Holocene extinctions in the sea

Nicholas K. Dulvy, John K. Pinnegar, and John D. Reynolds

6.1 Introduction

The Holocene is bounded at either end by pulses of terrestrial extinction. The beginning was marked by megafaunal extinctions associated with colonizing waves of hunter-gathering humans. The current pulse of terrestrial extinction is at least one to two orders of magnitude higher than the background rate, mainly due to large-scale habitat modification. By comparison, few extinctions of marine species have been recorded, and these have been of range-restricted species, mainly mammals and birds, over the past 300 years. Today's extensive overexploitation of global fisheries has a historical and prehistoric precedent in archaeological evidence for the local collapse of many fisheries and shellfish beds, and regional extinction of populations such as the Atlantic gray whale. Marine extinctions may be more widespread than is currently appreciated, largely because it is very difficult to observe the last days of the last individual of a marine species, and because of a fallacious but widespread perception that marine organisms cannot be driven to extinction. The observed human capacity for causing rapid and widespread terrestrial extinctions combined with the rapidly increasing scale of human impact on the sea forewarn of an impending marine extinction event. The scale of this may be the equivalent of concatenating both of the terrestrial Late Quaternary extinction waves into a much shorter time frame. Fortunately the opportunity to forestall major loss of ocean biodiversity has never been greater. While much megafaunal biomass has been depleted and some habitat has been lost, society, scientists, and managers are acutely aware of these problems and legislation and institutions are strengthening in response.

6.2 The origins of human exploitation of the sea

The Holocene is marked by a major transition in human social organization, from hunter-gathering to a settled agrarian lifestyle. This was made possible by domestication of a wide range of crops and animals. Prior to this, the expansion of hunter-gatherer populations across continents and islands led to waves of extinction of megafaunal mammals and birds (see Chapter 2 in this volume). Around 11 000 years ago prehistoric hunters in North America were probably responsible for causing the extinction of 34 genera of large-bodied mammals (including mastodons, ground sloths, artiodactyls, and perissodactyls) within a millennium of hunting (Martin and Steadman 1999). In Australia, human arrival around 46 000 years ago corresponds with the extinction of all mammal, reptile, and bird species weighing more than 100 kg (Roberts *et al.* 2001). Polynesians exterminated as many as 2000 bird species from Pacific Islands (Steadman 1995), and hunted 10 moa species to extinction soon after colonizing New Zealand (Holdaway and Jacomb 2000; see Chapter 2 in this volume). One-fifth of all the bird species extant at the beginning of the Holocene are now extinct (Milberg and Tyrberg 1993).

Environmental impacts associated with settled agrarian lifestyles led to a second wave of terrestrial extinctions towards the end of Holocene. At least 844 extinctions have been documented since AD 1500, and almost all have been of terrestrial plants and animals (Baillie *et al.* 2004). The main drivers of the recent extinction wave are habitat loss caused largely by forest clearance for agriculture, and predation and habitat degradation caused by invasive species such as dogs, cats, rats,

mongooses, pigs, and goats (Baillie *et al.* 2004). The terrestrial extinction rate is now one to two orders of magnitude higher than the background rate inferred from the fossil record (Mace *et al.* 2005).

Today the oceans may be in a state more akin to terrestrial ecosystems 10 000 to 50 000 years ago, at the Late Pleistocene or advent of the Holocene. There has been large-scale biomass removal of ocean megafauna, increasing extinctions of populations and species, and a rapid increase in the domestication of marine animals and plants (Dulvy *et al.* 2003; Lotze *et al.* 2006; Duarte *et al.* 2007). A hunting-to-cultivation transition is now gaining pace in the oceans, similar to the transition that began on land thousands of years ago (Fig. 6.1). One hundred million tonnes of food fish are extracted from oceans and coastal waters each year (2000–2006); most (85%) is still hunted from the wild, with the remainder provided by aquaculture of domesticated fish and invertebrates. Currently, the yield of aquaculture is small, but the rate of species domestication is rapid and the relative yield contribution has increased year on year since the 1980s (FAO 2007). Most (90%) cultivated marine species were domesticated in the last decade, whereas the majority of terrestrial species in cultivation were domesticated over 2000 years ago

(Fig. 6.1). Aquaculture is predicted to provide as much as 41% of global fish production by 2020, up from 31% in 1997 (Delgado *et al.* 2003).

This chapter documents the changing state of coastal and high-seas ocean ecosystem biodiversity, particularly over the last 1000 years, with occasional insights provided from the deeper Holocene. We summarize the main types of methods and data sets used to measure historic changes in marine biodiversity, and use this summary to justify limiting this chapter to the last millennium, instead of providing detailed treatment of the whole Holocene. We summarize the main causes of marine biodiversity loss, with a focus on overexploitation as the main driver of Holocene extinctions. Next, we outline the evidence for the spread of fishing impacts and habitat loss across the world and deeper into the oceans, and the sequential depletion of marine megafauna. Finally, we sketch out current knowledge of the number and taxonomic scale of marine extinctions.

6.3 Measuring marine biodiversity change over the holocene

It remains difficult for scientists to identify the causes of the major waves of terrestrial megafaunal
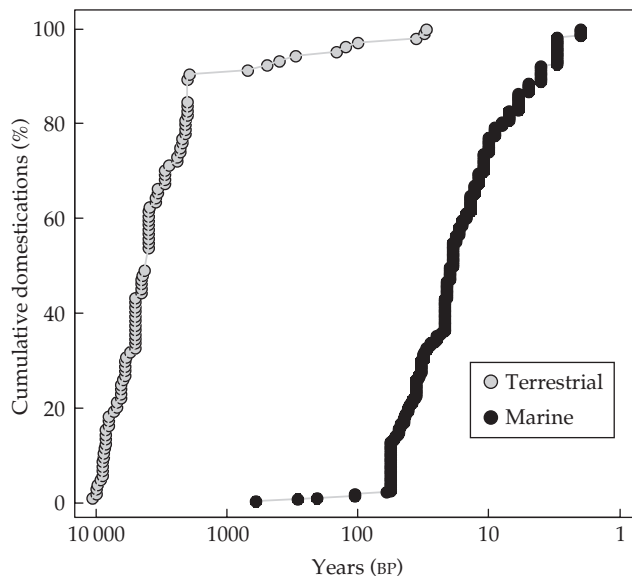

Figure 6.1 The cumulative number of domestications of terrestrial and marine plants and animals over the last 100 000 years. Most terrestrial domestications occurred around the beginning of the Holocene, whereas most domestications of marine species occurred in the last 100 years. Redrawn from Duarte *et al.* (2007).

extinction because these events took place several millennia or tens of millennia ago (Burney and Flannery 2005). The major loss of marine mega-fauna occurred more recently and largely within the period of increasing scientific knowledge, yet reconstructing the recent historical changes in marine biodiversity remains particularly challenging (Pinnegar and Engelhard 2008).

There is a relative paucity of observational data and knowledge of ecological conditions in the oceans for the prehistoric Holocene and Late Pleistocene (>1000 years before present). Humans inhabit the terrestrial portion of the Earth and frequent ocean travel has been largely restricted to the last millennium. The oldest perspective is provided by comparisons between fossil and modern coral reefs, providing insights into changing community structure from 125 000 to 17 000 years BP (Aronson *et al.* 2002; Pandolfi and Jackson 2006). Subfossil remains, such as fish bone deposits and kitchen middens (human refuse dumps), extend back several thousand years and can be used to demonstrate changing average fish size, changing fish community structure, and human economic and technological advances (Jackson *et al.* 2001; Wing and Wing 2001; Barrett *et al.* 2004b). However, many coastal archaeological and historical sites are now under water due to sea-level rise (W.J. Wolff, personal communication).

Historical documents and art, such as pottery and sculpture, depict catches and may hint at long-lost species (Pinnegar and Engelhard 2008). Documentary history, for example of trade and tax records, can often provide more complete information and may in exceptional cases be used to reconstruct the fate of populations, such as the 500 year span of Newfoundland cod catches (Rose 2004) or the 300 year span (AD 1650–1950) of Mediterranean tuna catches (Ravier and Fromentin 2001). The spread of exploration and rising interest in the natural world during the fifteenth to eighteenth centuries provided detailed taxonomic inventories and historical species distributions. Such information, when compared to modern surveys, is a major source of our knowledge on recent marine extinctions (e.g. Jackson *et al.* 2001; Dulvy *et al.* 2003).

The modern marine scientific era provides detailed fisheries and research surveys spanning large areas of coastal and oceanic seas, especially over the past 25–50 years (FAOSTAT 2004). Research surveys have provided considerable insight into the scale of human impact, particularly in temperate waters of the northern hemisphere, but they are rarely powerful enough or offer sufficient taxonomic resolution to be useful for detecting marine extinctions (Maxwell and Jennings 2005). Research time series are largely absent from the tropical oceans of developing nations. These knowledge gaps are now being filled through interviews with members of coastal communities for their traditional knowledge of species presence, behaviour, and ecology; for example, in Brazil, China, Palau, and Fiji (Johannes 1981; Sadovy and Cheung 2003; Dulvy and Polunin 2004; Silvano *et al.* 2006).

6.4 A millennium and more of fishing

Fishing or hunting is the greatest cause of threat and population extinctions in the sea, followed by habitat loss, pollution, and invasive species (Fig. 6.2). The last thousand years have seen great technological advances in fishing power and demand for fish from burgeoning human populations (Pauly *et al.* 2005). Industrial fishing fleets have expanded out over the oceans and into deeper waters, and the increasing densities of subsistence fishers make sustainability unlikely (Newton *et al.* 2007). Over a third of the human global population inhabits the seaward margins of the terrestrial realm (Cohen *et al.* 1997). The coastal seas provide abundant and easily accessible food that can be gleaned from tide pools, or caught in nets and traps or using lines of baited hooks. Fishing provides many nations with a large proportion of their dietary animal protein intake. For example, fish provide nearly two-thirds of the animal protein to people in the West African countries of Gambia, Ghana, and Sierra Leone, and over a third of the intake of the Asian countries of Vietnam, Malaysia, Thailand, Cambodia, and Bangladesh. In island nations fish are typically the major source of the average daily protein intake, for example for the Maldives (84%), Comoros (64%), Indonesia (57%), and Sri Lanka (52%) (FAO 2004b).

