15 Exploitation and other Threats to Fish Conservation

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15.1 INTRODUCTION

The traditional goal in fisheries management has been to obtain continuing yields from a living 'resource'. Concerns are raised when populations fall below levels that provide adequate yields or which fail to meet other specified reference points (Shepherd and Pope, Chapter 8, this volume). Unfortunately, fishers and fisheries biologists have had a lot to be concerned about lately, as maximum sustainable yields have been exceeded for many fisheries (Jennings et al. 2001b) with many stocks now in decline. There have been some spectacular declines of species with a wide spectrum of life histories and habitats, including various stocks of Atlantic cod, Gadus morhua, Peruvian anchoveta, Engraulis ringens, southern bluefin tuna, Thunnus maccoyii, swordfish, Xiphius gladius, and sablefish, Anoplopoma fimbrae (Fig. 15.1).

The economic and social hardships caused by population declines in so many fisheries around the world have received a great deal of deserved attention. The poorest of the world's countries (with a per capita gross domestic product <US\$5000) rely on fisheries to supply approximately 40% of their protein (Kent 1998). In richer countries, while diminished fisheries may not lead to starvation, the disruptions to livelihoods can still be enormous, as shown by the loss of 40 000 jobs in eastern Canada when the northern cod stock collapsed and was finally closed to fishing in 1992 (Hutchings and Myers 1994). Clearly, with such economic issues

at stake, politics has played a large role in the uptake of management advice, often erring on the side of continued employment rather than more stringent, less socially palatable management measures (Hart and Reynolds, Chapter 1, this volume).

Until recently, such failures of fisheries management policy have remained outside the mainstream conservation movement. Indeed, conservationists have generally taken much less interest in marine and freshwater environments than in terrestrial habitats. For example, a survey of papers published in the journal Conservation Biology found that only 5% were for marine species and habitats, 9% were freshwater, and 67% were terrestrial (Irish and Norse 1996). While there have been some notable public concerns about selected issues such as whaling, declines in fish populations have dwelt in the domain of 'management failures' rather than 'conservation problems' (Reynolds and Jennings 2000). This inattention to conservation issues in fishing has started to change during the past decade as conservationists have begun to worry about the possibility that fish populations may be unable to recover from severe declines (Reynolds and Mace 1999; Roberts and Hawkins 1999; Hutchings 2001a). Perhaps fishes may become extinct as a result of fisheries. We already know that they can be virtually eliminated from large parts of their ranges (Brander 1981; Casey and Myers 1998; Dulvy et al. 2000; Dulvy and Reynolds 2002). Thus, after swimming quietly in the backwaters of the environmental move-

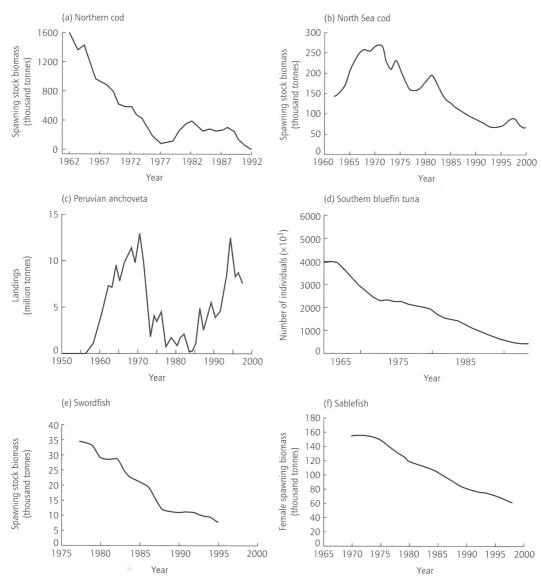


Fig. 15.1 Fish stock declines: (a) northern cod, *Gadus morhua* (Hutchings and Myers 1994); (b) North Sea cod, *Gadus morhua* (ICES 2001); (c) Peruvian anchoveta, *Engraulis ringens* (FAO 1999); (d) southern bluefin tuna, *Thunnus maccoyii* (Matsuda et al. 1998); (e) swordfish, *Xiphius gladius*; (f) sablefish, *Anoplopoma fimbrae* (http://www.mscs.dal.ca/~myers/welcome.html).

ment during the 1970s and 1980s, fishes are now featuring alongside other taxa as the public and scientists ask questions about links between exploitation and conservation (e.g. Mace and Hudson 1999; Hutchings 2001a; Reynolds et al. 2001al.

The goal of this chapter is to review the role of exploitation in causing conservation problems for fish species. We will review the evidence for severe declines in freshwater and marine fish populations which could lead to extirpation or extinction. We examine biological attributes of fishes and socioeconomic aspects of fisheries that render species vulnerable. This leads to a consideration of how 'conservation' of exploited species means different things to different people, as shown by difficulties in assessing the threatened status of marine fishes. We hope that this discussion will help to bridge the scientific gap between different approaches to 'conservation' of exploited species.

15.2 GLOBAL STATUS OF EXPLOITED FISH POPULATIONS

The fallacy that there are always more fish in the sea has officially ended. Marine capture fisheries produced 86 million tonnes in 1998, valued at US\$76 billion. The global marine fish catch was thought to have levelled out in the 1990s, but a predictive catch model suggests the global marine fish catch peaked in 1988 at 78 million tonnes and has since declined to 69 million tonnes (Watson and Pauly 2001; see Hart and Reynolds, Chapter 1, Volume 1). These figures omit the highly variable Peruvian achoveta catch and correct for massive misreporting by China (Watson and Pauly 2001). The FAO report that approximately half of the major fish stocks are fully exploited and very close to their maximum sustainable limits, with another quarter overexploited or depleted (Fig. 15.2). Only the remaining quarter of the world's fish stocks are considered to be under- or moderately exploited (FAO 1999).

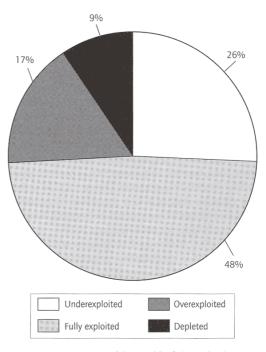


Fig. 15.2 Percentages of the world's fish stocks that range from underexploited to depleted. (Source: from FAO 1999.)

15.3 EXTINCTION

15.3.1 Recent extinctions

There are severe problems in estimating how many fish species have become extinct because of the difficulties of sampling aquatic habitats sufficiently well to be sure that a fish has truly disappeared from its entire range (Smith et al. 1993; Carlton et al. 1999; McKinney 1999). It is no longer fashionable for funding agencies to pay for basic taxonomy and collecting trips. Thus, lack of sampling effort as well as taxonomic uncertainties raise real difficulties in assessing accurately whether or not species have become extinct.

These problems are illustrated by an attempt to convey the strength of evidence for extinction of freshwater fishes, which has led to ongoing refinements of criteria and a database showing the level

of support for apparent recent (since AD 1500) extinctions of fishes (Harrison and Stiassny 1999; http://creo.amnh.org/). Examples of criteria that have been proposed include that the species' name should be taxonomically valid, and that attempts to collect the species during appropriate surveys have failed. Both of these requirements are often sticking points in conservation assessments of aquatic species. There has also been debate about whether one should wait some arbitrary period of time (e.g. 50 years) to be sure that a species has truly gone, but this requirement has been dropped by the World Conservation Union (IUCN's) Red List rules, as well as by the American Museum of Natural History's Committee on Recently Extinct Organisms (http://creo.amnh.org/).

