pornography: 'I shall not today attempt further to define the kinds of material I understand to be embraced within that shorthand description. . .*but I know it when I see it.*' That definition shall suffice for the purposes of this chapter. For more information about fishes in general and fish conservation in particular, we recommend the books by Facey et al. (2023) and Helfman (2007), respectively.

There are three major groups of living fishes:

'Living fossils' include the jawless hagfishes and lampreys, amazing relicts from a time before the vertebrate jaw evolved, dating back to about 530 Ma. Hagfishes are deep-sea scavengers (Figure 10.2B), whereas lampreys mostly persist in specialised freshwater habitats, although the largest are parasites on other fishes and can migrate to the ocean. Another living fossil is the coelacanth, the lobe-finned fish believed to have diverged near the origin of terrestrial vertebrates (tetrapods) (Figure 10.2C). Coelacanths were very abundant in the Jurassic and Cretaceous eras (240–65 Ma), but were believed to have perished with the dinosaurs about 65 Ma. This changed when a fresh specimen was captured in the southwestern Indian Ocean, as chronicled in J.L.B. Smith's classic 1956 adventure book entitled *Old Four Legs: The Story of the Coelacanth*. A second species of coelacanth was recently discovered in Indonesia and the hunt is on for additional species. The extant coelacanths are deepwater fishes that usually occur beyond the reach (and mostly without the knowledge) of local fishermen.

Chondrichthyan fishes are the sharks, rays and their relatives, known from a fossil record dating back to the Devonian (360–420 Ma). They have a cartilaginous skeleton rather

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than the bony skeleton of most vertebrates. Over 500 species of sharks and over 600 species of rays and ray-like fishes are recognised. Chondrichthyan fishes are overwhelmingly marine, although a few have moved into freshwater, with a stunning radiation of rays in the Amazon River basin. The bull shark (*Carcharhinus leucas*; Figure 10.2D), one of the most dangerous in terms of human attacks, can occur in freshwater, giving some unfortunate swimmers the surprise of a lifetime.

Teleost fishes, the modern bony fishes, are known from the fossil record back to the Triassic (200–250 Ma) and are by far the most abundant and diverse at 96% of living species. This category encompasses among the smallest and largest vertebrates, from the tiny male stout infantfish (*Schindleria brevipinguis*; Figure 10.2E) that measures less than one centimetre as an adult, to the giant ocean sunfish (*Mola mola*; Figure 10.2F) weighing over two tons. Teleosts also include such bizarre creatures as a frogfish that literally fishes for other fish with a fish-like lure (Figure 10.2G) and seahorses that closely resemble seaweeds (Figure 10.2H). Teleosts are *the* evolutionary success story among vertebrates.

Several groups of teleost fishes have shown explosive radiations in recent evolutionary history. The gobies (Family Gobiidae) are the most species-rich group, with over 2000 species. The rockfishes (Family Scorpaenidae) of the temperate eastern Pacific have radiated into over 70 species in a single genus (*Sebastes*). Some regions of the seas are known as wellsprings of species diversity, foremost among them being the Coral Triangle, the corners of which are formed by the Philippines, Indonesia and New Guinea (Allen, 2008). This area hosts over 3000 fish species, including over 50% of the Indo-Pacific fish fauna. By one estimate, 60% of Indo-Pacific reef fishes had ancestors in this region (Cowman and Bellwood, 2013). At the periphery of the Indo-Pacific basin are areas of high endemism (containing species occurring nowhere else) including the Red Sea (13% endemism in fishes) and Hawaiian Archipelago (25% endemism). These areas can also produce and export new species (Bowen et al., 2016). Clearly, regions like the Coral Triangle are conservation priorities to protect the progenitors of future biodiversity.

10.2 Marine Fishes at Risk

Box 10.1 summarises the marine fishes listed as threatened by IUCN. Here we review a half dozen examples in greater detail.

Atlantic halibut (*Hippoglossus hippoglossus;* Figure 10.3A) is among the largest flatfishes, growing to 3 m and exceeding 300 kg. Slow growth and a long time to maturity (over 10 years) make it especially susceptible to overfishing. Whereas European colonists found an abundance of this fish off the North Atlantic coast of America, this species is now rarely encountered. Overfishing has also caused Atlantic halibut to become sexually mature at much smaller sizes. Commercial fishing for this species, now IUCN listed as Endangered, is presently banned in US coastal waters.

Atlantic bluefin tuna (*Thunnus thynnus*; Figure 10.3B) is the largest member of the tuna family (3 m, 678 kg record) and highly prized for sushi and other dishes. It is the

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Box 10.1
IUCN Listed Marine Fishes

The International Union for the Conservation of Nature (IUCN) presently lists only six recent extinctions of fishes found in marine waters, all anadromous species (maturing in seawater, spawning in freshwater) that perished due to overfishing and other human activities: the New Zealand grayling (*Prototroctes oxyrhynchus*), the Adriatic Sea stock of the European sturgeon (*Huso huso*) and four populations of Columbia River sockeye salmon (*Oncorhynchus nerka*) (Figure 10.1). However, many marine fishes are threatened, defined by IUCN as having an elevated risk of

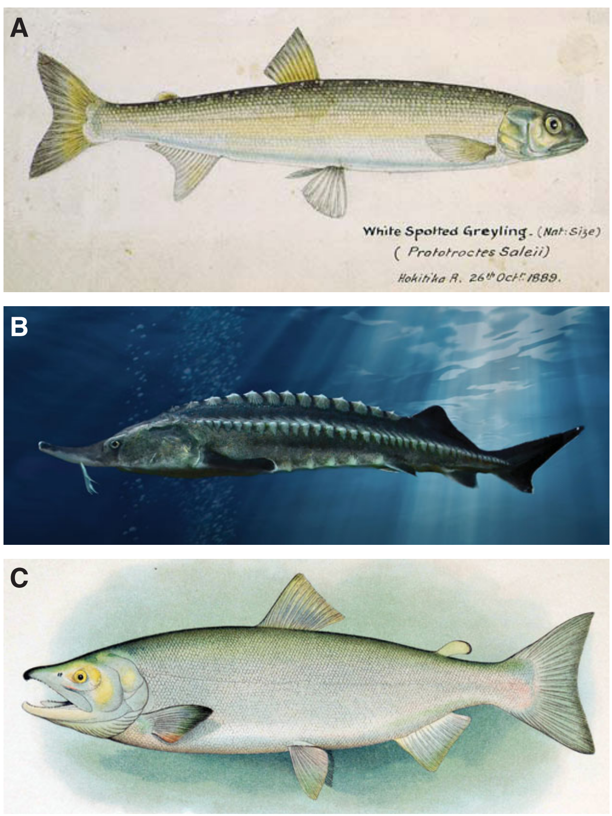

Figure 10.1 Fishes that inhabited seawater (all anadromous species) driven extinct by overfishing and other human activities, as documented by IUCN. (A) New Zealand grayling (*Prototroctes oxyrhynchus*, 22 cm FL) (credit: F.E. Clarke courtesy of the Museum of New Zealand Te Papa Tongarewa). (B) Adriatic Sea stock of the European sturgeon (*Huso huso*, 800 cm TL) (credit: Максим Яковлєв). (C) Four populations of Columbia River sockeye salmon (*Oncorhynchus nerka*, 84 cm TL) (credit: B.W. Evermann and E.D. Goldsborough). Maximum fork lengths (FL) and total lengths (TL) from fishbase.org.