In some parts of the world there is good reason to believe that human dependence on marine fish, molluscs, and crustaceans for food and dietary
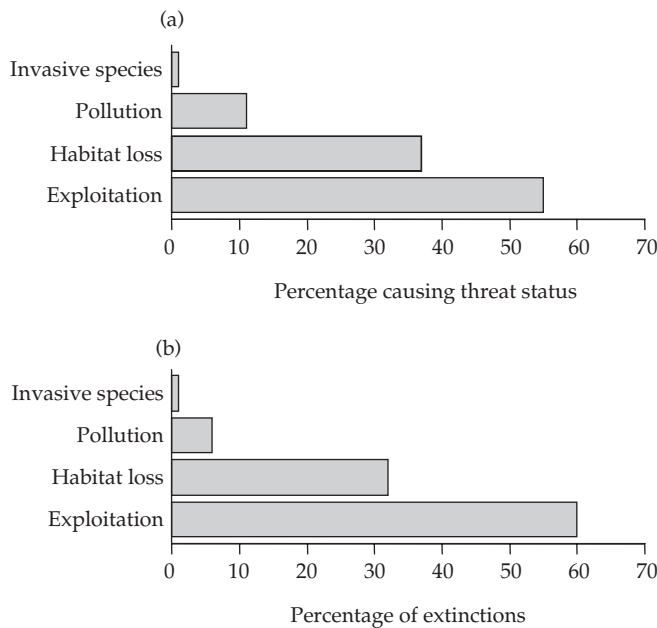
(a)

Percentage causing threat status

(b)

Percentage of extinctions

Figure 6.2 The main causes of (a) threat and (b) extinction risk for marine fish populations and species. The figures include cases where more than one cause of threat has been identified for a given population or species. (a) North American species threatened with extinction ($n=82$), including those considered Vulnerable, Endangered, or Critically Endangered (Musick *et al.* 2000). (b) Local, regional, and global marine fish extinctions ($n=65$) (Dulvy *et al.* 2003). In all cases exploitation and habitat loss were the primary causes of threat.

protein was just as great in our recent historical past. Pacific Island reef and lagoon fisheries resources have been continuously exploited for many centuries, and exploitation has been occurring in western Melanesia for 20 000–30 000 years (Dalzell 1998). Molluscs appear to have been extremely important as a food source for early Pacific Island human populations (Dalzell 1998). In some instances, declines in mollusc resources forced early human populations to increase exploitation of other marine resources, and to rely increasingly on agriculture.

The oldest evidence of marine harvesting is the presence of shellfish remains in two middens in Saldanha Bay, South Africa, dating from 60 000–70 000 years ago (Volman 1978). The earliest hunter-gatherers collected shellfish opportunistically, and hunted slow-moving terrestrial reptiles such as tortoises (Klein *et al.* 2004). By the early Holocene (11 500–8500 years BP), fishing technology had advanced considerably, broadly concurrent with the development of agriculture and crop domestication on land. The use of boats, hooks, and lines are known from a number of locations in the prehistoric Holocene, including the Northern Channel Islands, California (Rick *et al.* 2001). In Parita Bay, Panama, a comparison of fish faunas

from Cerro Mangote (6000 years BP) and Sitio Sierra (1800 years BP) suggests that regional fishing methods shifted between earlier and later periods from a shore-based, netless technique to a more complex one based on fine-meshed gill-nets and watercraft (Cooke 2001). Similar observations have been made for southern Taiwan (Kuang-Ti 2001) and northern Scotland (Barrett *et al.* 1999). At an early settlement on Cyprus, middens dated to 8000 years BP revealed that large individuals of certain species, notably sea breams (Sparidae) and groupers (Serranidae), were much more common during the Neolithic than they are now (Desse and Desse-Berset 1993). Similarly, fish faunal diversity and fish body size decreased over a 12 000 year period at a site in southern Spain (Morales *et al.* 1994).

Up to the turn of the first millennium AD, marine fisheries were a minor affair in Europe. For example, exploitation of fish resources in Britain during this period focused mainly on freshwater species such as northern pike, *Esox lucius*, and migratory species such as European eel, *Anguilla anguilla*, Atlantic salmon, *Salmo salar*, and European sturgeon, *Acipenser sturio*. The advent of the second millennium in Britain is marked by increasing quantities of marine fish remains in coastal and inland middens

(Barrett *et al.* 2004b). This increase in the consumption of marine fishes was repeated at a similar time or soon after in mainland Europe (Barrett *et al.* 2004a; Pauly 2004). The most parsimonious explanation for this transition was that increasing urbanization of European human populations led to increased food demand, concomitant with declining availability of freshwater fish. This led to the development of marine fisheries for Atlantic herring, *Clupea harengus*, and Atlantic cod, *Gadus morhua* (Barrett *et al.* 2004b). The decline of freshwater fisheries is thought to have stemmed from a combination of pollution from agricultural run-off, overexploitation, and damming (Hoffmann 1996; Barrett *et al.* 2004a, 2004b). Salmon were heavily overexploited, and populations of other freshwater fish species disappeared completely. The burbot, *Lota lota*, is common in archaeological deposits and was eaten in large numbers throughout Britain, but is now regionally extinct. Sturgeon were virtually extinct across much of northern Europe by the fourteenth century due to overexploitation, damming, and diking of key habitats (Hoffmann 1996), although they were still commercially exploited into the nineteenth and possibly the twentieth century in The Netherlands, Germany, and other countries (W.J. Wolff, personal communication). Climatic variability is not thought to have contributed significantly to the transition to marine fisheries; the transition occurred when environmental conditions were unlikely to promote such a switch, when local productivity of cod and herring in the southern North Sea was probably reduced, conditions which would be expected to have instead supported agricultural expansion (Barrett *et al.* 2004b).

Across the Atlantic Ocean, some subsistence Caribbean island fisheries had already begun to deplete their marine resources. Comparison of faunal remains between two time periods (early and late, 1850–1280 and 1415–560 years BP, respectively) on Puerto Rico, St Thomas, St Martin, Saba, and Nevis indicates that the average weight of reef fish declined between early and late periods on each island, with a decrease in representation of inshore reef fishes and increase in representation of offshore pelagic fishes (Wing and Wing 2001). These changes in species composition and average size resulted in a decrease in mean trophic level of the fish assemblage at each

island between early and late periods. However, this pattern is not widespread throughout the Caribbean, as there is evidence for sustainable fisheries (i.e. no change in average fish size or range in fish sizes) from AD 600/800 to AD 1500 on Anguilla in the northern Lesser Antilles (Carder *et al.* 2007).

Around the same time, Europeans were discovering new countries and new fishing grounds in the north-west Atlantic. In the eleventh century, Basque whalers from Spain and Portugal hunted around the coast of the Bay of Biscay, but from the twelfth century up to 600 Basque whalers caught bowhead, *Balaena mysticetus*, and North Atlantic right whale, *Eubalaena glacialis*, off the Labrador coast for their oil (Cumbaa 1986). The remnant bowhead population which survives in Baffin Bay–Davis Strait is thought to number between 450 and 1000 adults (IUCN 2006). The adjacent East Arctic bowhead population was exploited to near extinction by commercial whaling fleets from AD 1611 onwards (Allen and Keay 2006); this population now contains fewer than 100 individuals, and possibly fewer than 50 mature adults, and is listed as Critically Endangered (IUCN 2006). Portuguese and Norwegian fishermen also crossed the Atlantic to Newfoundland and stayed for the short summer season to fish the bountiful cod, drying and salting their catch before returning each winter (Kurlansky 1998). This was one of the world's largest ever fisheries and has been driven to collapse in 500 years or so, culminating in closure in 1992, with many sub-fisheries yet to be reopened (Hutchings 1996; Myers *et al.* 1996). As with the extinction of terrestrial megafauna, there has been debate over whether the ultimate cause of the decline of the fishery was environmental change or human exploitation. Long time series of Atlantic cod catch data from Newfoundland between 1505 and 2004 can be used to explore the relative explanatory power of climate and overfishing hypotheses (Rose 2004). Fishing or climate variability (as represented by interannual variation in tree-ring growth) alone did not mimic the observed catch trends; the model best describing the collapse and non-recovery of Newfoundland cod since 1505 incorporates climate variability, fishing mortality, and depensation (negative population growth at small population sizes) (Fig. 6.3).
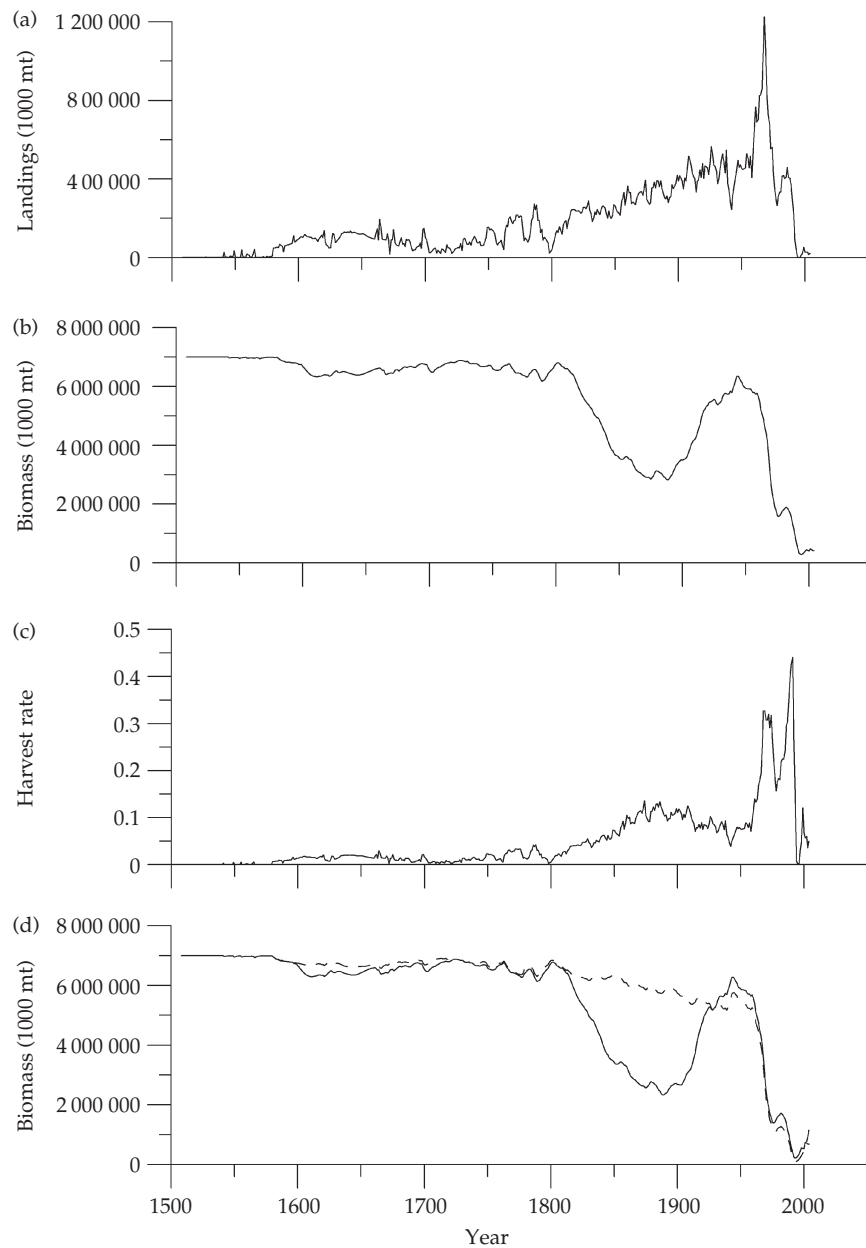
Figure 6.3 (a) Historical reconstruction of the landings of Atlantic cod, *Gadus morhua*, in Newfoundland and Labrador waters from 1505 to 2004; (b) stock biomass estimates based on a surplus production model incorporating climate forcing and depensation (Allee effects); (c) the annual harvest rate (landings per unit of biomass); and (d) stock biomass estimates derived from a surplus production model assuming constant *r* and *K* parameters (dashed line) and the climate forcing alone (solid line). The surplus production model was climate forced using a composite tree-ring data set, representing annual temperatures for northern North America (from Alaska to Quebec) from 1600 to 1974. Redrawn from Rose *et al.* (2004).