Table 15.1 shows 34 fish species whose taxonomic status is clear and for which surveys have been adequate to be reasonably certain that they are extinct. This list does not include Lake Victoria cichlids, largely because of inadequate surveys (Harrison and Stiassny 1999). When these species are included, along with other cases of unresolved extinctions, the database includes a total of 164 species.

It is noteworthy that all known cases of recent extinctions of fishes (since AD 1500) have happened to be freshwater species, despite the fact that marine taxa account for roughly 60% of described species (Gill and Mooi, Chapter 2, Volume 1). While the compilation by Harrison and Stiassny (1999) focused on freshwater taxa, our own survey of the literature and discussions with colleagues did not reveal any marine species that we could add to the list with complete confidence. However, there are at least three reasonable candidates that may well be extinct (Roberts and Hawkins 1999; Hawkins et al. 2000). The Galapagos damselfish (Azurina eupalama) is a planktivorous species which disappeared during the 1982-3 El Niño in the eastern Pacific, one of the most intense El Niños for the last several hundred years (Glynn 1988). The warming associated with the El Niño shut down the upwellings that fuelled plankton production for nearly one year and the Galapagos damselfish has not been seen since, despite thorough surveys. The green wrasse (Anampses

viridis) was described from shallow waters around the island of Mauritius in 1839 but has not been seen since. It may have suffered from degradation of reefs in the area, due to sedimentation and nutrient pollution. Similarly, the deepwater angelfish, Apolemichthys guezi, endemic to the nearby island of La Réunion, seems also to have disappeared, though further sampling will be necessary to confirm this. Morris et al. (2000) also noted that several species of tropical groupers have not been seen for long periods since their first description. Although general rarity and poor sampling are probably to blame for their 'disappearance', groupers are highly vulnerable to overfishing (Coleman et al. 1996). Thus, while some of these marine taxa may rise from the dead, extinction of highly localized species in areas subject to detrimental human activities cannot be ruled

15.3.2 Palaeoextinctions

The fossil record may shed some light on whether extinction rates in marine habitats are really lower than in non-marine habitats. McKinney (1998) showed that in a variety of non-fish taxa, marine lineages have persisted on average for five times longer in the fossil record than have non-marine lineages. However, it is not clear whether these differences are due to differences among habitats per se, or due to differences among the taxa themselves, since none of the taxa analysed had representatives in both environments. If these broad taxonomic comparisons also apply to fishes, they would support the impression of lower rates of recent extinctions in marine habitats.

McKinney (1998) also looked at how duration of species in the fossil record related to the fraction of a taxon that was listed as threatened by the World Conservation Union (IUCN 1996). Fishes represented one data point among a number of broad taxonomic groupings. There was a positive relationship between extinction rates in the geologic past and the percentage of species currently threatened. Of course, these data are confounded because the most threatened taxa also tend to be the largest and best known, and the best-known species do

 Table 15.1
 Species of fish for which there is strong evidence of extinction. This list does not include Lake Victoria cichlids, nor many other species, due to uncertainties about taxonomic status or incomplete surveys of appropriate habitat.

| Family | Cenus | Species | Соттоппате | Former distribution | Extinction year | Extinction cause |
|------------------|-----------------|---------------|---------------------------------|-----------------------|-----------------|------------------|
| Adrianichthyidae | Adrianichthys | kruyti | duck-billed buntingi | Indonesia | >1983 | P-IN-D |
| Aplocheilidae | Leptolebias | marmoratus | gingerpearlfish | Brazil | >1944 | HM-P |
| Catostomidae | Chasmistes | muriei | Snake River sucker | United States | >1927 | HM |
| Catostomidae | Moxostoma | lacerum | harelip sucker | United States | 1893 | ΣI |
| Cyprinidae | Cephalakompsus | pachycheilus | | Philippines | >1921 | HM-IN-OE |
| Cyprinidae | Chondrostoma | scodrensis | | Yugoslavia | >1881 | P-0E |
| Cyprinidae | Cyprinus | yilongensis | | China | >1977 | 모 |
| Cyprinidae | Evarra | bustamantei | Mexican dace | Mexico | >1957 | HM-P-HD |
| Cyprinidae | Evarra | eigenmanni | plateau dace | Mexico | >1954 | HM-P-HD |
| Cyprinidae | Evarra | tlahuacensis | endorheic dace | Mexico | >1957 | HM-P-HD |
| Cyprinidae | Gila | crassicauda | thicktail chub | United States | >1957 | NI-MH |
| Cyprinidae | Lepidomeda | altivelis | pahranagatspinedace | United States | >1938 | 2 |
| Cyprinidae | Mandibularca | resinus | bagangan | Philippines | >1922 | HM-IN-0E |
| Cyprinidae | Notropis | атесае | Ameca shiner | Mexico | >1969 | HM-P-IN |
| Cyprinidae | Notropis | aulidion | Durango shiner | Mexico | >1961 | HM-P-IN |
| Cyprinidae | Ospatulus | palaemophagus | | Philippines | >1924 | HM-IN-OE |
| Cyprinidae | Ospatulus | trunculatus | bitungu | Philippines | >1921 | HM-IN-OE |
| Cyprinidae | Pogonichthys | ciscoides | Clear Lake splittail | United States | >1970 | HM-P-IN |
| Cyprinidae | Rhinichthys | deaconi | Las Vegas dace | United States | >1940 | MΗ |
| Cyprinidae | Sprattelicypris | palata | palata | Philippines | >1922 | HM-IN-OE |
| Cyprinidae | Stypodon | signifer | stumptooth minnow | Mexico | >1903 | HM-P |
| Cyprinodontidae | Cyprinodon | ceciliae | pupfish | Mexico | >1988 | WH |
| Cyprinodontidae | Cyprinodon | inmemoriam | cachorrito del la Presa | Mexico | >1984 | WH |
| Cyprinodontidae | Cyprinodon | latifasciatus | Parras pupfish | Mexico | >1903 | HM-P |
| Cyprinodontidae | Orestias | cuvieri | Lake Titicaca orestias | Bolivia, Peru | >1937 | Z |
| Fundulidae | Fundulus | albolineatus | whiteline topminnow | United States | >1889 | NI-WH |
| Gastoresteidae | Pungitius | kaibarae | Kyoyto ninespine stickleback | Japan | >1959 | HM-P |
| Gobiidae | Weberogobius | amadi | Poso bungu | Indonesia | >1985 | P-IN-D |
| Goodeidae | Characodon | garmani | Parras characodon | Mexico | >1880 | HM-P |
| Goodeidae | Empetrichthys | merriami | Ash Meadows killifish | United States | >1948 | NI-MH |
| Poeciliidae | Gambusia | amistadensis | Amistad gambusia | United States | >1968 | NI-WH |
| Retropinnidae | Prototroctes | oxyrhynchus | New Zealand grayling | New Zealand | >1923 | HM-IN-D |
| Salmonidae | Coregonus | johannae | deepwaterciscoe | Canada, United States | >1952 | IN-OH-HY |
| Salmonidae | Salvelinus | agassizi | silvertrout | United States | >1930 | HM-IN-0E |

Notes: Codes for cause of extinction: HD, habitat destruction, HM, habitat modification, HY, hybridization; IN, introduced species, OE, overexploitation, P, pollution, D, disease. [Source: American Museum of Natural History's Committee on Recently Extinct Organisms [http://creo.amnh.org/h.]

not live in the sea. We are therefore most likely to identify a species as threatened if it lives in a non-marine habitat. Nonetheless, McKinney concluded that the perception that marine species are less extinction prone is valid. Subsequent work has argued that the extinction rate of poorly known taxa in well-studied regions equals that of the best studied taxa – mammals (McKinney 1999). Thus, the appearance of relatively low extinction rates of fishes and other marine organisms may simply stem from artefacts of sampling biases and undersampling.