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extinction, the risk categorised along a gradient from Vulnerable to Endangered to Critically Endangered. Of 988 marine fish species assessed in European waters alone, 15 are Critically Endangered, 22 are Endangered and 22 are Vulnerable, mostly due to overfishing (Nieto et al., 2015). Of 519 Mediterranean species assessed, 15 are Critically Endangered, 13 are Endangered and 15 are Vulnerable, again due to overfishing (Abdul Malak et al., 2011). Most listed species are chondrichthyan fishes (sharks, rays and relatives), of which 36% of over 1000 assessed species are threatened at some level or categorised as Data Deficient (IUCN, 2022). Globally, IUCN currently lists 65 marine fish species as Critically Endangered, 141 as Endangered and 372 as Vulnerable. Importantly, most marine fishes have not been assessed. Beyond IUCN listings, 60% of 825 exploited marine fish species worldwide are projected to experience very high extinction risk from a combination of overfishing and ocean climate disruption if present trends continue (Cheung et al., 2018), especially on coral reefs (McClenachan, 2015).

target of a very lucrative fishery, with individual fish being sold for hundreds of thousands of dollars, and a recent record of 3 million US dollars for a single fish in Tokyo. Management is confounded by the long migrations made by adults, traversing international boundaries and multiple management zones. While other fisheries tend to abate as fish get scarce, the high price of bluefin tuna makes it profitable to hunt them down to the last fish. As a result, the IUCN status for bluefin tuna is Endangered.

Atlantic goliath grouper (*Epinephelus itajara*; Figure 10.3C) exceeds 2 m in length, grows to 300 kg and can live past 40 years. There is a sister (closely related) species in the East Pacific (*Epinephelus quinquefasciatus*). These species are subject to a triple whammy of low reproduction relative to other groupers, overfishing of juveniles before they can reproduce and capture of reproductive adults in spawning aggregations. The Atlantic Goliath Grouper is IUCN listed as Endangered in the Gulf of Mexico, and Vulnerable elsewhere in the West Atlantic. Following a 1990 moratorium on fishing for this species, numbers in US waters are showing impressive signs of recovery.

Orange roughy (*Hoplostethus atlanticus*; Figure 10.3D), originally known as the Slimehead, was rebranded by fisheries to increase appeal to consumers. It is extremely long-lived (up to 149 years) and takes 20–30 years to mature. The damage done by overfishing is amplified by the tendency of this fish to congregate in spawning aggregations, making it easy prey and wiping out reproductive adults. IUCN lists this fish as Vulnerable, likely headed towards Endangered unless overfishing is eliminated.

Smalltooth sawfish (*Pristis pectinata*; Figure 10.3E) is Critically Endangered throughout the Atlantic, with populations reduced by more than 95% over the last century. The primary culprit is mortality in coastal fisheries. While this sawfish is not sought in commercial fisheries, it overlaps extensively with other fishery targets in coastal waters. In these areas, the toothy rostrum ('saw') makes this fish very vulnerable to entanglement

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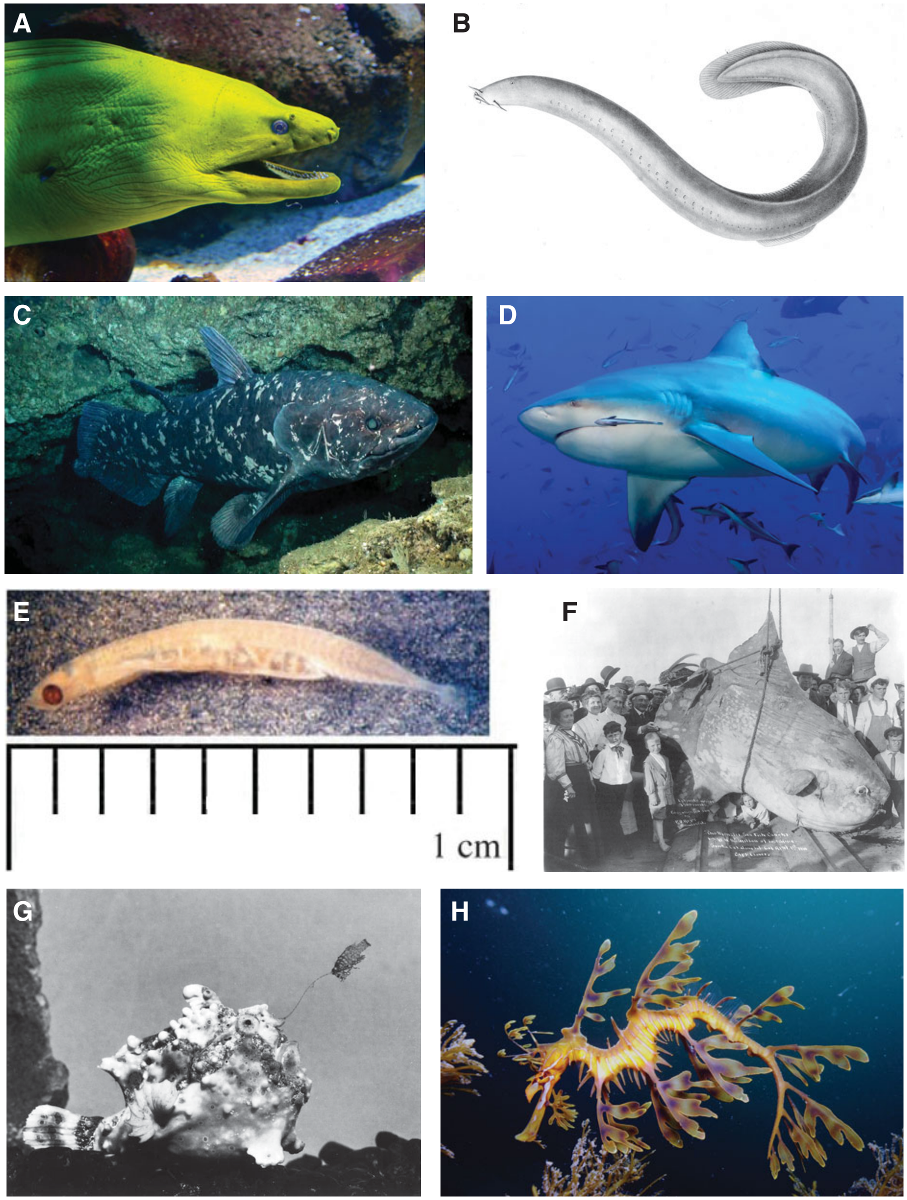