6.5 The expansion of fishing into deep water

In recent years, fishing in deep waters (>400 m) has increased as traditional shallow-water stocks have declined (Devine *et al.* 2006). The target deep-water fish (e.g. roundnose grenadier, *Coryphaenoides rupestris*, and orange roughy, *Hoplostethus atlanticus*) are often long-lived and late-maturing, and hence intrinsically vulnerable (Morato *et al.* 2006a, 2006b). Orange roughy can live to over 125 years of age and may not mature until 20 years. Fishing by factory trawlers and modern long-line fleets started in the late 1960s. Analyses of several of the most important deep-sea fishes, using a widely used index of abundance (catch-per-unit fishing effort, CPUE), have indicated a clear declining trend in abundance. For orange roughy in the north-east Atlantic, the CPUE in 1994 was only 25% of initial catch rates when the fishery commenced in 1991 (ICES 2003). Since 1964, deep-water fisheries have contributed 800 000–1 000 000 tonnes annually to global marine fish landings. The average depth from which catches of both pelagic and bottom-dwelling species are taken has been deepening over time across all oceans (Fig. 6.4). This trend has been accelerating since 2001 (Pauly *et al.* 2003; Morato *et al.* 2006b).

6.6 Declines of marine megafauna

6.6.1 The great whale hunt

As with terrestrial extinctions (Stuart 1991), population declines of large-bodied, long-lived animals are typical of historical and modern fisheries. In some cases, this has led to regional extinctions. The gray whale *Eschrichtius robustus* now occurs only in the North Pacific, but this species first became known to science through the discovery of subfossil remains in England and Sweden (Bryant 1995). Radiocarbon dating of fossil and subfossil remains indicate that a gray whale population existed in the Atlantic until the seventeenth century AD. Coastal whaling has occurred in the North Atlantic since at least AD 1000, and historical accounts suggest that the Atlantic gray whale may have been among the species hunted by the first whalers (Bryant 1995).
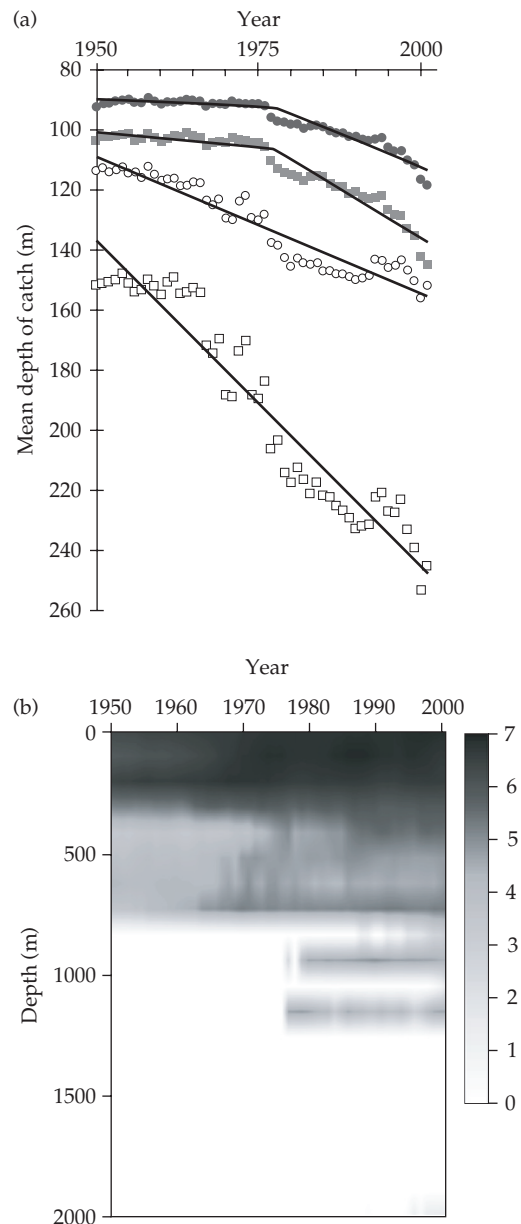

Figure 6.4 (a) Deepening of the global marine fisheries catches from 1950 to 2001 for surface dwelling (pelagic) fishes (dark grey circles) and for bottom marine (demersal) fishes (light grey squares). Open symbols are corresponding estimates for high-seas areas only (beyond Exclusive Economic Zones). (b) Time series of world marine bottom fisheries catches by depth strata. Catch in tonnes are $\log_{10}$ transformed. Redrawn from Morato *et al.* (2006b).

From AD 1059 onwards Basque whalers killed large numbers of whales as they migrated close to shore through the Bay of Biscay. By the fifteenth century, Basque whalers travelled as far as Iceland, Greenland, and Canada in search of whales. It is widely assumed that the primary target species for these whalers was the North Atlantic right whale; however, if the gray whale inhabited nearshore waters in the Atlantic, as surviving populations do in the Pacific, then it is plausible that they may have been an even likelier target for Basque whalers (Bryant 1995).

More recently, industrial whalers fished down and sequentially depleted the great whales in 50 years or less. Depletion of the largest species (the blue whale, *Balaenoptera musculus*) occurred first, followed by the North Pacific right whale, *Eubalaena japonica*, humpback whale, *Megaptera novaeangliae*, fin whale, *Balaenoptera physalus*, and eventually moving on to the smaller sei whale, *Balaenoptera borealis*, and minke whale, *Balaenoptera acutorostrata* (Gulland 1974) (Fig. 6.5). Many populations of these species are now at a fraction of their former abundance, and are listed in one of the three threat categories (Vulnerable, Endangered, or Critically Endangered) on the IUCN Red List. Although cetaceans are the subject of a great deal of attention and controversy, it is interesting to note that out of the 84 known species, only one (freshwater) species is believed to have become globally extinct, and one coastal species is Critically Endangered. While not a marine species, it is worth considering the decline of the Yangtze River dolphin or baiji, *Lipotes vexillifer*. This dolphin is endemic to the middle-lower Yangtze River system in eastern China and was long recognized as one of the world's rarest and most threatened mammal species. Chinese scientists reported a steady decline in the baiji population from an estimated 400 individuals in 1979–1981 to as few as 13 individuals in 1997–1999 (Zhang *et al.* 2003), due largely to by-catch in local fisheries, pollution, boat collisions, and dam construction instead of direct persecution. Even though efforts were proposed to conserve the species, an expedition towards the end of 2006 failed to find any baiji in the river. In 2007 the organizers were forced to conclude that the baiji is now very likely to be extinct (Turvey *et al.* 2007b). The Critically Endangered vaquita, *Phocoena sinus*, is a small porpoise endemic to the northern Gulf of California (Sea of Cortez). This species numbers in the low hundreds, and again suffers from incidental by-catch mortality from fisheries; it is predicted to become extinct within the next few years without intensive conservation efforts (Rojas-Bracho *et al.* 2006; Jaramillo-Legorreta *et al.* 2007).
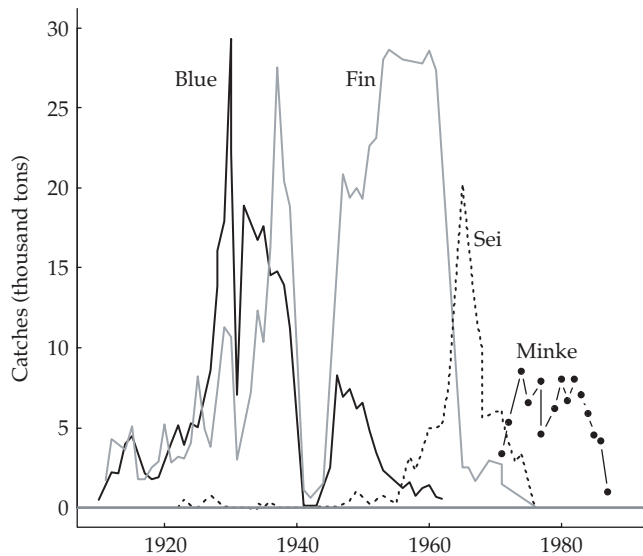

Figure 6.5 Sequential depletion of the great whales in the Antarctic Ocean. Redrawn from Allen (1980).