15.3.3 Causes of extinction

Human activities have been held responsible for all known cases of recent extinction (Fig. 15.3). Remember that, so far, all known extinctions have occurred in freshwater fishes (Section 15.3.1). Habitat alteration is the most important problem, and includes construction of dams and channels, as well as siltation and water extraction (e.g. Minkley and Deacon, 1991; Miller et al. 1999). The World Conservation Union's most recent *Red List* (Hilton-Taylor 2000) also lists habitat destruction as the most important cause of threats to birds, mammals and plants.

Introduced species pose a major threat to native fishes (Courtney and Sauffer 1984; Froese and Torres 1999). They rank as the second most important threat to freshwater fishes, again mirroring the threats posed to birds, mammals and plants, where introduced species rank as either the third or fourth most important threat, depending on the taxon. Over a decade ago, Welcomme (1988) was able to compile data on 1354 introductions of 237 alien fish species into inland waters. For 72 species, it was possible to document the outcome of the introduction in terms of impacts on the environment, including native fish species. Twenty-five of these introduced species had harmful impacts, including reduction or elimination of native fish populations, introductions of parasites to native fishes, physical disturbance of habitats, or severe depletion of native fishes due to predation.

Introductions can also cause problems through direct and indirect interactions with native populations of the same species (Ward, Chapter 9, Volume 1). Escapes of farmed fishes are widespread; for example 20–30% of spawning Atlantic salmon (Salmo salar) in Norway are of farmed origin. Various studies have shown genetic differences between farmed and wild salmon in important

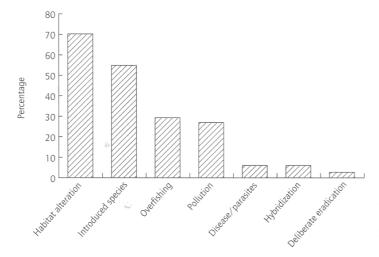


Fig. 15.3 Percentages of fish extinctions attributed to specific causes. The percentages pertain to a total of 70 species of fish, all occurring in freshwater habitats (see text) but excluding Lake Victoria cichlids. Many species were affected by more than one problem. (Source: from Harrison and Stiassny 1999.)

fitness traits (e.g. Einum and Fleming 1997; Fleming and Einum 1997). An ambitious field study in Norway showed that farm fish were competitively inferior to wild fish, with a lifetime reproductive success of 16% of that of wild fish (Fleming et al. 2000). Males were particularly inferior, courting females about one-third as often as did wild males, and obtaining only 24% of the breeding success of wild males. Thus, the main route of gene flow was from wild males mating with farm females. Overall, farm fish contributed to a reduction in productivity by wild fish by over 30%.

Pressures to farm genetically modified fishes have brought concerns about introduction of alien species and genes into uncharted waters. For example, transgenic salmonids have been created with the objective of enhancing growth rates of fish used in aquaculture (e.g. Devlin et al. 2001). The environmental impacts of escapes to the wild are unknown, but the lessons from studies of farmed fish described above suggest that concerns would be well founded (Hedrick, 2001). Thus, while no species is known to have become extinct as a result of competition with non-native populations of the same species, hybridization between wild and domesticated fishes has certainly led to the loss of genetically distinct native populations, which we expect to accelerate with the use of transgenic fishes. There may be impacts on wild populations through competitive interactions, as well as genetic introgression, because it is doubtful that sterility can be achieved with 100% success.

Overfishing ranks as the third most important cause of extinction of fishes (Fig. 15.3). The importance of exploitation in general rises if we consider secondary activities related to it, such as introductions of alien species. The most notorious case has been the introduction of the Nile perch (*Lates niloticus*) to a fishery in Lake Victoria (Witte et al. 1992). This predatory species has had a devastating impact on rock-dwelling haplochromine cichlids, though estimates of the exact number of species lost are severely hampered by uncertainties about taxonomic relationships, incomplete sampling, and the role of additional threats such as ecosystem alterations due to eutrophication and introduced macrophytes (Harrison and Stiassny 1999).

The problems faced by Lake Victoria cichlids exemplify the typical situation whereby fish populations are rarely threatened by a single process. Instead, the direct impacts of fishing, as well as indirect impacts related to fishing, often combine with various forms of habitat degradation to threaten species (Beverton 1992). These problems are particularly acute in freshwater bodies and in coastal zones, as these waters are the recipients of virtually every form of human waste (Moyle and Leidy 1992). In North America, multiple factors were implicated in 82% of extinctions of 27 species and 13 subspecies during the past 100 years (Miller et al. 1999).

Although there is a paucity of known extinctions of marine fish species, we can gain some insights into differences between marine and freshwater environments in processes that may lead to extinction by making comparisons among taxa. A comparison of threatened species of freshwater fishes confirms the findings for extinction risk, with species most heavily threatened by habitat loss and introductions (Froese and Torres 1999). Indeed, there is a correlation between the number of introductions and the number of IUCN threatened species at a national level. In contrast, marine introductions have not been linked to any extinctions of native fauna. An analysis of the relative importance of different causal factors of extinctions in the Wadden Sea over the past 2000 years suggested that overexploitation was responsible for the loss of six species of fishes, with habitat loss responsible for the loss of four additional species (Wolff 2000). These two factors together are thought to have contributed to the loss of two more fish species, and pollution together with habitat loss has caused the loss of one more species.

15.4 EXPLOITATION AS A CAUSE OF DECLINES AND EXTINCTION

Comparatively little is known of the disappearances of some fishes. For example, declines of the

endemic New Zealand grayling (*Prototroctes oxyrhynchus*) were first noted in the year in which the species was described, 1870. This species is presumed to have become extinct by 1930 from a combination of habitat degradation due to deforestation plus the impacts of introduced salmonids. Exploitation may not have been a major culprit here, though neither of the two proposed explanations is conclusive (McDowall 1996).