Figure 10.2 Some of the fantastic diversity of marine fishes. (A) Green moray eel (*Gymnothorax funebris*, 250 cm TL) (credit: J. Wilder). (B) Fourteen-gill hagfish (*Eptatretus polytrema*, 93 cm TL) (credit: J.H. Richard). (C) Coelacanth (*Latimeria chalumnae*, 200 cm TL) (credit: R.L. Pyle). (D) Bull shark (*Carcharhinus leucas*) (credit: T. Sinclair-Taylor). (E) One of the smallest vertebrates next to a 1 cm scale, the stout infantfish (*Schindleria brevipinguis*, 0.8 cm SL) of the Great Barrier Reef (credit: Scripps Institution of Oceanography). (F) One of largest fishes, captured at Catalina Island, California, in 1910, the ocean sunfish (*Mola mola*, 333 cm TL) (credit: P.V. Reyes). (G) Warty frogfish (*Antennarius maculatus*, 15 cm TL), showing the modified dorsal spine that resembles a small fish and acts as a fishing lure for this highly cryptic ambush predator (credit: T.W. Pietsch). (H) Leafy sea dragon (*Phycodurus eques*, 35 cm TL), a relative of seahorses that mimics seaweed (credit: J. Rosindell). Maximum total lengths (TL) and standard lengths (SL) from fishbase.org.

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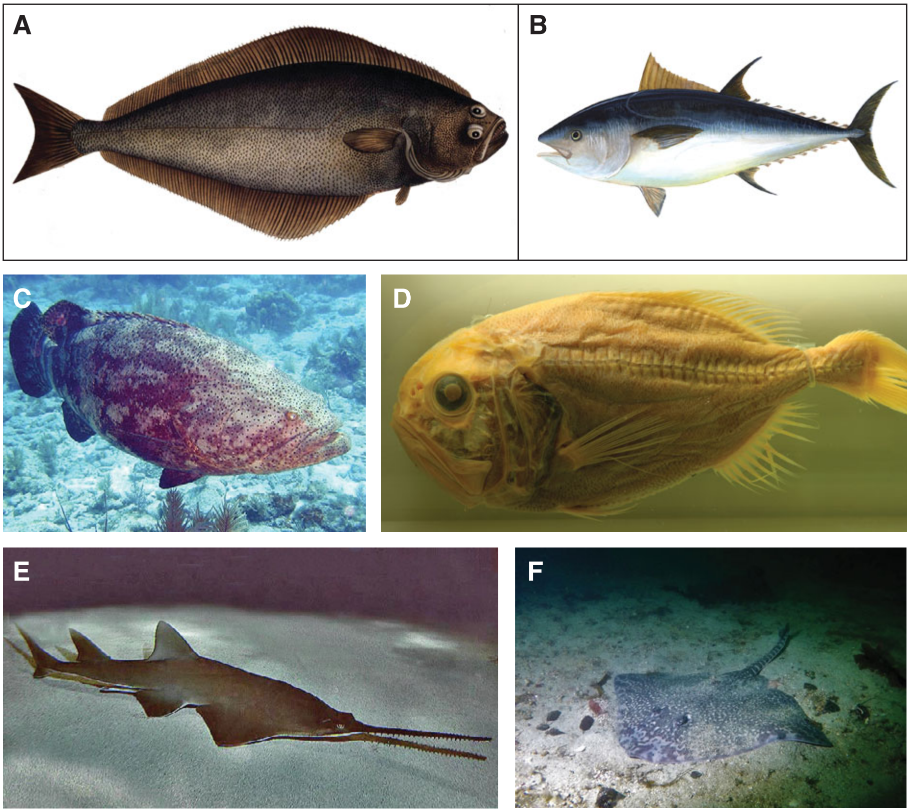

Figure 10.3 Some threatened marine fishes. (A) Atlantic halibut (*Hippoglossus hippoglossus*, 470 cm TL) (credit: Wikipedia). (B) Atlantic bluefin tuna (*Thunnus thynnus*, 458 cm TL) (credit: NOAA). (C) Goliath grouper (*Epinephelus itajara*, 250 cm TL) (credit: J.E. Randall). (D) Orange roughy (*Hoplostethus atlanticus*, 75 cm TL) (credit: Pengo). (E) Smalltooth sawfish (*Pristis pectinata*, 760 cm TL) (credit: D.R. Robertson). (F) Winter skate (*Leucoraja ocellata*, 110 cm TL) (credit: NOAA). Maximum total lengths (TL) from fishbase.org.

in fishing nets. A second factor is the desirability of the fins, esteemed in the shark fin trade. The low fecundity of this species, typical of chondrichthyans, limits potential for recovery. In response to these dire population trends, international trade is prohibited under the Convention on International Trade in Endangered Species (CITES), and many nations have imposed total fishing bans, including Brazil, Nicaragua, Mexico and the USA. A decade of intensive management in the USA has paid off in that population trends indicate the beginning of a recovery in US Atlantic waters. However, all sawfish genera (*Pristis* and *Anoxypristis*) are imperilled globally, with two of five species listed by IUCN as Endangered, and the other three listed as Critically Endangered (IUCN, 2022).

Winter skate (*Leucoraja ocellata*; Figure 10.3F) inhabit the northwest Atlantic Ocean and are harvested for fish meal, lobster bait and human consumption. Over the last three decades numbers have dropped by 90%, prompting IUCN to label this species as Critically

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Endangered. Due to the low fecundity of skates (like other chondrichthyans), the species will recover slowly if at all, especially because fisheries continue to capture it and remaining numbers are subject to predation from a rebounding population of grey seal (*Haliochoerus grypus*).

10.3 Causes of Extinction Risk

While freshwater fishes have suffered devastating losses from water diversion and habitat disruption (Chapter 9), the fate of marine fishes has not yet been as severe. Documented recent extinctions among marine fishes have been rare so far (Box 10.1). Ignorance about the status of most species may be the primary reason. It may also be that extinction from overfishing is prevented by natural limits on the efficiency of exploitation, with the physical inability or lack of economic incentive to catch the few remaining members of a species (with notable exceptions, such as Atlantic bluefin tuna). Additionally, the paucity of documented extinctions may be due to the enormous expanses of the ocean, where some fish can disperse over entire ocean basins with population sizes in the millions. Coral reef fishes in the vast Indo-Pacific region (which covers over half the planet) have geographic ranges averaging about 9 million km^2, about the size of China (Allen, 2008). Given these possibilities and our lack of knowledge of most species, official tallies presume that marine fish diversity is intact relative to other vertebrates, yet there are clearly important and rapidly multiplying exceptions.