A striking feature of the Red List status of the world's cetaceans is that the IUCN has been unable to determine the status of 48% of the world's 84 species. One reason for this is that it has proven difficult to obtain good estimates for current or historic population sizes of many of the world's beaked whales, dolphins, and porpoises. One approach that has been used with some success for baleen whales has involved estimates of long-term effective population sizes based on genetic diversity and rates of gene substitution. In the North Atlantic, the historic population estimates of humpback, fin, and minke whales are 240000, 360000, and 265000 respectively. Current population sizes (and overall percentage decline) are 10000 (96%), 56000 (84%), and 149000 (44%) (Roman and Palumbi 2003). Records of historical catches from ship logbooks during the eighteenth and nineteenth centuries are regularly used by the International Whaling Commission (IWC) to reconstruct the population dynamics of whales before, during, and after exploitation (Baker and Clapham 2004). The historical trajectories for southern right whale, *Eubalaena australis*, one of the most vulnerable species, show a sharp decline during the mid-1800s, with a slow increase following international protection in 1931 and another decline resulting from illegal Soviet catches during the 1960s. The lowest point of population abundance was in 1920, when as few as 60 adult females were estimated to have survived.

6.6.2 Sea cows, seals, and otters

Only 27 years after the discovery of Steller's sea cow, *Hydrodamalis gigas*, in 1741, this species was driven to extinction as a result of excessive, and wasteful, hunting to provision Russian fur-hunting expeditions (Anderson 1995; Turvey and Risley 2006). The four extant sirenian species (dugong and manatees) are currently listed as Vulnerable by the IUCN Red List. The dugong, *Dugong dugon*, was once distributed widely throughout the tropical South Pacific and Indian Oceans. The primary causes for population declines include hunting, habitat degradation, and fishing-related fatalities. Along the coast of Queensland, where the most robust quantitative data on population trends are available, analyses have suggested that the region supported 72000

dugongs in the early 1960s compared with an estimated 4220 in the mid-1990s (Marsh *et al.* 2005). Similar declines have been experienced by the West Indian manatee, *Trichechus manatus*, which is particularly at risk from boat strikes (Marmontel *et al.* 1997).

The Caribbean monk seal, *Monachus tropicalis*, the only seal known to be native to the Caribbean Sea and the Gulf of Mexico, is now considered globally extinct. This species was estimated to have originally consisted of more than a quarter of a million individuals divided among 13 populations spread throughout the Caribbean (McClenachan and Cooper 2008). This species was hunted for food and oil by European explorers and plantation settlers. Hunting rapidly eliminated the outer populations, substantially contracting the spatial extent of the seal's range (Fig. 6.6). The last reliable sighting of the Caribbean monk seal was of a small colony at Seranilla Bank, Jamaica, in 1952, but it had been substantially depleted throughout the Caribbean since at least the 1850s (Timm *et al.* 1997). The world's two other monk seal species are also considered highly threatened. The Mediterranean monk seal, *Monachus monachus*, is believed to be the world's rarest pinniped and one of the most endangered mammals on Earth. It is listed as Critically Endangered (IUCN 2006). A dramatic population decrease over time has been attributed to several distinct causes, in particular commercial hunting (especially during the Roman period and the Middle Ages) and eradication by fishermen during the twentieth century, but also coastal urbanization. As a result of these factors, the entire population is estimated to consist of fewer than 600 individuals scattered throughout a wide geographic range (Forcada *et al.* 1999). The Hawai'ian monk seal *Monachus schauinslandi* has also suffered severe population declines in recent years, due to the spread of human activity to even the most remote and isolated areas in the north-west Hawai'ian Islands. It is estimated that fewer than 1400 Hawai'ian monk seals exist today (Antonelis *et al.* 2006).

Sea otter (*Enhydra lutris*) populations were hunted for their fur, initially by indigenous Aleut people and later on more extensively by Europeans, and were reduced to local extinction in many parts of
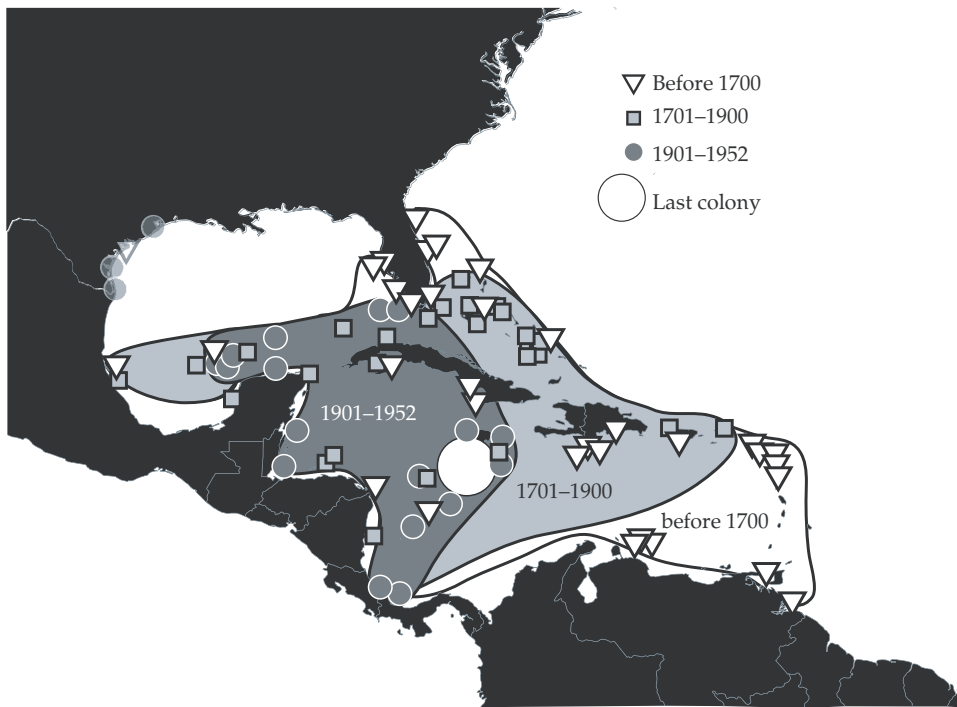
Figure 6.6 Decline in the total geographic extent of the Caribbean monk seal over time. Early observations (triangles, before the eighteenth century) were recorded as far east as the Lesser Antilles and Guyana. Observations from the eighteenth and nineteenth centuries (squares) were recorded in most of the Caribbean basin, but by 1900 observations (small circles) were restricted to the western Caribbean and Gulf of Mexico. The most persistent population (large circle, last colony) was found on the Serranilla Bank. Observations in the western Gulf of Mexico are unconfirmed. Redrawn from McClenachan and Cooper (2008).

their historic range, for example Mexico and British Columbia (Simenstad *et al.* 1978). By 1911 the global population was estimated to be only 1000–2000 individuals (mostly in the Aleutian Islands), compared to as many as 300 000 before the years of the great hunt (Kenyon 1975). So few individuals remained that many authorities assumed they would become extinct. However, in 1938 biologists found a small group of about 50 sea otters along the coast south of Carmel, California. These few animals (together with the last remaining animals in Alaska) formed the nucleus of a breeding population for restoration efforts. Currently the sea otter is listed as Endangered; the current global population estimate for *E. lutris* is approximately 108 000, although the Alaskan and Californian populations are declining due to killer whale, *Orcinus orca*, predation and disease respectively.

The sea otter remains regionally extinct in Mexico and Japan (Springer *et al.* 2003; IUCN 2006).

6.6.3 Seabirds

Many species of seabirds are severely threatened. For example, the long-lived ocean-going albatrosses (Diomedeidae) are threatened from high-seas long-line fisheries, such as those that target southern bluefin tuna, *Thunnus maccoyi*, and albacore, *Thunnus obesus*, in the Southern Ocean. The birds are attracted to the baited hooks as they are deployed from the fishing vessels, and are often hooked and drown. The total reported fishing effort was at least 60 million hooks set per year in the 1960s and is presently greater than 180 million hooks and increasing (Tuck *et al.* 2001). The Red List threat status of albatrosses worsened in the

decade after 1994 (Butchart *et al.* 2004). All 21 species of albatross are now listed as globally threatened (compared to just three species in 1996 and 16 species in 2000) (IUCN 2006).

Studies of other species of seabirds have shown that impacts of fisheries can be mixed. For example, the Balearic shearwater, *Puffinus mauretanicus*, which breeds in the Mediterranean, is listed as Critically Endangered. Population models suggest that by-catch of adults by long-line fisheries is probably the main cause of a declining population trend (Oro *et al.* 2004). Yet the birds benefit from foraging on small fish that are discarded by fisheries, with over 40% of the energetic requirements of chicks being met from this source (Arcos and Oro 2002). Such subsidies from fisheries discards are typical for a range of seabirds (Lewison *et al.* 2004). There is now concern that efforts by the European Union to reduce the amount of fisheries discards may remove a critical food source and push this species more quickly towards extinction.