15.4.1 Targeted species

The common sturgeon (Acipenser sturio) is now captured only rarely in Europe. Historically this species was highly regarded as a food fish, contributing 70% of the fish consumed around the southern Baltic Sea during the 7th-8th century. By the 11th century this species was extinct in the Netherlands and by the 12th century sturgeon were so rare that all captures in the United Kingdom and France were reserved for kings. So by the 14th century sturgeon had been reduced from a common to a quantitatively insignificant portion of the fish catch (Hoffmann 1996). International trade in this species has been restricted under the Convention on International Trade in Endangered Species (CITES) since 1983 and the species is listed under the IUCN Red List as critically endangered and it is protected under Appendix III of the Berne Convention. All other species of sturgeons and paddlefishes (Acipenseriformes) are threatened by multiple factors including overexploitation for caviar, habitat loss through dams, channelization, degradation of spawning habitat and pollution. To date one species and one population of Acipenseriformes are listed as extinct, 6 species are critically endangered, 10 species are endangered and 7 are listed as vulnerable (Hilton-Taylor 2000). Two species, Acipenser sturio and A. brevirostrum, are listed in Appendix I of CITES. At the time of writing, Russia, Kazakhstan and Azerbaijan have declared a complete moratorium on the capture of sturgeon species from the Caspian Sea, and Iran exercises strict controls.

Direct exploitation has caused the collapse of many targeted fish stocks. There are some cases where fishing alone has caused the collapse, such as the Georges Bank haddock and various cod stocks on both sides of the Atlantic (Fig. 15.1). The decline of the sablefish (*Anoplopoma fimbrae*) off the west coast of the United States provides another example, with stocks reduced by half over a period of 27 years (Fig. 15.1f).

Declines have often been assisted by unfavourable environmental conditions, as illustrated by the short-lived early maturing herring-like fishes - clupeoids. For example, Peruvian anchoveta stocks crashed dramatically in 1972 as a result of a strong El Niño event that moved warmer waters nearshore and led to the shutdown of upwelling, consequently reducing availability of their planktonic food (Fig. 15.1c) (Glantz 1979). Intense fishing continued on the now more vulnerable schools that had been pushed shorewards. The anchoveta has taken 25 years to recover, and this process was hindered by smaller El Niño events after the initial collapse. There are numerous other examples of combinations of exploitation and environmental problems causing collapses of stocks, such as the Monterey Bay sardine fishery (Chapter 1, this volume) and the southern North Sea herring fishery.

A marine fish that is listed under the United States Endangered Species Act is the the totoaba (Totoaba macdonaldi). The plight of this species highlights several impacts of exploitation and the ways in which they interact with other environmental problems. The totoaba is a huge species of croaker (Sciaenidae) which is restricted entirely to the northern half of the Gulf of California. In the early 20th century, when directed fishing on the species first began, each year the fish migrated in huge shoals, following the coast north to their spawning grounds at the mouth of the Colorado River. The fish were enormous, reaching lengths of more than 2m and weights upwards of 100 kg (Cisneros-Mata et al. 1995, 1997). Initially, they were caught simply for their swim bladders, which were sent to the Far East for thickening soups. The bodies were piled on the shore to rot or were used as fertilizer. It was only in the 1930s that a market developed in California for the meat and the fishery prospered, peaking at 2300 tonnes per year in 1942 (Cisneros-Mata et al. 1995).

Totoaba were just too easy to catch. Sometimes the shoals ran so thick and close to the coast that the fish could be pitchforked out of the water. But gill-net fisheries began the real decline and the fishery soon crashed, falling to just 59 tonnes in 1975. Fishing for totoaba has been banned in Mexico since 1975, but the species has continued to decline due to bycatch in gill-nets set for other species, and increasing bycatch of juveniles by shrimp trawlers near the Colorado River estuary (Roberts and Hawkins 1999). Added to the problems of bycatch, the estuarine nursery habitat has been transformed over this period from brackish to predominantly saline, a consequence of abstraction of water upstream for irrigation. The case of the totoaba demonstrates how marine species can be reduced from prolific abundance to the edge of extinction just as surely as terrestrial

It is relatively easy to track declines of important target fishery species such as the totoaba. It is much more difficult to document declines in nontarget species, or species of minor commercial importance. For example, the smalltooth sawfish has never been of much commercial interest. Like the totoaba, this estuarine species has been badly hit by bycatch in fish nets and habitat degradation. It has been extirpated sequentially from estuaries on the Atlantic and Gulf of Mexico coasts, and is now largely restricted to a few lagoons off the Florida coast (Anon. 2001).

Another example of severe population declines involves rockfishes (Scorpaenidae) off the west coasts of Canada and the United States. This complex of 72 species supports important commercial and recreational fisheries (Yoklavich 1998; Glavin 2001). However, only a few are common enough for the US National Marine Fisheries Service or the Canadian Department of Fisheries and Oceans to be able to collect reliable data on their rates of capture. Those data show such steep declines in abundance for several species that extinction is possible. One of them, the bocaccio (Sebastes paucispinis), has been added to the World Conservation Union's Red List of Threatened Animals, but it is far from being the least common rockfish, or the most threatened. We simply lack good data on

the status of the many species that are rarer than bocaccio.

Artisanal fisheries are often thought to be less damaging than industrial ones, but there is extensive evidence that they also cause species extirpations, which may be the first steps on the road to extinction (Roberts 1997). What is important is not the fishing methods employed, but the intensity of fishing. Tropical reef fisheries are often pursued at a subsistence level and may be the last resort of poor people in developing countries (Polunin and Roberts 1996). The rapid expansion of human populations in coastal areas has driven enormous increases in exploitation rates. In the Caribbean, for example, several of the larger species of groupers have been extirpated from intensively fished islands such as St Lucia and Dominica (Hawkins and Roberts, unpublished data; see also Section 15.5.2, below). Such extirpations have also been documented in the Indo-Pacific, especially in southeast Asia where the growing live-food fish trade targets larger species like groupers (Bryant et al. 1998). Extirpations have even been recorded in subsistence fisheries, where fish and other organisms are captured solely for local consumption. Extirpations of the giant clam (Tridacna gigas) and the bumphead parrotfish (Bolbometopon muricatum) have been documented from subsistence fisheries of the isolated Lau Island group, Fiji (Lewis et al. 1988; Dulvy and Polunin unpublished data). Human populations on these islands have not expanded significantly and they still have poor trade links (Zann 1992).

So widespread is overexploitation on coral reefs that even species with large geographic ranges may be at risk of extinction. Morris et al. (2000) recently examined the status of 85 species of epinephelinae groupers (Serranidae) that inhabit coral reefs. They found evidence for serious declines in 37 species, two of which they proposed for 'endangered' status in the World Conservation Union's *Red List* and a further 35 as 'threatened'.

Hawkins et al. (2000) drew attention to the fact that there are far more species of small island endemics than had been believed previously. They found that nearly 10% of a sample of 1677 coral reef fish species had geographic ranges <50000 km²

(equivalent to an area of reef habitat of perhaps as little as a few hundred square kilometres). Many restricted-range species are small, like damselfish and wrasses, but direct exploitation for the ornamental fish trade may put some of them at risk. For example, the Banggai cardinalfish (*Apogon kauderni*) has an extremely limited distribution in central Indonesia, where it has been heavily collected for the aquarium trade (Allen 2000). As it can be bred in aquaria, it is unlikely to go extinct, but it could disappear from the wild.