10.3.1 Diadromous Fishes: Marine–Freshwater Double Jeopardy

Diadromous fishes, those that use both marine and freshwater habitats, have been very successful in terms of both abundance and diversity. However, in the age of human exploitation, double benefits can capsize into double jeopardy, as these species are prone to the same hazards as purely marine and purely freshwater fishes. These double-dipping fishes come in two primary varieties.

Anadromous fishes are hatched in freshwater, eat, grow and mature at sea, then return to freshwater and spawn. The most famous example are salmon (Family Salmonidae), a group of very successful fishes that have nourished coastal peoples for thousands of years, becoming cultural icons in the process. Salmon are easy to catch when they return to rivers and hence very vulnerable to overexploitation. While no entire species has yet gone extinct, hundreds of breeding populations have been wiped out by all the various factors that depress freshwater fishes (Chapter 9). The US National Marine Fisheries Service estimates that about one-third of the genetically distinct populations of salmon on the west coast of North America have gone extinct in the last 250 years (Gustafson et al., 2007). Additional anadromous fishes include Striped bass (*Morone saxatilis*), Shad (genus *Alosa*) and Sturgeon (family Acipenseridae), the last being valued for their eggs, known in culinary circles as caviar. Unfortunately for sturgeon, the caviar cannot be extracted without killing the female, and for that reason many species are endangered. Atlantic sturgeon (*Acipenser oxyrhynchus*) longer than 3 m used to be so common that they posed a hazard to river navigation in New England, flipping canoes with the casual swipe of a tail. They are now rarely encountered, and may be effectively extinct in the northern part of

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their range. As summarised in Box 10.1, all documented extinctions of fishes that inhabit seawater have been anadromous species.

Catadromous fishes do the opposite, living primarily in freshwater but migrating to the ocean where they spawn. The most spectacular examples are the freshwater eels (Family Anguillidae). The European and American freshwater eels inhabit rivers and lakes for most of their lives, then migrate to the Sargasso Sea in the central western Atlantic, where they mass spawn and die. The resulting larva is a bizarre translucent ribbon-like creature known as a leptocephalus (Figure 10.4A) that spends a year or more in oceanic gyres before

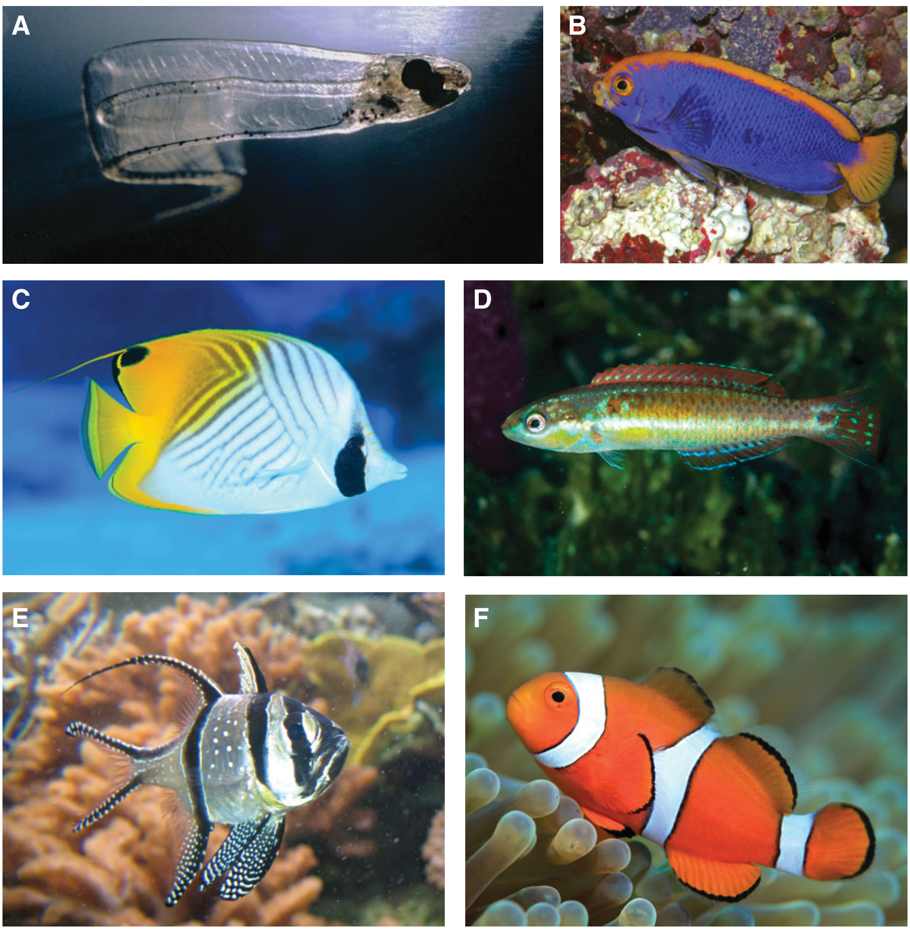

Figure 10.4 Some marine fishes of various levels of conservation concern. (A) Leptocephalus eel larva (8 cm TL, credit: U. Kils). (B) Resplendent angelfish (*Centropyge resplendens*, 6 cm TL) (credit: F. Baensch). (C) Threadfin butterflyfish (*Chaetodon auriga*, 23 cm TL) (credit: T. Sinclair-Taylor). (D) Social wrasse (*Halichoeres socialis*, 5 cm TL) (credit: L. Rocha). (E) Banggai cardinalfish (*Pterapogon kauderni*, 9 cm TL) (credit: P. Hound). (F) Orange clownfish (*Amphiprion percula*, 11 cm TL) (credit: T. Sinclair-Taylor). Maximum total lengths (TL) from fishbase.org, except actual length of leptocephalus eel larva photographed.

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transforming into a juvenile eel and returning to freshwater. It is this stage, the so-called glass eels, that are subject to intense fishing for subsequent aquaculture or direct consumption. The European eel (*Anguilla anguilla*) has declined by an estimated 80% in the last 50 years. On an evolutionary timescale, switching from marine to freshwater habitats has been a very successful form of exploiting two completely different environments. However, in the age of humans, the confines of a riverine migration expose fish to all the factors that cause declines in freshwater fishes, such as overexploitation, habitat destruction and water quality degradation.