6.6.4 Turtles

Jackson (1997) highlighted the difference between how we see the seascape today and how early Europeans visiting America witnessed it. Old hunting data from the Cayman Islands together with reports from early explorers indicate that green turtle (*Chelonia mydas*) populations in the Caribbean may have declined by at least 99% since the arrival of Christopher Columbus in 1492. Turtles suffer many threats worldwide; chief among these is by-catch in offshore long-line fisheries, either on baited hooks or through entanglement, and in inshore shrimp trawls. A recent global estimate of the effect of fisheries on marine turtles suggests that some 260 000 loggerheads and 50 000 leatherbacks are captured incidentally by long lines each year, a large proportion of which die as a consequence (Lewison *et al.* 2004). In addition, turtles suffer overexploitation of eggs and habitat loss from human development of their nesting beaches. Analyses of green turtle subpopulation changes at 32 index sites across the world suggest a 48–67% decline in the number of mature females nesting annually over the last three generations (IUCN 2006). Analysis of published estimates for leatherback turtle, *Dermochelys*

coriacea, suggests a reduction of over 70% for the global population of adult females in less than one generation (Pritchard 1982; Spotila *et al.* 1996).

All five species of sea turtles in US waters are listed as threatened or endangered under the US Endangered Species Act. A major source of mortality for these turtles is drowning in shrimp trawls. Most (70–80%) strandings of dead turtles on US beaches are thought to be related to interactions with this fishery (Crowder *et al.* 1995). Efforts are underway to introduce turtle excluder devices (TEDs) in trawl nets in both the USA and northern Australia, although trawl fisheries remain a major problem for turtles elsewhere (FAO 2004a). It has been estimated that the US shrimp fleet alone caught 47 000 sea turtles each year prior to the introduction of TEDs in 1989 (FAO 2004a).

6.6.5 Large predatory fishes

Many fishes, particularly the larger-bodied predatory species, have declined massively. This has become particularly apparent in the past half century. The Food and Agriculture Organization (FAO) of the United Nations, the collector of world fishery statistics, has calculated that more than 77% of the world's fisheries are fully or overexploited, 8% have collapsed, and only a quarter remain 'under-exploited' (Garcia and Newton 1995; FAO 2007). An independent analysis of the same data suggests that one-quarter (366 of 1519) of fish stocks have collapsed in the last 50 years (Mullon *et al.* 2005). These figures may be conservative, as discarded fishes and other animals go unreported in these statistics, as do the catches of artisanal and subsistence fishers (Sadovy 2005; Zeller *et al.* 2006; Andrew *et al.* 2007). While trends in aggregated taxa are widely available, there are few data on the fate of individual species and populations. A more detailed picture of the fate of populations and species comes from the analysis of assessed exploited stocks of the northern temperature fisheries of Europe, Canada, and the USA. Of these 232 stocks (populations) the median decline in adult abundance has been 83% from known historical levels; however, these declines are usually measured from the beginning of the time series, which often started long after exploitation began. Few of these populations

have recovered 15 years later (roughly equivalent to three generations; a time scale used in the extinction risk assessments of the IUCN Red List criteria) (Hutchings 2000; Hutchings and Reynolds 2004). A large number of these populations exhibit reduction in age and size of maturity, consistent with an evolutionary response to the effects of overfishing of adults (Law and Grey 1989; Olsen *et al.* 2004; Hutchings 2005; Hutchings and Baum 2005).

Large predatory fishes have undergone the steepest declines due to their lower intrinsic rate of population increase and hence lower resilience to fishing mortality (Reynolds *et al.* 2005). The average trophic level of this global catch has declined as predatory fishes have been sequentially depleted and fishers target more productive species at lower trophic levels (Pauly *et al.* 1998; Essington *et al.* 2006). In the North Atlantic, predatory fishes have declined by two-thirds over the twentieth century (Christensen *et al.* 2003). A compilation of research survey data suggests that severe reductions in populations of the largest fishes span all oceans. More than 70–90% of the biomass of predatory fishes has been removed in the first 15 years after surveys began (Myers and Worm 2003); however, scientific surveys typically begin long after the onset of fishing, and the true extent of decline may again have been underestimated (Pinnegar and Engelhard 2008). It is incredibly difficult to go back much further in time to estimate the true extent of the decline in predatory fishes. Some insight of the overall impact of fishing compared to the ecological baseline comes from a macroecological energetic analysis that does not suffer from a limited time horizon of data availability. Such analysis suggests that fishing has resulted in a 99.9% decline in North Sea fish ranging in size from 16 to 66 kg (Jennings and Blanchard 2004).

6.6.6 Sharks, rays, and chimaeras

Many sharks and rays (elasmobranchs) are large and feed at or near the top of food webs (Cortés 1999; Stevens *et al.* 2000). Many elasmobranchs are taken as incidental by-catch of the high-seas fisheries for tuna and billfishes, and the great mechanized fisheries targeting cod and other bottom-dwelling fishes.

Some of the great pelagic sharks in the north-west Atlantic, such as the great white shark, *Carcharodon carcharias*, scalloped hammerhead, *Sphyrna* spp., and thresher shark, *Alopias* spp., have declined by approximately 75% in 15 years, which is less than the typical pelagic shark generation span (Baum *et al.* 2003; Myers *et al.* 2007). The oceanic white-tip, *Carcharhinus longimanus*, and silky shark, *Carcharhinus falciformis*, have declined by 99 and 90% respectively in the Gulf of Mexico (Baum and Myers 2004). Overall, three-quarters (16 of 21) of the species of oceanic pelagic sharks and rays face an elevated risk of extinction. Many of these species are caught regularly as incidental by-catch in widespread long-line, purse seine, and gill-net fisheries targeting more productive tunas, swordfishes, and other billfishes, as well as in midwater trawl fisheries for small pelagic fishes in boundary current systems, and swordfish fisheries on the high seas (Dulvy *et al.* 2008). Some elasmobranch species are also increasingly targeted for their meat, such as the shortfin mako, *Isurus oxyrhinchus*, porbeagle, *Lamna nasus*, and blue shark, *Prionace glauca*. However, shark fins are often worth more than the meat and these are removed (and body is discarded); the fins are then dried and sold on in the lucrative Asian shark-fin soup trade (Clarke *et al.* 2006b). There is strong concern about directed fishing to support the demand of the shark-fin soup trade in China and Hong Kong (Clarke *et al.* 2006a, 2006b). The weight of fins imported to Hong Kong each year amounts to approximately 5930 tonnes and the amount traded has been growing by approximately 6% per year (1991–2000) (Clarke 2004). It is estimated that 38 million individuals weighing a total of 1.7 million tonnes are killed each year and pass through the Hong Kong shark-fin market (Clarke *et al.* 2006b).

Smaller bottom-dwelling sharks, skates, and rays have declined severely as a result of incidental capture in bottom-trawl fisheries. The 2 m-long barndoor skate, *Dipturus laevis*, formerly widespread along the north-west Atlantic coast of USA and Canada, has largely been eliminated from Canadian shelf seas, but still persists on deeper slopes 1200 m deep beyond the reach of most fisheries and around protected areas on Georges Banks (Simon *et al.* 2002). On the other side of the Atlantic the largest skate in

the world, the unfortunately named common skate, *Dipturus batis*, has been eliminated from much of its range (Brander 1981; Dulvy *et al.* 2000). The angel shark, *Squatina squatina*, was the original monkfish, but as their catches declined they were substituted by anglerfishes, *Lophius* spp. This shark species disappeared virtually unnoticed from around the north-west Atlantic and the Mediterranean Sea. Research surveys throughout the west, north, and east Mediterranean Sea suggest that fewer than a couple of hundred adults remain (Baino *et al.* 2001). More recent surveys did not find any around the Balearic Islands, where the last known catches were taken (Massuti and Moranta 2003).

Sharks, rays, and chimaeras are one of the first marine groups subject to comprehensive assessment of threat status. The World Conservation Union (IUCN) Global Shark Assessment has documented a large number of local regional and global declines and near extinctions of oceanic and coastal sharks and rays (Cavanagh and Dulvy 2004). To date the IUCN/SSC Shark Specialist Group has assessed almost half (591 species) of the world's 1100 species of sharks, rays, and chimaeras and found that 21% are threatened (Dulvy *et al.* 2008).

6.7 Our emerging understanding of marine habitat loss

Habitat loss is currently the major driver of terrestrial extinctions, and is an increasingly important cause of threat and extinctions in the sea (Fig. 6.2). Our understanding of the scale of marine habitat loss and degradation is hampered by the difficulty of measuring and monitoring marine habitats, especially those beyond the view of satellite and airborne remote-sensing cameras (Green *et al.* 1996). Coral reefs, mangroves, and temperate estuaries provide the best understood examples of marine habitat loss and the consequences for marine biodiversity, and here we highlight some case studies.