15.4.2 Non-target species

Many other species of vertebrates, fishes and invertebrates are captured alongside the target species in the relatively non-selective fishing gears commonly used, predominantly trawl nets on temperate shelves and encirclement nets, traps and hook-and-line gears in reef fisheries. In the north Australian prawn trawl fishery there are 411 species of fish bycatch alone (Stobutzki et al. 2001). Many species are simply thrown back, while others are retained as they have some commercial value, such as skates. The North American barndoor skate (Dipturus laevis) (Casey and Myers 1998) and the European common skate (D. batis) (Rijnsdorp et al. 1996; Walker and Hislop 1998) have similar problems due to bycatch in trawl fisheries directed at groundfish stocks. Brander (1981) conceded that we may have to accept the possible extinction of such low-value bycatch species as a consequence of capturing more valuable species. It was suggested that the barndoor skate may be close to extinction, although recent surveys suggest a comeback, restricted to large, no-trawl areas on Georges Bank (S. Murawksi, personal communication). The common skate is restricted to a few de facto refuges where the bottom is too rough to fish. Dulvy et al. (2000) argued that the problem of skate extirpations is more general than for these species alone, but the problems of detecting declines and extirpations of individual species have usually been masked by the lumping of different species into general categories in fishery statistics a common practice for low-value fishes. We are only just beginning to look into how many other species are threatened by industrial-scale fisheries.

15.4.3 Ecosystem impacts

Exploited species are connected to many others by reticulate webs of behavioural and trophic interactions, the simplest of which are direct interactions such as predation, competition and mutualisms (Chapters 11-16, Volume 1). Furthermore, there are many less direct interactions through which exploitation, pollution and dam construction may have profound and less predictable consequences (Menge 1995; Pinnegar et al. 2000). In freshwater systems eutrophication can lead to phase shifts from macrophyte- to phytoplankton-dominated production systems (Strong 1992; Pace et al. 1999; Scheffer et al. 2001). Such phase shifts can stem from trophic cascades, where the removal of a top predator, which controls the abundance of a herbivore, affects the abundance of key basal species, such as algae (Pinnegar et al. 2000; Kaiser and Jennings, Chapter 16, this volume). In hard substrate marine ecosystems trophic cascades have been found to control coral-algal abundance in tropical systems and kelp-coralline algal abundance in temperate systems. One of the key problems is that there is currently no way of predicting which species have critical ecosystem roles.

Fishing down food webs, the removal of top predatory fishes, and subsequent targeting of species further down the food chain, is globally widespread; although the details can be disputed, the pattern is consistent (Caddy et al. 1998; Pauly et al. 1998a,b). Unfortunately, the ecosystem implications of removing top predators (such as sharks) is at best unclear and at worst may be idiosyncratic or unpredictable (Stevens et al. 2000). One suggested consequence of fishing down food webs is that it could lead to ecosystems dominated by microbial loops (Jackson 2001). There have been various pathogen outbreaks resulting in the dieoffs of Caribbean seagrass beds, corals and remaining herbivores, which may be connected with overexploitation of megafauna, such as manatees, turtles, large predatory fishes and herbivores (Jackson 1997; Wing 2001).

Recent attention has focused on the disturbance effects of trawl gears on the benthos. Heavy, mobile trawl gears resuspend sediments and kill or injure benthic invertebrates, which are then eaten by scavengers (Hall 1994; Kaiser and Spencer 1996; Jennings and Kaiser 1998). This has resulted in declines of benthic invertebrates (Collie et al. 2000). Recently, an analysis of benthic invertebrate community production: biomass ratios along a fishing gradient has demonstrated that trawling has negative impacts on secondary benthic production (Jennings et al. 2001a).

Habitat degradation is responsible for estuarine species topping the list of threatened species in the sea, largely through human development and pollution (Roberts and Hawkins 1999). Estuarine and nearshore habitats like salt-marshes, mangroves and seagrass beds provide critical spawning and nursery habitats for a wide range of species, including many that we exploit. Such habitats have been cleared extensively for aquaculture, agriculture, development and timber. The US has lost more than 50% of its salt-marshes during the last century (Agardy 1997), while many countries in southeast Asia have cleared as much as 80% of their mangroves in recent decades (Spalding 1998). By interrupting critical phases of the life cycles of species, habitat destruction has caused many species to decline. Estuaries are also foci for introductions of invasive species that may threaten native fauna (Cohen and Carlton 1998). For example, the spotted handfish (Brachionichthys hirsutus) is restricted entirely to the Derwent River estuary in Tasmania and may be threatened by predation on its benthic egg clusters by starfish (Roberts and Hawkins 1999).

Other marine habitats are also being damaged and destroyed at accelerating rates. For example, the widespread use of highly destructive blast fishing in southeast Asia is converting diverse and complex habitats to rubble (Cesar et al. 1997). Local impacts and habitat loss such as the construction of a military airbase in Castle Harbour, Bermuda, has led to the local extirpation of 10–14 species of reef fishes (Smith-Vaniz et al. 1999). Furthermore, habitat destruction is sufficiently widespread that it could cause global extinctions,

especially for species with small ranges. Many of the restricted-range coral reef fish species documented by Hawkins et al. (2000) had ranges overlapping regions where reef habitats are under growing pressure. For example, the damselfish (*Chromis pelloura*) is restricted entirely to the far northern Gulf of Aqaba in the Red Sea, where it is hemmed in by intensive coastal development. The splendid toadfish (*Sanopus splendidus*) occurs only on reefs around the island of Cozumel in the Mexican Caribbean, an area undergoing rapid tourism development.

Recently, it has become clear that coral reef environments are highly sensitive to seawater warming associated with global climate change (Reaser et al. 2000). The year 1998 saw the most widespread coral bleaching and subsequent mortality so far documented. Coral mortality reached 70-90% throughout large regions of the Indian Ocean (Wilkinson 2000). Such large-scale habitat degradation, especially if combined with other human pressures such as overfishing, could trigger extinctions. Indeed theoretical estimates of the number of extinctions likely to have been caused by coral bleaching have been calculated using the species-area curve method. This approach indicates that about 1000 species may already have been lost if we accept the most conservative estimate of a loss of 5% of the world's reefs (Carlton et al. 1999). The key caveat is that bleaching causes hard and soft coral loss alone, rather than complete loss of all reef microhabitats. There are bound to be species thriving on reefs with little or no remaining coral as a consequence of bleaching.

15.5 WHAT RENDERS SPECIES SUSCEPTIBLE TO OVERFISHING?

From the foregoing discussion and various reviews (e.g. Beverton 1992; Roberts and Hawkins 1999; Reynolds et al. 2001b), we have picked out five key features of the biology of fishes and the motivations of fishers that render fish populations susceptible to overfishing.

15.5.1 Catchability remains high as population size decreases

Species that form shoals can still be targeted profitably by fishers even as the total population sizes decline (Pitcher 1995; Mackinson et al. 1997). Thus, species such as herring and Peruvian anchoveta can still be caught effectively by purse seines as populations decline. This continuing efficiency works against the old concept that as fish became rare, they would become unprofitable and therefore subject to lower mortality (see also next section).