10.3.2 Small-Range Endemics

Restricted geographic range (endemism) is recognised as a primary factor in extinction risk, and some marine fishes have very small ranges that make them more vulnerable to catastrophic decline (Hobbs et al., 2011). The resplendent angelfish (*Centropyge resplendens*; Figure 10.4B) is a living jewel, highly sought after in the aquarium trade, but native only to Ascension Island, a rocky outpost on the Mid-Atlantic Ridge. While it is locally abundant, the restricted range was a primary reason IUCN listed the species as threatened. In contrast, the threadfin butterflyfish (*Chaetodon auriga*) occupies reefs from the Hawaiian Islands to the Red Sea (Figure 10.4C). Such large geographic ranges may be a buffer against extinction, as any catastrophic declines are likely limited to only part of the range. Overall the broad range of most marine species may be their salvation in terms of extinction risk.

10.3.3 Invasive Species

Harmful introduced species are recognised as one of the foremost conservation issues in ecosystems both above and below the waterline. Invasive species seem to be a greater problem for freshwater habitats, perhaps due to the higher population connectivity and fewer barriers in the oceans (Chapter 9). Nonetheless, invasive species also disrupt coastal ecosystems.

For a species introduced by humans to be considered 'invasive,' it must cause declines in the abundance of native species or otherwise be considered a pest. In the 1950s and 1960s, a variety of non-native coral reef fishes were introduced to Hawaii from the South Pacific in an attempt to enhance local fisheries. Unfortunately, the Peacock grouper (*Cephalopholus argus*) has proven to be an unpopular fishery target, due to the accumulation of toxins in its flesh from a dinoflagellate that causes ciguatera (tropical fish poisoning). Another reef fish introduced to Hawaii, the Bluestripe snapper (*Lutjanus kasmira*), brought a nematode parasite that has spread to local fishes.

By far the most devastating invaders among marine fishes have been Indo-Pacific lionfishes (genus *Pterois*), which were likely introduced to the Atlantic sometime in the 1980s, probably the result of multiple aquarium releases. From an initial breeding population in the vicinity of Florida, lionfish have spread across the greater Caribbean region and most recently to Brazil. Lionfishes are very effective predators of small reef fishes, reducing their abundance, in some cases perhaps sufficient to alter coral reef ecosystems (Albins and

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Hixon, 2013). Maybe the greatest risk that lionfish pose is to the small-range endemics. The Mardi Gras wrasse (*Halichoeres burekae*), restricted to a few reefs in the Gulf of Mexico, and the Social wrasse (*Halichoeres socialis*; Figure 10.4D) found only on reefs of Belize in Central America, are both regarded as Endangered by IUCN because of restricted ranges and habitat degradation. Predation by lionfish, which target small-bodied fishes, may be sufficient to drive such species to extinction (Rocha et al., 2015). One prominent remedial measure is targeted removals combined with culinary lessons in lionfish as seafood, which seem to be effective in some areas as community events.

10.3.4 Floating Marine Debris

Persistent plastics and other flotsam in the ocean may provide an underappreciated pathway for invasive marine species. The abundance of marine debris in the vast reaches of the North Pacific has allowed a damselfish (*Abudefduf vaigiensis*) to colonise Hawaii. Juveniles of these species inhabit floating ghost nets (abandoned fishing gear) and other marine debris, creating a dispersal mechanism that did not exist previously. The invader is now interbreeding with the Hawaiian Archipelago endemic species (*Abudefduf abdominalis*), which may be genetically swamped out of existence by hybridisation (Coleman et al., 2014). Following the massive 2011 tsunami in Japan, West Pacific fishes such as the striped beakfish (*Oplegnathus fasciatus*) were transported to the other side of the Pacific Ocean with floating debris.

In addition to providing a mechanism for dispersing invasive species, plastic debris has a more insidious negative effect on marine fishes as it breaks down into small particles. These plastic fragments, including microplastics that are often bonded with pollutants, are ingested by marine fishes and their larvae (Worm et al., 2017).

10.3.5 Low Reproductive Potential

Most teleost fishes can produce thousands to millions of eggs, perhaps allowing populations to rebound when adverse conditions are alleviated. In contrast, the sharks, rays and their relatives have a reproductive strategy that is similar to mammals, producing small numbers of well-developed progeny. Overfishing is by far the greatest threat to these fishes, because they cannot quickly rebound from a population crash. The demand for shark fin soup is especially devastating, inducing a barbaric fishery in which sharks are stripped of their fins on the boat deck, and then thrown overboard to die. Similarly, demand for the gill plates of manta and devil rays for traditional Chinese medicine has led to severe overfishing of manta and devil rays. An estimated 36% of sharks and rays are threatened according to IUCN criteria (IUCN, 2022).

Seahorses, pipefish and their relatives (Figure 10.2H) are another group with low reproductive output, in this case coupled with high parental care. Young are born as miniature adults, bypassing the larval stage, and are protected during the first few weeks of life in the father's brood pouch. This strategy has proven successful as seahorses thrive in all tropical oceans. However, this life history becomes a vulnerability under exploitation or habitat loss (Vincent et al., 2011). The Cape seahorse (*Hippocampus capensis*) is the most

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endangered member of this group. It has a restricted range in a few bays and estuaries in South Africa and is subject to habitat degradation by development and pollution. Millions of seahorses enter the Chinese medicinal trade each year, and hundreds of thousands more are shipped in the aquarium trade. The international trade agreement CITES list them as 'not yet endangered but a species of high concern', with voluntary trade limits observed by the United States and other nations.

The cardinalfishes (Family Apogonidae) are another group with small reproductive potential and unusual breeding habits. They are mouthbrooders, a common strategy in freshwater fishes that protects the young, but rarely seen in marine fishes. The higher survivorship of mouthbrooded young is coupled with a lower reproductive output, as only a few baby fish can fit in dad's mouth. This low reproductive potential, as with the sharks, creates a vulnerability to human disturbances. One extreme example is the Banggai cardinalfish (*Pterapogon kauderni*; Figure 10.4E), native to a few islands in eastern Indonesia. This attractive fish has a small geographic range (5500 km^2, contrasting with the average Indo-Pacific reef fish range of 9 million km^2) and like the seahorses, it lacks a pelagic larval stage. It has been intensively exploited by the aquarium trade, with some collection estimates exceeding 100,000 per month, and numbers are drastically reduced in some parts of the range. As a result of low fecundity, small range and high exploitation, IUCN regards this fish as Endangered. Fortunately, the Banggai cardinalfish can be bred in captivity, which may ultimately provide relief from overexploitation.