6.7.1 Coral reefs

Coral reefs are among the most diverse ecosystems and also one of the most threatened, suffering multiple human impacts that occur at a range of spatial and temporal scales (Côté and Reynolds 2006). The scale of human impact on coral reefs over the last century is unprecedented in recent geological history. Recent human impacts have changed modern coral reef structure in a manner not previously observed in a 220 000 year sequence of fossil reefs in the Bahamas (Pandolfi and Jackson 2006). Unprecedented rates of coral reef loss have resulted from climate change-induced coral bleaching, the cascading effects of overfishing, emerging coral diseases, pollution, and hurricane disturbance (Côté and Reynolds 2006). In addition to these more immediate threats, the increase in anthropogenic CO_2 will largely be absorbed by the oceans, resulting in the acidification of surface waters and a reduction in the saturation state of the carbonate mineral aragonite by 30% by 2100 (Kleypas *et al.* 1999). The calcification of coral reefs is highly correlated with the aragonite saturation state, and the predicted 10–20% deficit in calcium carbonate accretion will render reef-building corals increasingly rare (Kleypas *et al.* 1999; Hoegh-Guldberg *et al.* 2007). Fish catches from island coral reefs are currently 64% higher than can be sustained (Newton *et al.* 2007). Overfishing may result in habitat degradation through herbivore removal, which reduces grazing pressure on algae that compete with and overgrow hard corals, and the release of coral predators resulting in coral mortality (McClanahan 1995; McCook *et al.* 2001; Dulvy *et al.* 2004). The rate of coral reef degradation has increased with predictions that up to 60% of reefs may be lost by 2030, not least due to increasing frequency of coral bleaching events (Hoegh-Guldburg 1999; Wilkinson 2000; Pandolfi *et al.* 2003; Sheppard 2003). The loss of hard coral cover, particularly due to global coral bleaching event associated with the 1998–2000 El Niño/La Niña Southern Oscillation, has led to the local extinction of fishes that specialize in feeding on corals or dwell within corals. The harlequin leatherjacket, *Oxymonocanthus longirostris*, is an obligate corallivore that disappeared from small study sites in southern Japan and elsewhere soon after a coral bleaching event (Kokita and Nakazono 2001; Dulvy *et al.* 2003). Coral-dwelling gobies (Gobiidae) and hawkfishes (Cirrhitidae) dwelling among branching *Acropora* corals declined by 59% between 1996 and 1997
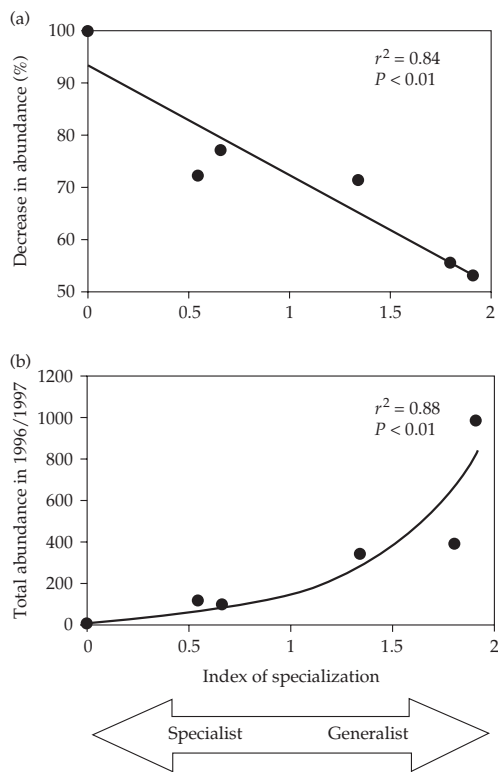
(a)

(b)

Figure 6.7 Decline (%) in abundance of coral-dwelling fishes compared to their habitat specialization (Shannon index of the diversity of coral species inhabited). (b) The relationship between the habitat specialization index and the total number of gobies of each species recorded in Kimbe Bay in 1996–1997. Redrawn from Munday (2004).

and 2003 in Kimbe Bay, Papua New Guinea due to coral bleaching and sedimentation (Munday 2004). This resulted in a 59% decline in the abundance of coral-dwelling gobies. The most specialist species typically had the smallest initial population sizes and suffered the most from the coral mortality. One undescribed goby species endemic to Kimbe Bay (*Gobiodon* sp. C.) may well have become globally extinct and another more widespread species (*Gobiodon* sp. A.) suffered local extinction (Munday 2004) (Fig. 6.7).

Reef-building corals also exist as patch reefs and mounds in deep coldwater habitats, such as continental shelf edges and seamounts (Roberts *et al.* 2006). There are more than 800 species of shallow-water reef-building corals; in the deep sea there are

eight described reef-building species as well as a wide array of soft corals, sea fans and bamboo corals (Octocorallia), black corals (Antipatharia), and hydrocorals (Stylasteridae) that can form or contribute to large structures. Deep-water coral reefs harbour considerable diversity: for example, over 1300 species have been found on *Lophelia pertusa* reefs in the north-east Atlantic (Roberts *et al.* 2006). Deep-water coral reefs are threatened by bottom trawling, oil exploration, and a shallowing aragonite saturation horizon due to ocean acidification (Roberts *et al.* 2006; Turley *et al.* 2007). The corals comprising or associated with deep-water reefs are very long lived and therefore unlikely to recover from impacts within a human time frame (Roberts *et al.* 2006). Hawai'ian coral-like species were radiocarbon-aged and found to be 450–2742 years old (Roark *et al.* 2006), New Zealand deep-sea corals were aged between 45 and 1200 years (Sikes *et al.* 2008), and dead portions of reef matrix taken in by-catch from commercial trawls targeting deep-water fishes off western Ireland was found to be at least 4500 years old (Hall-Spencer *et al.* 2002). However, a large Norwegian deep-water reef on the Sula ridge comprised of *Lophelia pertusa*, 13 km long and 10–35 m in height, was found to have reef-accumulation rates comparable to shallow tropical coral reefs (Freiwald *et al.* 1999). The most widespread and pressing threat is bottom trawling; in trawled areas reef-building corals are broken and dislodged by the heavy otter boards of the trawl gear. Several nations have acted swiftly to close newly discovered reef to fishing activity. However, much habitat exists beyond the 200 mile limit of Exclusive Economic Zones and outside national jurisdictions (Roberts *et al.* 2006).

6.7.2 Estuaries and coastal seas

Estuaries have suffered multiple impacts over the course of human history. They provide focal points for human activity, providing river access to the interior of countries and sheltered harbours and ports allowing the development of sea-going trade. Consequently, major settlements and ports have expanded rapidly along estuarine coastlines and into salt marshes. A well-documented case study is the Wadden Sea in The Netherlands, Germany, and

Denmark. Large-scale embankments and drainage of coastal marshes began approximately 1000 years ago (Wolff 2000a; Lotze 2005; Reise 2005). We will never know precisely how many species became extinct over any region across such a large time scale, but there is good evidence for extinction or severe depletion of 144 species in the twentieth century, with at least nine species having been lost in earlier times (Wolff 2000b; Lotze 2005). As is typical for most extinctions around the world (but see below), habitat loss has been the most important extinction driver, especially for invertebrates, seaweeds, and birds, followed by exploitation (invertebrates, bird, fishes, and marine mammals). So far, invasive species have not yet been blamed for the loss of any native species. However, the rate of invasion is increasing rapidly to the extent that, in some European port and harbour areas, non-native species may represent as much as 60% of the biomass of all species present (e.g. Eno *et al.* 1997).

An analysis of depletions and extinctions in 12 major coastal seas and estuaries around the world suggests that the Wadden Sea may be typical of heavily industrialized regions (Lotze *et al.* 2006). Key species groups from all regions showed similar patterns of gradual decline until the last 150–300 years, followed by recent rapid depletion of over 90% of formerly important species. For the species in this study, exploitation was responsible for approximately 95% of depletions and extinctions, followed by habitat loss.

6.7.3 Mangroves

Mangroves trap sediment along tropical coastlines, creating natural barriers to sea-level rise and storm surges and saltwater intrusion into coastal soils and estuaries (Spalding *et al.* 1997; Danielson *et al.* 2005). They also function as key nursery habitats for fishes and invertebrates and are likely to contribute to ecosystem resilience and fisheries productivity (Mumby *et al.* 2004). Mangroves are threatened by deforestation for firewood, coastal development, the expansion of shrimp aquaculture, and rising sea levels. The global extent of mangrove forest has declined by a third over the last 50 years (Alongi 2002). The greatest cause of deforestation is shrimp aquaculture: the rich mangrove soils support highly

productive growing conditions for shrimp, but productivity declines within a few years and the farming operation moves on, clearing more mangrove forest (EJF 2004). Shrimp farming has caused the loss of 20–50% of mangroves worldwide, particularly in developing countries where mangroves are predicted to decline by another 25% by 2025. The loss of mangroves has affected local populations of plants and animals, but it is not yet known whether deforestation has led to extinctions (Dulvy *et al.* 2003). Mangrove loss is expected to increase due to anthropogenically induced sea-level rise; mangrove habitat will be trapped between rising sea levels and coastal development. In the Pacific Ocean sea level is (conservatively) predicted to rise by 0.5–0.8 m by 2100 (Church *et al.* 2001) and is predicted to reduce mangrove area by 12% by 2100 (Gilman *et al.* 2007). However, there is a possibility that sea-level rise may be an order of magnitude greater as these estimates do not incorporate emerging evidence of rapid dynamic melting of west Antarctic and Greenland ice sheets (Hansen 2007).

6.7.4 Overfishing-induced habitat transformation

The effects of overfishing and habitat loss may be more difficult to disentangle, as the depletion of predatory fishes has led to habitat degradation and transformed the production base of some marine ecosystems through trophic cascades (Pace *et al.* 1999; Pinnegar *et al.* 2000; Tittensor *et al.* 2008). A top-down view of many ecosystems is emerging whereby top predators control herbivore abundance, biomass, and behaviour with cascading effects on the structure and dynamics of the resource base (Micheli 1999; Shurin and Seabloom 2005; Heithaus *et al.* 2008). Overfishing-induced proliferations of urchins and starfish have transformed coral communities into algal-dominated states (Carreiro-Silva and McClanahan 2001; Dulvy *et al.* 2004). For example, hunting and elevated predation on Pacific sea otters has led to urchin proliferation and shifts from kelp forests to coralline algal barrens (Estes 1998; Steneck *et al.* 2003). While it is difficult to demonstrate causality, compelling evidence suggests the massive-scale population collapses of the great whales by post-World War II

industrial whaling caused killer whales to begin feeding more intensively on smaller marine mammals such as sea otters (Springer *et al.* 2003). The collapse of Atlantic cod is associated with increases in northern snow crab, *Chionoecetes opilio*, northern shrimp, *Pandalus borealis*, urchins, and small pelagic fishes (Worm and Myers 2003; Frank *et al.* 2005). The increase in urchins has denuded coastal kelp forests in the Gulf of Maine (Jackson *et al.* 2001) and increase in small pelagic fishes was associated with lower abundance of large zooplankton and elevated phytoplankton abundance on the eastern Scotian shelf, off Nova Scotia, Canada (Frank *et al.* 2005). Such trophic cascades are relatively commonplace and have been reported for marine ecosystems all around the world (for recent reviews see Pinnegar *et al.* 2000; Lees *et al.* 2006).