Species that migrate through physical bottlenecks, such as diadromous salmonids, shads and sturgeons, are susceptible to high mortality due to focused fishing effort and pollution outputs associated with the dense human populations of river mouths (McDowall 1992). The impact of dams on freshwater fish populations, particularly the Atlantic salmon (Salmo salar), has been known since before 1214, when a Scottish statute required that all dams be fitted with an opening (Hoffmann 1996; unpublished data). Damming and the introduction of dikes also contributed to the decline of the common sturgeon. This was confirmed by the revival of catches after floods destroyed barriers in the southern Baltic in the 1400s. The catches remained high until new reclamation works in the 1800s (Hoffmann 1996; unpublished data). Conservation of salmonids remains a serious concern, as their discrete freshwater spawning populations remain subject to a variety of threats, including forestry and damming (Jonsson et al., 1999). To date, 55 evolutionarily significant units (ESUs) are recognized for the seven anadromous species of Pacific salmon, of which 23 ESUs are listed as endangered under the US Endangered Species Act (R.S. Waples, personal communication).

Species with limited physiogeographic ranges, living in small catchments, with specific breeding and feeding habitats appear to be particularly vulnerable to extinction in freshwater habitats (Angermeier 1995; Parent and Schriml 1995). In the sea critical habitats such as locations where groupers aggregate to spawn are vulnerable. The loss of subpopulations may result in the loss of be-

havioural resilience in the population as a whole. There is growing evidence of assortative mating and genetic substructuring on even spatially diffuse breeding grounds of more wide-ranging species such as cod (Hutchings et al. 2000; Nordeide and Folstad 2000; Ruzzante et al. 2000). Such aggregations are easily targeted.

The classic example of vulnerability due to fishers targeting spawning aggregations concerns the Nassau grouper (*Epinephelus striatus*) (Sadovy and Eklund 1999). In some areas of the Caribbean approximately 90% of commercial and recreational landings of this species came from spawning sites. Aggregations no longer form at some previously known traditional sites in Belize, the Dominican Republic, Honduras, Mexico and the Bahamas, while none of the previously known aggregations remain in Bermuda, Puerto Rico, or the US Virgin Islands. In Cuba, 21 aggregations were known in the 1800s. Today, however, only one of these sites is known to remain in use. The status of many other spawning aggregations is unknown.

15.5.2 Fish are highly valuable

Some fish derive their value not only as a source of protein, but also from cultural or social values leading to premium prices. Buyers capable of paying for rare species may advertise their wealth and social status. The reservation of caviar and sturgeon for English and French nobility in the 14th century is testament to the deep-rooted existence of this behaviour, which continues today in fine restaurants. Raw tuna or sashimi is highly coveted by rich restaurant-goers in Japan. The most prized species is the southern bluefin tuna. It set a new price record early in 2001, when US\$178 000 was paid for one individual (Watts 2001). Western Atlantic bluefin tuna (Thunnus thynnus) has sold for up to US\$83 500 for a single individual. It provided 2400 servings of sushi, worth US\$180000. Another expensive fish is the giant yellow croaker (Bahaba taipingensis), which has been exploited for its swimbladder in the South and East China seas from Shanghai to Hong Kong. In recent years the swimbladder, or maw, has been called 'soft gold' due to market prices of US\$20000-64000 per kg

(Sadovy and Leung 2001). It is highly valued for its medicinal properties, and as a health tonic, and is typically boiled and drunk as a soup. Despite the near extinction of this species, 100–200 boats still target its historical spawning sites in the hope of netting a windfall (Sadovy and Leung 2001).

Unfortunately for conservation efforts the high prestige and price of rare species often widen the geographical net to meet demand, thereby threatening even those species that have large ranges. The humphead, maori or Napoleon wrasse (Cheilinus undulatus) is a highly valued commodity in the live reef fish trade centred in Hong Kong and reaching Taiwan, Singapore and China. It is worth a retail price of up to US\$130 per kg, with parts of this fish reaching much higher prices (Lau and Parry-Jones 1999). As southeast Asian sources have been overfished, demand has led to fishing explorations and export operations as far away as the Seychelles, Fiji and Kiribati (Bentley and Aumeeruddy 1999). This increasing price associated with biological and market rarity has meant that it is economically viable to fly fish to markets from such distant sources. This species is now listed as threatened under IUCN criteria (Donaldson and Sadovy, 2001). Given the role that increasing 'rarity value' has had in depleting terrestrial species such as African elephants, rhinoceroses, tigers and musk deer, it is difficult to see how current aquatic conservation methods can protect such species. International trade can be prevented through CITES Appendix I listing, if enforcement is adequate. However, this would not prevent trade within countries, and this measure would only be introduced after species had already declined seriously.

15.5.3 Fish are susceptible to capture as non-target species

If fish are caught as a byproduct of other activities, they again defy the hope that unprofitability at low population sizes might protect their populations. We have already described several examples of this problem for species such as skates and rays (Section 15.4.2). Stevens et al. (2000) noted that roughly 50% of elasmobranchs are taken as bycatch

without any regulations, and these species rarely appear in catch statistics. Non-target species thus inhabit the poorly known underworld of fisheries conservation. They are either discarded at sea or, if landed, they often fetch a lower price than the species being targeted. Therefore they do not attract much attention from assessment biologists or managers.

15.5.4 Life histories result in low productivity

Species with long generation times, low natural mortality rates and slow body growth are expected to be less able to withstand elevated mortality (reviewed by Musick 1999b; Reynolds et al. 2001b). This has been shown on theoretical grounds (e.g. Adams 1980; Kirkwood et al. 1994; Pope et al. 2000), and it has been borne out by comparisons among diverse taxa (e.g. Jennings et al. 1998, 1999a, 1999b; Dulvy et al. 2000). Thus, sharks and rays feature prominently in the Red List of Threatened Animals (Hilton-Taylor 2000), on the basis of severe population declines under exploitation. Other examples of species with life histories that are incompatible with elevated mortality include sturgeons, rockfishes (Sebastes) (Section 15.4.1) and orange roughy (Hoplostethus atlanticus) in New Zealand, which reaches maturity in its twenties to thirties and may live to a maximum age of 150 years (Smith et al. 1995; Horn et al. 1998). The coelacanth (Latimeria chalumnae) also fits this category. While most details of its life history remain unknown, this species has the lowest metabolic rate known for any fish (Fricke and Hissmann 2000). This suggests a very slow life history, which would render the species susceptible to the mortality that individuals suffer as a result of bycatches in deepwater artisanal fisheries in the Comoros and in Indonesia (reviewed by Fricke 2001).

15.5.5 Per capita recruitment decreases as population size decreases

Depensation, called the 'Allee effect' in terrestrial systems, occurs when there is a positive relationship between individual productivity and popula-

tion size (Myers, Chapter 6, Volume 1). In fisheries, depensation can occur due to a reduced ability to aggregate and find mates, reduced fertilization success, or increased predation rates (reviewed by Petersen and Levitan 2001). The concern here is that as fish stocks are pushed downwards, they may fall over a cliff of recruitment from which they cannot climb back. A Bayesian analysis of various fish stocks by Liermann and Hilborn (1997) showed that scatter in relationships between stock sizes and recruitment cause considerable difficulties in detecting depensation, if it exists. For a number of species of cod relatives (Gadiformes), flatfishes (Pleuronectiformes) and herring relatives (Clupeiformes), the authors found that the tails of probability distributions for the likelihood of depensation extended well into the depensation range. However, attempts to quantify the prevalence of depensation based on current stockrecruitment (S-R) models may be too conservative. This is because current models assume that recruitment is zero only when the stock is extinct. However, Allee effects, by definition, involve low recruitment despite the continued presence of spawners. Therefore, future assessments of the existence of depensation in fishes may need a new family of S-R models, which do not necessarily have their origin at zero (Frank and Brickman