10.3.6 Evolutionary Twilight

As noted above, coelacanths were diverse, abundant and widespread in the age of dinosaurs, but are now limited to a few species in deepwater habitats. It is likely that the evolutionary history of coelacanths is almost over. However, natural extinction is a process that may play out over thousands to millions of years, whereas human perturbations occur over periods of decades and centuries. While some of the living fossils may be persisting on borrowed time, we should not hasten their demise by short-term assaults. It is possible that living fossils can break out with new evolutionary innovations (Bowen, 2016), so they have been recognised as Evolutionarily Distinct and Globally Endangered (EDGE) species worthy of conservation in their own right.

10.3.7 Overfishing

To date, the greatest threat to marine fishes has been overfishing: removing more fish from a population faster than the fish can reproduce. Much has been written on this topic, and we refer interested readers to the excellent book by Callum Roberts (2007). Overfishing has occurred since the dawn of civilisation, yet overexploitation skyrocketed with the Industrial Revolution. Large-scale commercial fishing began in the late 1800s with the introduction of steam trawlers in the British Isles. Within a few years, trawlers depleted local flatfish stocks, and began to fish further afield. From that time forward, the major threat to marine fishes has been increasingly efficient industrialised harvest. Reynolds et al. (2005) estimated that commercially exploited marine fishes have declined by 65% in

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breeding biomass relative to historical levels. Industrial fishing now occurs in >55% of the world ocean and has a spatial extent more than four times that of agriculture on land (Kroodsma et al., 2018). The fishes hardest hit are those with large body size and late maturity, and the net result is depleted continental shelves and a decline in the trophic level of fishery targets, a process known as fishing down the food web (Pauly et al., 1998). As noted above, low fecundity is also a factor, most especially for sharks and rays. The sea yields about 82 million tons of fisheries products per year, compared to about 12 million tons from freshwater.

The overfishing problem is severe. Worm et al. (2009) estimate that 63% of fish stocks are overexploited. Especially troublesome is the practice of targeting the largest fish, which are often the most productive and effective spawners (Hixon et al., 2014). Solutions to overfishing include catch restrictions that are not unduly swayed by political pressures, designating protected areas free from fishing to replenish fished areas and gear modifications to eliminate the most destructive practices. In the last category, bottom trawling can be especially damaging to fish populations as well as seafloor habitats. In addition to clear-cutting the seafloor habitat, trawls tend to produce huge volumes of discarded bycatch (Watling and Norse 1998), unwanted sea life that is mutilated, crushed and usually dead, including the young of many commercially valuable fishes.

10.4 Evil Twins of Ocean Warming and Acidification

Although overfishing has been the greatest threat to marine fishes historically, the twin threats of ocean warming and ocean acidification are rapidly becoming even greater challenges to life in the sea (Gattuso et al., 2015). Because ocean climate disruption is a looming catastrophe unknown to most non-experts, we dedicate much of the chapter to this growing threat. It is as yet uncertain whether these evil twins will merely produce both winners and losers among the fishes in the sea, or only losers.

By way of introduction, recent warming of the ocean as well as the atmosphere is caused by human activities, primarily excessive combustion of fossil fuels (coal, oil, natural gas) and burning of forests. These activities are releasing carbon dioxide and other gases that enhance the heat-trapping greenhouse effect, causing heat waves in the ocean as on land (Oliver et al., 2018). About 93% of the excess heat accumulates in the seas (Cheng et al., 2019), and from 1948 to 1998, the upper layers of the world ocean warmed by over 0.3 °C on average (Levitus et al., 2000). This seemingly small change has already caused intensified storms, altered rainfall patterns, rising sea levels, declining ocean productivity and oxygen levels, bleaching of reef-building corals and melting of polar ice (Gattuso et al., 2015).

Ocean acidification is the other pernicious effect of excess carbon emissions (Doney et al., 2009). About a quarter to a third of the carbon dioxide emitted into the atmosphere by human activities is absorbed directly by the oceans, where it chemically reacts with water and forms carbonic acid. The mean pH (an inverse measure of acidity) of the world ocean has dropped 0.1 units since the industrial era began, and like changes in ocean temperature, this seemingly tiny change has major ramifications for fishes and other sea

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life. Acidification robs seawater of dissolved carbonate, making it difficult for marine creatures to grow calcium carbonate (limestone) structures. This physiological inhibition has two major effects on marine fishes: direct and indirect. Directly, the inner ear stones or otoliths of fishes are affected, being the only bones of fishes made of calcium carbonate (most of the vertebrate skeleton is made of calcium phosphate). Indirectly, many single-celled planktonic organisms, invertebrates (including corals that build reefs) and even some seaweeds have calcium carbonate skeletons that are inhibited by ocean acidification. These changes are affecting both the food supply and the habitats of marine fishes.

Importantly, the rates at which the oceans are warming and acidifying are accelerating exponentially (Cheng et al., 2019), and these combined threats paint a dire picture for the future oceans (Gattuso et al., 2015). Bryndum-Buchholz et al. (2019) predicted that, if current rates of carbon emissions continue, marine animal biomass will decline by 15–30% in temperate and tropical seas by 2100. Some 60% of 825 exploited marine fish species are projected to experience very high extinction risk from a combination of overfishing and ocean climate disruption (Cheung et al., 2018). Time is short to reverse these dangerous trends (IPCC, 2018), and both grassroots activism and governmental action will be essential to curb carbon emissions and increase carbon sequestration. These are scientific facts which will not go away, even if ignored by corporations and politicians. As Aldous Huxley admonished denialists in his 1927 book *Proper Studies*, 'Facts do not cease to exist because they are ignored.'

10.4.1 Ocean Warming

Accelerating global warming has four major negative ramifications for ocean species and their ecosystems (Gattuso et al., 2015). Like all species, each marine fish has a preferred temperature range to which it is adapted. When the climate warms beyond normal preferences, affected organisms have only three choices: adapt in evolutionary time (centuries to millennia), move in ecological time (years to decades) or suffer physiological stress and increased mortality. With the rapid warming occurring today, the immediate solution is to move, and for marine fishes, this translates to following preferred cooler temperatures by drifting as larvae and/or swimming as juveniles and adults either into higher latitudes or deeper water. The ultimate result of fishes shifting their latitudinal or depth distributions is ecological reorganisation at best, and ecological catastrophe at worst, likely accompanied by lower fishery production (Free et al., 2019). New assemblages of species will eventually form, and there will likely be both winners and losers, with some species or populations going extinct. As reviewed below, those fishes that cannot shift their distributions are already facing physiological costs.

Second, as oceans warm, the timing of reproduction, larval development and other key population processes (i.e. phenology) are disrupted with largely unknown consequences. Species in warming seas have already advanced the timing of important activities, such as spawning, by an average of 4.4 days per decade during the late twentieth century (Poloczanska et al., 2013), with likely negative ramifications for fisheries.