6.8 A brief overview of known marine extinctions

There is unequivocal evidence for at least 20 global marine extinctions during the historical era (Table 6.1), an increase on the last estimate of 12 reported in 1999 (Norse 1993; Vermeij 1993; Carlton *et al.* 1999). As far as we are aware there have not been any global marine extinctions in the past two decades. The most recent extinction, that of the Galapagos damselfish, *Azurina eupalama*, occurred at some point after 1983. The cause of the increase in the number of documented global marine extinctions is instead our more detailed understanding of the taxonomy of extinct species and the discovery of previously unknown historic extinctions. For example, the Japanese sea lion, *Zalophus japonicus*, was previously thought to be a subspecies of the California sea lion, *Zalophus californianus*, but is now recognized as a separate species (Wilson and Reeder 2005). Among the newly discovered extinctions is Bennett's seaweed, *Vanvoortsia bennettiana*, which was last recorded in Sydney harbour in 1916. This extinction was only uncovered by the diligent efforts of a taxonomist compiling a regional species list. Not included in this list of marine extinctions are the species on 'death row'; these include European sturgeon and white abalone, *Haliotis sorenseni* (Dulvy *et al.* 2003), neither of which has bred successfully in the past two decades. There

may be hope for the white abalone, as captive breeding appears increasingly feasible. However, the prognosis for the European sturgeon is poor; it is now only found in one river system in Europe, the Gironde system in France, and is also threatened by the accidental escape of Siberian sturgeon, *Acipenser baerii*, into this river.

More biodiversity has been permanently lost during the Holocene than might be inferred from this relatively low number of known historical-era marine species extinctions (Knowlton 1993; Reaka-Kudla 1997). The 20 known marine species extinctions documented here include only two procellariiform species: the St. Helena Bulwer's petrel, *Bulweria bifax*, and the large St. Helena petrel, *Pteroderma rupinarum* (Table 6.1). However, a further 11 species and 79 populations of procellariiforms may have gone extinct in the prehistoric Holocene (see Chapter 4 in this volume). The recent survey of Dulvy *et al.* (2003) has highlighted that numerous population extinctions have occurred at the local and regional level, and there may be more impending global-scale extinctions that have yet to be discovered. This survey focused on local and regional population-scale extinctions for four reasons. First, populations are often morphologically and genetically distinct (Carlton *et al.* 1999; Ruzzante *et al.* 2000; McIntyre and Hutchings 2004). Second, source populations may also rescue other sink populations contributing to the resilience of the species as a whole (Smedbol *et al.* 2002). Third, population extinctions usually precede global extinction (King 1987; Pitcher 1998). Finally, impacts and management typically occur at the population scale. This survey uncovered evidence for 133 local, regional, and global extinctions. Local- and regional-scale extinctions cover the scale of small semi-enclosed seas such as the Irish Sea up to the Mediterranean Sea and ocean quadrants. There was evidence for at least seven new possible global extinctions of fishes, corals, and algae. Four of these are now recognized are global marine extinctions (Table 6.1), leaving three whose status has yet to be confirmed (two eastern Pacific corals, *Millepora boschmai* and *Siderastrea glynni*, and Turkish towel algae, *Gigartina australis*) (Dulvy *et al.* 2003).

A key assumption of this analysis is that the populations have truly become extinct. A proposed

Table 6.1 Twenty historical-era global marine extinctions of mammals (4), birds (8), fishes (3), molluscs (4), and algae (1).

Common name (order, family: species name)	Historical range	Last known date of occurrence	Cause of extinction	Source
Mammals				
Steller's sea cow (Sirenia, Dugongidae: *Hydrodamalis gigas*)	Commander Islands (Bering Sea, north-west Pacific Ocean)	1768	Overexploitation	Anderson (1995); Carlton *et al.* (1999); Turvey and Risley (2006)
Sea mink (Carnivora, Mustelidae: *Neovison macrodon*)	Canadian (New Brunswick) and USA (Maine) coasts	1860	Overexploitation	Campbell (1988); Youngman (1989); Carlton *et al.* (1999); IUCN (2006); Sealfon (2007)
Japanese sea lion (Carnivora, Otariidae: *Zalophus japonicus*)	Japan (Sea of Japan), Russia (Kamchatka)	No credible sightings since late 1950s		Rice (1998); Carlton *et al.* (1999); Wilson and Reeder (2005); IUCN (2006)
Caribbean monk seal (Carnivora, Phocidae: *Monachus tropicalis*)	Coastal Caribbean Sea and Yucatan, including Mexico, Bahamas, Guadeloupe, Jamaica, Puerto Rico, USA (Florida)	1952	Overexploitation	Carlton *et al.* (1999); Wilson and Reeder (2005); IUCN (2006); McClenachan and Cooper (2008)
Birds				
Pallas's cormorant (Pelecaniformes, Phalacrocoracidae: *Phalacrocorax perspicillatus*)	North-west Pacific	*c.*1850	Overexploitation	Greenway (1967); Carlton *et al.* (1999)
Tasman booby (Pelecaniformes, Sulidae: *Sula tasmani*)	Lord Howe and Norfolk Islands (Australia)	Nineteenth century?; last seen in 1788	Overexploitation and introduced species	BirdLife International (2004); IUCN (2006)
St. Helena Bulwer's petrel (Procellariiformes, Procellariidae: *Bulweria bifax*)	St Helena, central Atlantic	Sixteenth century	Overexploitation	BirdLife International (2004); IUCN (2006)
Large St. Helena petrel (Procellariiformes, Procellariidae: *Pteroderma rupinarum*)	St. Helena, central Atlantic	Sixteenth century	Overexploitation and introduced species	BirdLife International (2004); IUCN (2006)
Auckland Island merganser (Anseriformes, Anatidae: *Mergus australis*)	South-west Pacific	1902	Overexploitation	Carlton *et al.* (1999)
Labrador duck (Anseriformes, Anatidae: *Camptorhynchus labradorius*)	Breeding habitat in Gulf of St. Lawrence and coastal Canada, north-west Atlantic	1875	Overexploitation of adults and eggs	Carlton *et al.* (1999); BirdLife International (2004); IUCN (2006)
Great auk (Charadriiformes, Charadriidae: *Pinguinus impennis*)	North Atlantic	1844	Overexploitation	Carlton *et al.* (1999)
Canary Islands oystercatcher (Charadriiformes, Charadriidae: *Haematopus meadewaldoni*)	North-east Atlantic	1913	Invasive species	Carlton *et al.* (1999)
Fishes				
Galapagos damselfish (Perciformes, Pomacentridae: *Azurina eupalama*)	Galapagos Islands	1982	Habitat loss, climate change	Jennings *et al.* (1994); Roberts and Hawkins (1999); G.J. Edgar *et al.* (unpublished work)

Table 6.1 *Continued*

Common name (order, family: species name)	Historical range	Last known date of occurrence	Cause of extinction	Source
Mauritius green wrasse (Perciformes, Labridae: *Anampses viridis*)	Mauritius	1839	Unknown	Hawkins *et al.* (2000)
New Zealand grayling (Salmoniformes, Retropinnidae: *Prototroctes oxyrhinchus*)	New Zealand	1923	Exploitation and invasive species	Balouet and Alibert (1990); McDowell (1996)
Invertebrates				
Atlantic eelgrass limpet (Archaeoastropoda, Lottidae: *Lottia alveus*)	North-west Atlantic	1929	Habitat loss	Carlton *et al.* (1991, 1999); Carlton (1993)
Rocky shore limpet (Archaeoastropoda, Nacellidae: *Collisella edmitchelli*)	North Pacific	1861	Habitat loss	Carlton (1993); Carlton *et al.* (1999)
Horn snail (Gastropoda, Cerithideidae: *Cerithidea fuscata*)	North-east Pacific	1935	Overexploitation	Carlton (1993); Carlton *et al.* (1999)
Periwinkle (Mesogastropoda, Littorinidae: *Littoraria flammea*)	China	1840	Habitat loss	Carlton (1993); Carlton *et al.* (1999)
Algae				
Bennett's seaweed (Ceraniales, Delesseriaceae: *Vanvoortsia bennettiana*)	Sydney Harbour, eastern Australia	1916	Habitat loss	Millar (2001); IUCN (2006)

alternative is that they represent shifts in dynamic geography, whereby reduced abundance is associated with reduced spatial occupancy, and these disappearances merely represent temporary extinction and recolonization events which may be particularly likely at the edge of a species' geographic range (MacCall 1990; Hanski 1998; del Monte-Luna *et al.* 2007; Webb *et al.* 2007). However, permanent range contractions at local scales are the stepping stones toward species extinction (King 1987). The population extinctions reported by Dulvy *et al.* (2003) are unlikely to be temporary patch extinctions. These extinctions are long-standing; the local extinctions have persisted on average for 64 years, and global extinctions for 77 years on average (Fig. 6.8a). Comparatively less time (33 years) has elapsed for regional extinctions, largely due to the inclusion of numerous recent fish population extinctions (Fig. 6.8b).