15.6 CONSERVATION MEETS SUSTAINABLE USE

Conservationists traditionally worry about preventing extinction, whereas resource managers in fisheries and forestry traditionally ignore extinction risk, and worry instead about obtaining high sustained yields (Mace and Hudson 1999). Of course, if the yield objective is achieved, we won't have to worry about extinction! However, most of the world's exploited fish species are not being assessed or managed. Therefore, extinction cannot be ruled out for many species that have the vulnerable characteristics listed in the previous section, especially if exploitation exacerbates other problems such as habitat degradation, pollution and

introductions of alien species. These problems are particularly acute in freshwater habitats. Furthermore, many conservationists point to the repeated failure of fisheries management to maintain adequate populations, even when fisheries are under the 'control' of single nations or unions of member states. The northern cod stock(s) off Newfoundland, which has still not shown convincing signs of recovery since a ban on fishing was imposed in 1992, is the most recent notorious example. Some resource managers counter that there are still millions of Atlantic cod in the sea, and that you couldn't kill off this species if you tried. At this point, conservationists tend to bring up the fate of the passenger pigeon (Ectopistes migratorius), which once numbered between 3 and 5 billion in the mid-1800s, but became extinct in 1914. The debate continues from there.

How did we come to this? We blame cod and haddock. Specifically, it was their listing as 'vulnerable' (to extinction) by the Red List of Threatened Species (IUCN 1996) that triggered a confrontation between some conservationists and some resource biologists. The species were listed on the basis of their population declines within the previous three generations. Rate of decline is one of five criteria under which a species can be listed as threatened. The others are small distribution combined with declines or fluctuations, small populations combined with declines, very small or restricted ranges, and quantitative population models that vield pessimistic outcomes. A caveat was published with the Red List, which noted that its designations may not be appropriate for fish species that are subject to management by fisheries. However, this did not save the Red List's rate-of-decline criterion from criticism by many fisheries biologists (e.g. Musick 1999a; Butterworth 2000).

One criticism of the *Red List*'s treatment of exploited fishes is that traditional management practice suggests that populations should decline to about 50% of virgin population sizes in order to maximize productivity (e.g., Schnute and Richards, Chapter 6, this volume). So in theory, a perfectly well-managed abundant species could be brought quickly to 50% of its population size and provide a maximum yield, only to be listed by a

globally recognized conservation body as threatened with extinction. In practice, of course, one could suggest that this is all a moot point, because there are few examples of any virgin population of fishes being brought down to 50% (and not beyond) in the controlled way envisaged by this hypothetical scenario. But even if this situation is only hypothetical, it does suggest an anomaly, which the IUCN has been trying to fix (see below).

Another problem that has been raised is that it is difficult to distinguish between 'real' declines and population fluctuations in many marine fishes (Butterworth 2000). A recent study by Hutchings (2001b) suggested that fish populations do not fluctuate more than populations of terrestrial animals. So, while the problem certainly deserves to be taken seriously, it is not unique to fishes.

Finally, the high fecundity of many exploited fish species has been taken to imply that such stocks have high potential to bounce back from low numbers (Musick 1999a). The theory and evidence in support of this assumption have been questioned (Sadovy 2001). Indeed, Hutchings (2000) found little evidence of recovery for most of the 90 stocks that he has examined. Although his analyses did not take fishing mortality following population declines into account explicitly, subsequent analyses have shown that recoveries remain slower than generally expected even when the data are restricted to stocks in which fishing mortality during the recovery phase is extremely low (Hutchings 2001b).

After the uproar over the listing of commercially exploited fishes, there was a careful rethinking of the *Red List*'s main criteria for listing species. CITES has also been grappling with these issues, with advice from the FAO (Butterworth 2000), as have the Committee on the Status of Endangered Wildlife in Canada (COSEWIC), the Australian Society for Fish Biology and the American Fisheries Society (Musick 1999a). The American Fisheries Society has adopted a two-step listing process, under which species with life history characteristics that imply high productivity and resilience would be allowed to decline more steeply than the IUCN suggests before triggering a listing. Elsewhere, we have argued that the high rates of

decline required for a listing under this proposal are not sufficiently precautionary (Reynolds et al. 2001b). For example, a species deemed to have high productivity would be allowed to decline by 99% over 10 years or three generations, whichever is longest, before it would be listed as 'vulnerable' (Musick 1999a).

In the meantime, after a series of scientific workshops, the World Conservation Union brought out a refined set of criteria in 2001. Among various refinements there were two key changes. First, for any taxon to be listed as 'vulnerable' (the lowest threat status), the species must have declined by 30% (formerly 20%) over the previous 10 years or three generations (whichever is longest). Second, and particularly relevant to exploited species, higher declines are allowed before triggering a listing if the causes of the decline are understood, clearly reversible, and have ceased (IUCN 2001). Now, the species in our hypothetically controlled fishery can decline by at least 50% before being listed as 'vulnerable' (formerly 20%), 70% for 'endangered' status (formerly 50%), and 90% for 'critically endangered' status (formerly 80%).

The *Red List* has taken on the ambitious task of combining versatility with practicality so that the same criteria can be applied to a wide variety of plant and animal taxa. Thus, the aim is to draw attention to species when they show at least one of the symptoms of vulnerability towards extinction, including severe population declines (Mace and Hudson 1999). Defenders of this approach argue that the *Red List* is intended as precautionary flag, not a prescription for action, though it is hoped that it might lead to careful assessment, and management if required.

Perhaps the best way to bridge this divide between conservationists and resource managers is to incorporate extinction risk explicitly into population models, so that traditional fisheries reference points such as maximum sustainable yield (MSY) can be compared with the probability of extinction. Several researchers have begun to build this bridge. Matsuda et al. (1998) used three methods to evaluate the probability that the southern bluefin tuna would become extinct (less than 500 individuals) within the next 100 years: a simple

simulation model, a model that used a diffusion approximation of births and deaths, and a fluctuating age-structured model. None of these found support for a high probability of extinction under current circumstances, contrary to the IUCN's 1996 and 2000 listing of this species as critically endangered. This was largely due to the large current population sizes of these fish, despite their high rates of decline. Matsuda et al. (1998) concluded that the decline criterion should be linked to population sizes to give a better reflection of extinction probability.

A direct comparison of traditional fisheries reference points with extinction risk has been made by Punt (2000). He used a deterministic population model that compared the level of fishing mortality that achieves maximum sustainable yield (F_{MSV}) with that which causes the population to become extinct, defined as 1/1000th of initial population size (F_{crash}) . At this point, depensation might occur, whereby per capita recruitment might decline, thus potentially spiralling the population downwards to extinction (Section 15.5.5; see also Myers, Chapter 6, Volume 1). The analyses confirmed the expectation that F_{crash} was highest for highly productive populations, and that depensation greatly reduced the ratio of F_{crash} : F_{MSY} . In tests with case studies, Punt found that in two shark species F_{crash} was only about twice F_{MSY} . This is worrying because F_{MSY} cannot be estimated with much precision in many fisheries, so one cannot be certain how far above or below it the actual fishing mortality is.