Third, both horizontal and vertical ocean currents are being affected, which can drastically change productivity and thus food sources available to fishes. Typically, as the

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upper layers of the ocean warm, the ocean stratifies, meaning that a cap of warm water prevents deeper, cooler, nutrient-rich water from reaching the well-lit shallows. Without those upwelled nutrients, many marine plants – mainly the single-celled phytoplankton – cannot grow sufficiently to support complex ocean food webs. As Bakun et al. (2015) concluded bluntly, 'Ecosystem productivity in coastal ocean upwelling systems is threatened by climate change.' Ironically, not only does a warmer ocean provide less food for fishes, but also, because most fishes are 'cold-blooded' (with internal temperature the same as the environment), warmer fish require more food to survive. This situation is a negative double whammy. The resulting increase in respiration by affected sea life, combined with the fact that warmer water necessarily holds less oxygen, has caused the fish-free oxygen minimum zones at 300 m depth and elsewhere in the world ocean to expand.

Fourth, as detailed below, excessively warm seawater causes tropical corals to bleach and die, resulting in loss of coral reefs, which are the rainforests of the sea and the most species-rich assemblages in the ocean.

Distributional Shifts. As the oceans warm, many marine species are moving poleward (into higher latitudes) to match preferred water temperatures (Poloczanska et al., 2013). In general, the species that are shifting successfully are both mobile and ecologically generalised – i.e. not requiring special diets or habitats – criteria which fortunately include many fishes. There is also evidence of fishes moving into deeper, cooler waters as the surface layers warm. For example, a variety of North Sea fishes have not only shifted their geographical distributions poleward an average of 100 km over the past several decades (Perry et al., 2005), but also have moved into deeper water at a rate of nearly 4 m per decade (Dulvy et al., 2008). Simultaneous increases in latitude and depth have also been observed in various continental shelf fishes off the northeastern United States, and poleward shifts in the distributions of marine fishes have been documented worldwide.

The anchovies (genus *Engraulis*) that inhabit cold-temperate upwelling zones may be at special risk because they depend on upwelling of nutrient-rich waters. At peak abundance these species yield millions of tons for regional fisheries, the largest fisheries in the world by biomass. Anchovies along continental coastlines may shift into higher latitudes in response to warming. This is feasible along continental coastlines such as Chile and California. However, the anchovies that inhabit the southern tip of Africa have nowhere to go, as a shift into higher latitudes would deprive them of coastal upwelling.

In northern latitudes, boreal (cold-temperate) marine fishes have shifted northward and pushed Arctic fishes out of the Barents Sea, which connects the North Atlantic Ocean to the Arctic Ocean (Fossheim et al., 2015). The good news is that Atlantic cod (*Gadus morhua*) has reached a record high population size in the Barents Sea, despite being severely overfished to the south. Unfortunately, Arctic fishes, including various snailfishes, sculpins and eelpouts, are not coping well with the warming seas. These species are stressed physiologically by warmer temperatures, on top of facing competition and predation by northward-moving boreal fishes. Like the South African anchovy, Arctic species have

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nowhere to go, and are expected to suffer catastrophic losses. The analogues on land are cool-climate species that eventually become stranded at the tops of mountain peaks, unable to ascend to cooler altitudes as the world warms.

Because there are more species at lower latitudes closer to the equator, as fishes shift their distributions poleward, one would expect the number of species to increase in temperate and polar regions, all else being equal. This pattern has been observed in the North Sea. However, because new mixes of species may cause intensified competition and other negative interactions among species, diversity may also decline. Off southern California, warm-temperate species have displaced cool-water species that originally inhabited this region, resulting in a 15–25% reduction in the number of coastal marine fish species. Exacerbating this decline has been an overall decline in ocean productivity as the ocean warms (Gattuso et al., 2015). On average, with increasing ocean temperatures, marine fish communities become dominated by warmer-water species (Cheung et al., 2013). For example, a 29-year time series of the North Atlantic over 5 degrees of latitude west of Scotland detected a homogenisation of fish assemblages, such that what used to be cooler-water communities are increasingly resembling warmer-water communities (Magurran et al., 2015).

Note that shifts in the geographical ranges of most marine fishes will depend on successful larval dispersal, the drifting and swimming of tiny baby fish in the open ocean that ultimately replenish the adult population. Warming waters are expected to accelerate larval development, thereby reducing larval durations and thus the distance larvae can disperse. Less productive warming oceans may also provide less food for developing larvae (Gattuso et al., 2015). Overall patterns of larval dispersal are likely to shift substantially as the ocean warms (Gerber et al., 2014).

Physiological Effects. Tropical and polar fishes, as well as fish larvae in general, usually are most sensitive to ocean warming because they have narrower temperature tolerances. Over normal environmental ranges, metabolic activity in fish increases by about 10% for every 1°C rise in temperature, and increased metabolism requires additional food. If food is available, then warmer waters result in faster growth of fish. However, given that less food is available in a warming ocean (Gattuso et al., 2015), warmer waters result in decreased activity, decreased growth rates, and increased mortality. Overall, the ability of marine fishes to acclimate to a rapidly warming ocean appears to be limited, and there is evidence that maximum body size of marine fishes may decrease, further negatively affecting fisheries due to altered ecological interactions and reduced fecundity (Cheung et al., 2013).

Habitat Loss. The vast majority of marine fish species inhabit tropical coral reefs (Allen, 2008), which support over 25% of all marine species. Unfortunately, these rainbow gardens of the seas are not only among the rarest of marine habitats – occupying only 0.02% (250,000 km^2) of the surface area of the world ocean – but also the most endangered. Globally, 25–50% of our coral reefs have already been lost due to human activities (Eddy et al., 2021).

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One of the main reasons for the death of coral reefs is a phenomenon called ‘coral bleaching’ (Hoegh-Guldberg, 1999). Reef-building corals provide the structural foundation of coral reefs. These animals are actually partnerships of two organisms: the anemone-like polyp that we see, and special single-celled, plant-like dinoflagellates that live inside the polyp, called zooxanthellae (or simply ‘zoox’ by coral experts), which give the coral its colour. The association involves mutual feeding: the polyp feeds the zoox nitrogenous wastes that fertilise the microscopic plants, and the zoox in turn provide products of their photosynthesis. (By the way, because the zoox require access to sunlight, corals often assume leaf-like shapes similar to land plants. And corals are often greenish in colour because of the chlorophyll in the zoox.) Healthy corals secrete calcium carbonate (technically, aragonite) skeletons that create the structure of the reef, in turn providing food and shelter for a vast variety of species, especially fishes.