A third approach towards bridging conservation and sustainable use has examined the effects of various exploitation strategies on yields and long-term risks of population collapse and extinction in populations that undergo strong natural fluctuations (Lande et al. 1995, 1997; reviewed by Lande et al. 2001). These studies suggest that if the goal is to maximize the cumulative yield before extinction or population collapse, the best approach is to use threshold exploitation, whereby populations are fished only when they overshoot their carrying capacities. A more prudent strategy, appropriate when there is considerable uncertainty about population sizes, is to use proportional threshold

exploitation, whereby only a fraction of the estimated surplus above the threshold is taken, rather than aiming for maximum exploitation of the surplus. These models are noteworthy not only for their contributions to the theory of exploitation of fluctuating populations, but also because they explicitly incorporate extinction risk, unlike traditional models such as yield-per-recruit, which are in widespread use (see Shepherd and Pope, Chapter 8, this volume, and Sparre and Hart, Chapter 13, this volume).

15.7 WHAT IS NEEDED TO SAFEGUARD FISH BIODIVERSITY?

It should be clear from this review that freshwater and marine biodiversity is seriously threatened. The bright side is that although many populations have undergone steep declines no species of marine fishes is known for certain to have become extinct. As we have argued in Section 15.3, there is good reason for thinking that we are less able to detect extinctions in marine environments. But at least we can say that no fisheries manager goes to bed at night with a conscience laden with the guilt of having seen a species of targeted marine fish become extinct during their watch.

The situation for freshwater fishes is far more dire in many parts of the world. Direct and indirect effects of exploitation, habitat destruction and degradation loom large among the drivers of decline. As demand for freshwater increases, and technologies for catching fish have improved, so the areas free from exploitation and habitat loss have diminished. We treat inland water bodies as sources of irrigation and hydroelectric power, at the expense of aquatic biodiversity.

15.7.1 Marine reserves

Marine reserves are often championed as one mechanism for protecting marine biodiversity (Watling and Norse 1998; NRC 2000; Roberts and Hawkins 2000). The evidence for and against this viewpoint is reviewed critically by Polunin

(Chapter 14, this volume). Syntheses of research from around the world have shown that the creation of reserves closed to fishing does yield rapid increases in abundance, body size and diversity of marine communities (Mosquera et al. 2000; Côté et al. 2001; Halpern, in press). Reserves can therefore provide an important fishery management tool by putting back the refuges that fishing has eroded away during the last century. Furthermore, fully protected reserves can begin the process of habitat recovery from fishing disturbances such as trawling or blast fishing.

Because of their promising role in fishery management, reserves are viewed as a potential ecological–economic win–win tool (Pezzey et al. 2000; Rodwell and Roberts 2000), providing an economic rationale for doing what is also sensible from a conservation perspective. Current understanding of marine reserves suggests that they will deliver maximum benefits when they cover between 20% and 50% of every habitat and biogeographic region of the oceans (NRC 2000). Theoretical studies suggest that they will be most effective when established in dense networks consisting of areas of a few to a few tens of kilometres across, and which are separated by a few to a few tens of kilometres (Roberts et al., in press).

Of course marine reserves will not be sufficient to protect high seas and migratory fish stocks like swordfish, marlin and tuna, and their use in freshwater has barely been explored. Furthermore, their implementation needs to be augmented by overall reductions in fishing effort and other technical measures (Murawski et al. 2000; Wabnitz and Polunin 2001; Polunin, Chapter 14, this volume). Otherwise, reserves may simply cause a redistribution of fishing effort, without leading to reduced mortality.

15.7.2 The precautionary principle and reference points

The precautionary principle is now being implemented in fisheries management in many parts of the world (FAO 1995). The elements of this principle are simple, such as taking account of uncertainty, being cautious with new fisheries, not

using lack of information as an excuse for inaction, and using reference points. Reference points include benchmark population sizes or mortality rates that are not to be exceeded ('limit reference points') or which are desirable ('target reference points') (see also Shepherd and Pope, Chapter 8, this volume). However, for precautionary reference points to be successful it is critical that once a benchmark is agreed upon the conservation goalpost is not shifted. Powles et al. (2000) outlined the continuum and overlap of both fisheries management and conservation benchmarks. As some species have declined management has shifted from one benchmark to the next, allowing populations to go from growth overfishing to recruitment overfishing, and up the scale to a critically endangered listing under IUCN criteria.

15.7.3 Targeted management at key points in the life history

Identifying key points in the life history of organisms could prove to be a fruitful approach for focusing often-limited management efforts. However, identification of critically important ages, stages, habitats or even sexes is still in its infancy. Guesses can be made based on experience; salmon are clearly more vulnerable in estuaries than in the open sea, and females usually limit populations more strongly than do males. However, we still have a lot to learn. For example, at present managers are unsure as to whether is it better to protect juvenile skates or mature females. While control of mortality in either life stage would be difficult, one can imagine that closed areas could be applied to nursery areas or locations that are primarily used by adults.

One way forward is the application of elasticity analyses, based on demographic matrix models (e.g. Kokko et al. 2001). These can be used to determine the relative importance of various stages of the life cycle for the population growth rate. One of the first uses of this method was to examine the conservation method of 'head starting', which is widely applied to a bycatch turtle species. This involves enhancing the hatching and survival rate of turtles, which was previously assumed to be the

critical stage for population growth. However, demographic modelling and elasticity analyses demonstrated that this life stage contributed little to population growth rate compared to the subadult and adult stages (Heppell et al. 1996). Similarly, while fishery scientists often focus on understanding what determines survival in the first year of life, elasticity analyses hint that it is more critical to protect fishes between the first year and maturation (Heppell et al. 1996). For example, in the North Sea haddock survival in the first year of life contributes only approximately 30% to the overall population growth rate, whereas survival from the first year to maturity contributes approximately 60%. We should therefore focus conservation effort on allowing juveniles to reach maturity rather than focusing on first-year juveniles (Heppell et al. 1999). Though such approaches are data-intensive, the information should be generally applicable to species that have similar life histories to those studied so far.

There is a critical need for more precautionary and ecosystem-based approaches in fishery management (NRC 1999). What has become clear is that present approaches to fishery management are too risk-prone, failing to take adequate account of irreducible uncertainties in fishing mortality rates or future environmental conditions (Ludwig et al. 1993; Mangel 2000; Roberts 2000). In combination, reduced fishing effort, extensive use of reserves in both marine and freshwater habitats and management focused on critical life stages will do much to secure the future of fish species.

15.8 CONCLUSIONS

For too long, fisheries biologists and conservation biologists have been attending different conferences, publishing in different journals, and worrying about different things. Extinction risk has not usually been a concern in marine fisheries, but the collapses of fish stocks, extirpations and damage to ecosystems, combined with considerable uncertainty about risks of cryptic extinctions, are causing conservationists to ask resource biologists awkward questions. Furthermore, there is no

question about the vulnerability of freshwater fishes to extinction, and the potential for exploitation to exacerbate the threats. There have been positive developments in the field of fisheries conservation, including studies of marine reserves, ecosystem-based analyses, adoption of precautionary reference points that embrace the uncertainty that pervades fisheries, and theoretical studies that bridge between management targets and risks of extinction. We look forward to further progress in all of these fields, which should lead to more prudent use of fishes as resources while protecting them and the environment.

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