When the surrounding seawater becomes too warm, sometimes as little as 1°C above the normal summer maximum, the marvellous symbiosis between polyp and zoox breaks down and the zoox become more like parasites than mutualists. The coral then expels the zoox, leaving the colourless polyp (hence the term ‘bleaching’). If the water does not cool shortly thereafter, the polyp may die. Once the coral dies, the reef begins to erode and crumble, denying fishes and other creatures the shelter and food that the reef once provided. One of us wept in his facemask upon witnessing the complete death and collapse of his favourite coral reef in the Bahamas during the first global coral bleaching event in 1998 (Hixon, 2009).

To date, coral bleaching has been sporadic, yet its frequency and severity is increasing rapidly. It has been projected that tropical coral reefs worldwide will bleach every year by 2040, and that the oceans will be too warm for 46% of the world’s coral reefs by 2100. Currently bleached reefs provide a window to the future. One global survey found that 62% of reef fish species declined in abundance within 3 years following 10% (or more) loss of live coral cover (Wilson et al., 2006). Loss of coral due to bleaching can render some fish species more susceptible to predation and intensify competition in other species. Moreover, 10 times as many larval fish settle on healthy corals as on bleached corals. Pratchett et al. (2008) concluded ominously, ‘Coral loss has the greatest and most immediate effect on fishes that depend on live corals for food or shelter, and many such fishes may face considerable risk of extinction with increasing frequency and severity of bleaching.’ Such losses will directly affect nearby human communities due to declines in fisheries and other reef products.

10.4.2 Ocean Acidification

Ocean acidification is negatively affecting marine fishes directly in terms of developmental and physiological stress, as well as indirectly in terms of food and habitat loss. Because a broad range of marine species are likely to be negatively affected by an acidifying ocean (Doney et al., 2009), the food supply and ecological interactions of marine fishes will certainly shift, mostly in unpredictable ways. As experts Branch et al. (2013) warn, ‘Overall

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effects of ocean acidification on primary productivity and, hence, on food webs will result in hard-to-predict winners and losers.' The ramifications for marine fisheries are even less certain.

Physiological Effects. Efforts to understand the effects of ocean acidification have focused mostly on rearing larval fish in seawater at future low pH values, yet there have also been field studies at locations where natural carbon dioxide vents acidify seawater locally. For most marine fish species studied, ocean acidification causes a variety of physiological and associated sensory and behavioural problems (Heuer and Grosell, 2014). Underlying these problems, acidification negatively affects both protein synthesis and neurotransmitter function. A frequent result is that larval growth and development are stunted.

Declining pH also affects the growth and function of otoliths, the calcium carbonate inner ear stones of fish involved in orientation and hearing. Paradoxically, acidification may result in larger otoliths, yet often disorientation and reduced hearing capabilities. The sense of smell is also inhibited in acidified oceans, negatively affecting both sharks and bony fishes. Some fish even suffer neurological anxiety.

Habitat Loss. Coral reefs are expected to wither tremendously under the combination of coral bleaching caused by ocean warming (discussed above) and ocean acidification, which will likely inhibit the ability of corals to grow their calcium carbonate skeletons (Hoegh-Guldberg, 1999). As corals die, the entire reef ecosystem will shift in unpredictable ways, and may eventually collapse. Indeed, the Great Barrier Reef in Australia has already lost over 50% of the live coral cover. Coral loss in the Indo-Pacific region is increasing at about 2% per year, and it is projected that one-third of reef-building corals face elevated risk of extinction. Given that upwards of 8000 marine fish species are associated with tropical coral reefs (Victor, 2015), and that 8% of assessed reef fish species are already threatened with extinction (McClenachan, 2015), the long-term outlook for coral-reef fishes is dire.

10.5 The Future

We have summarised the life history factors and human assaults that push marine fishes toward extinction, including very small geographic ranges, invasive species, plastic debris, low reproductive rates, overfishing, habitat loss, and the multiple pernicious effects of ocean warming and acidification. However, the extinction crisis that is apparent in terrestrial and freshwater ecosystems has not yet reached the marine fishes. This situation perhaps reflects our ignorance of the trends and status of most species. Large geographic ranges, large population sizes, high fecundity and economic constraints on extreme overfishing may buffer many marine fishes from catastrophic loss. Alternately, these factors may merely slow the process of collapse due to ocean warming and acidification. Many researchers believe that the factors protecting marine fish populations are merely causing a slower march towards extinction. The reduction of many fishes to small populations, due to overfishing and other threats, puts previously abundant species at the same risk as small-range endemics. In other words, there may be an extinction debt that falls due if overfished species are not allowed to recover.

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Yet there is also good news. The cases of the Goliath grouper and Smalltooth sawfish reviewed above show that conservation can halt declines and promote recovery in a surprisingly short time. Additionally, marine conservation programmes have increasingly turned from single-species management to ecosystem-based approaches that explicitly include entire ecological systems as well as humans, so-called 'social-ecological systems' (Francis et al., 2007). This holistic perspective now dominates international conservation efforts, as indicated by the United Nations Global Centre for Ecosystem Management and the IUCN Commission on Ecosystem Management. Major tools for ecosystem-based management include marine protected areas (MPAs) where human activities are minimised (Cabral et al., 2020). In keeping with the vast geographic scale of many marine ecosystems and corresponding conservation issues, IUCN has set a goal of permanently protecting 30% of the world's oceans by 2030. It is fortunate that the number of large MPAs is steadily increasing, including the Ross Sea MPA in Antarctica, the Papahānaumokuākea Marine National Monument in the Hawaiian Islands and the Great Barrier Reef Marine Park in Australia. It is unfortunate that meeting the above goals is unlikely, given that, as of 2021, only about 7% of the world ocean is in designated or proposed MPAs, and only 2.7% is in fully implemented, strongly protected areas (Sala et al., 2021).

Fishes are the crowning achievement of vertebrate biodiversity and evolution. As such they have weathered climate changes throughout their 500 million year history, with planetary temperatures and seawater acidity both higher and lower than today. The key understanding for the contemporary climate crisis is not whether the oceans will warm and acidify – which is already happening – it is that ocean temperature and pH are changing extremely rapidly. To some extent the marine fishes will adapt, and they may shift habitats much more easily than their freshwater cousins. However, evolution and adaptation usually work on the scale of millennia, while damage wrought by humanity on our oceans, the cradle of life on Earth, is moving at the timescale of decades.

Many of the threats that beset marine fishes can be addressed by effective ecosystem-based management, yet the issues of ocean warming and acidification are global in scale and require committed governmental efforts to reduce and sequester carbon emissions (Mumby et al., 2017). The fate of marine fishes, and ocean life in general, is contingent on humanity working in common cause. The essential solution is maturation of the human species involving a 'great turning' toward true sustainability and an end to the culture of overconsumption (Korten, 2006).

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