Since the review by Dulvy *et al.* (2003) was published there have been several recolonizations in the Dutch Wadden Sea, including grey seal, *Halichoerus grypus*, eider duck, *Somateria mollissima*, common gull, *Larus canus*, and lesser black-backed gull, *Larus fuscus*. All of these cases may be attributed to strongly improved protection (W.J. Wolff, personal communication). While these recolonizations are a important sign of changing management focus and efficacy, they are unlikely to mitigate against the likely loss of genetic, morphological, and behavioural diversity associated with the original population extinctions. Population extinctions are turning up with greater frequency, as predicted in the original study. The authors originally stressed that this data set was far from definitive, because of the problems of recognizing and defining extinctions; however, they provided the first systematic review of the evidence
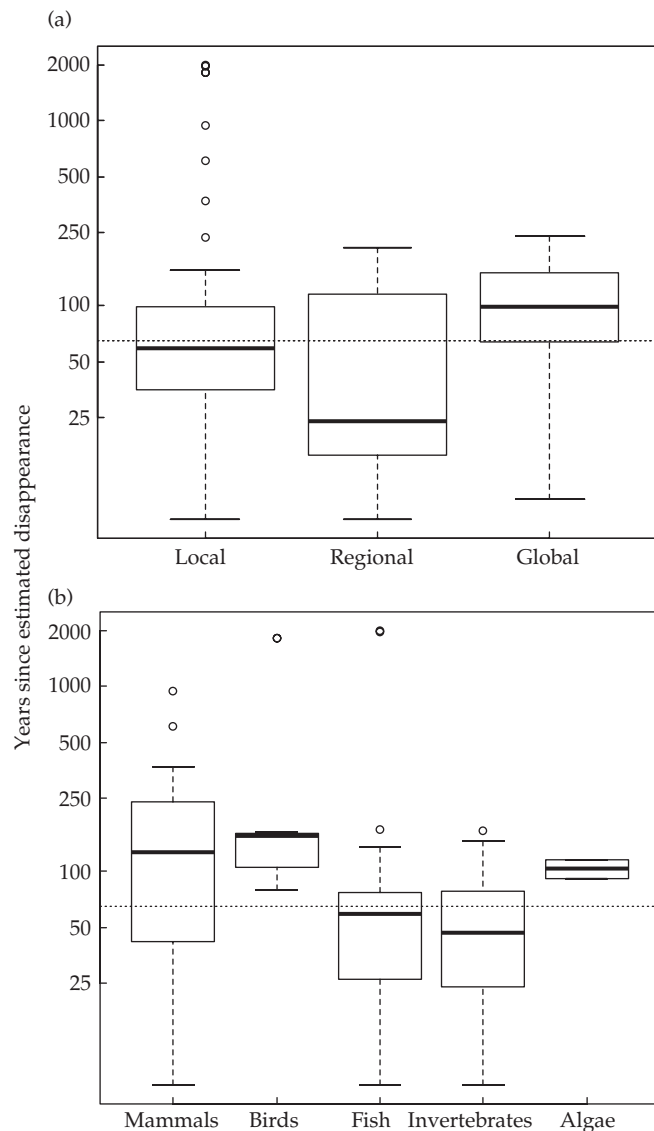
(a)

Years since estimated disappearance

(b)

Figure 6.8 The persistence of marine extinctions. Time elapsed since the estimated extinction date, split by (a) geographical scale and (a) taxon. The average time elapsed since the estimated extinction date is 65 years, and is represented by the dotted line. There is no significant difference in the time elapsed since estimated extinction among the differing spatial scales of extinctions ($F_{2,97} = 0.7$, $P = 0.48$). Bird and mammal disappearances were detected earlier and/or happened longer ago compared with the estimations of fishes and invertebrates ($F_{4,95} = 5.3$, $P < 0.001$), but only pairwise comparisons between birds versus either fish or invertebrates are significant (Tukey's HSD, $P < 0.05$). This test is robust to the exclusion of algae. Estimated extinction dates were available for 13 of the 14 mammals, 11 of the 12 birds, 57 of the 65 fishes, 17 of the 31 invertebrates, and 2 of the 12 algae. Data from table 1 in Dulvy *et al.* (2003).

and concluded that marine extinctions were being overlooked (Dulvy *et al.* 2003). The detection and reporting of marine extinctions lags behind the date of actual extinction by about 50 years. However, this detection lag is becoming shorter over time, suggesting that scientific capacity to detect marine extinctions is steadily improving (Dulvy *et al.* 2003). Indeed, since the original review was published, additional population-level extinctions have been discovered, particularly on coral reefs.

These include: the disappearance of the rainbow parrotfish, *Scarus guacamaia*, from the coastline of Brazil (Ferreira *et al.* 2005); population extinctions in the world's largest parrotfish, the giant bumphead parrotfish, *Bolbometopon muricatum*, from Guam and the Marshall Islands (Bellwood *et al.* 2003; Hamilton 2003; Donaldson and Dulvy 2004; Dulvy and Polunin 2004); the local and near-global extinction of two coral-dwelling gobies (Gobiidae) (Munday 2004); and the probable global extinction

of the endemic Galapagos stringweed, *Bifurcaria galapagensis*, and possible local extinction of another seven species (G.J. Edgar *et al.*, unpublished work). The recent increase in the number of documented global extinctions and these newly discovered extinctions may reflect an elevated marine extinction rate, and they refute recent assertions by del Monte-Luna *et al.* (2007) that the marine extinction rate is overestimated and overstated. The increase in extinctions is a more likely hypothesis for two reasons: evidence for accelerating threats such as exploitation, climate change, and habitat loss (Edgar *et al.* 2005), and increased likelihood of extinction detection due to greater awareness of the potential for marine extinctions (Dulvy *et al.* 2003).

A major barrier to raising awareness of the likelihood that marine populations and species have gone extinct is a highly risk-averse attitude towards evaluating evidence for marine extinctions. Some scientists believe that species extinctions should not be highlighted until there is sufficient evidence has been accumulated (del Monte-Luna *et al.* 2007). Raising false alarms—incorrectly flagging the extinction of an extant marine population or species—should be avoided at all costs because a high rate of false alarms would devalue the credibility of threat assessments and be used to question the integrity of conservation and management policies (del Monte-Luna *et al.* 2007). However, while a more stringent approach to defining and documenting marine extinctions appears highly risk-adverse, this strategy runs the risk of allowing extinctions to go unnoticed and undocumented (Peterman and M'Gonigle 1992). Given (1) the rise in the scale of human activity in the seas, (2) the clear link between human-induced habitat transformation and terrestrial extinctions over the last 10 000 years, and (3) the documented evidence that marine extinctions are underestimated, it seems less precautionary to wait until sufficient evidence is available to ensure the accurate documentation of a species extinction. Instead it may be more appropriate to focus on identifying local marine extinction and biodiversity loss with a view to conserving and managing remaining populations (Peterman and M'Gonigle 1992). The choice lies somewhere between providing sound defensible assessments based on the currently available evidence that can be used to prioritize conservation action, or waiting until *all* evidence is available and taking the risk of presiding over a post mortem of marine biodiversity loss.

While scientists can provide and describe the consequences of these options, to a large degree the choice lies with society rather than scientists. This choice depends on the degree to which human societies are able to move towards bearing the social and economic cost of the lost opportunity to exploit provisioning ecological services, such as fisheries, to ensure that all biodiversity is preserved (Jennings 2007). Historically, (European) society has been more concerned with maintaining food supply and minimizing conflict (e.g. Icelandic cod wars) in fisheries (Holden 1992), although now there is an increasing and concerted effort to ensure biodiversity protection and maintenance of ecosystem function and processes through the Ecosystem Approach to Fisheries (Sainsbury and Sumaila 2003; Pikitch *et al.* 2004; ICES 2005). However, we recognize that other less developed nations, which are yet to experience the human demographic transition and reduced population growth rates, may face a more difficult or delayed transition towards sustainability.

6.9 Can we avert a double extinction wave in the sea?

The evidence for loss of marine megafaunal biomass and alterations to marine ecosystems over the last thousand years is incontrovertible. So far most marine extinctions have been of local and regional populations: relatively few species extinctions have been documented. The depletion of marine biomass is a price paid as a consequence of supplying considerable provisioning ecosystem services for the development and benefit of human societies (Pauly and Alder 2006). There is increasing recognition that even greater benefits can be derived while sustaining rather than depleting biodiversity (Worm *et al.* 2006). For example, a large stock size and a multistock portfolio policy allows sustainable yields to be taken in perpetuity while minimizing the risks and insecurity of environmental variability and long-term change (Hilborn *et al.* 2003; DEFRA 2004). Not only will reduction

of fishing capacity and effort on target stocks help build resilience; the integration of fisheries considerations within a wider management framework is well advanced, for example through development of the ecosystem approach to fisheries management, thereby addressing the World Summit on Sustainable Development 2010 target to halt the loss of global biodiversity by 2010 (Sainsbury and Sumaila 2003; Pikitch *et al.* 2004; ICES 2005). The scientific knowledge, institutional capacity, and political commitment available to avert a marine megafaunal extinction wave is greater now than in the past, and our capacity to recognize and avert serious environmental damage has never been greater in the Holocene. The first fishes have been listed on international conventions typically used to restrict the trade in endangered plants, mammals, and birds (including sea horses, humphead wrasse, *Cheilinus undulatus*, basking shark, *Cetorhinus maximus*, whale shark, *Rhincodon typus*, and great white shark). Regionally and nationally there is increasing use of wildlife conservation legislation to assess and protect exploited fishes, such as the Endangered Species Act (USA), the Species at Risk Act (Canada), the Wildlife and Countryside Act (UK), and the Bern Convention (Europe). This is clearly an optimistic view and one more typical of European and North American fisheries science; research capacity and the strength of institutions may not be as favourable elsewhere in the world, and there is still scope for the development of novel fisheries diagnostics and management (Andrew *et al.* 2007).

Some populations of marine species have been brought 'back from the brink', notably sea otters in the western Pacific and some whale species. This has required draconian measures, including a complete moratorium on hunting or whaling. Several species of marine mammals and birds in the countries around the North Sea have recovered spectacularly thanks to a range of concerted conservation measures in these countries (W.J. Wolff, personal communication). Similarly, a few fish and invertebrate stocks have been allowed to recover from overexploitation (Caddy and Agnew 2004; Mace 2004). More successes have been documented for invertebrate pelagic fisheries than demersal species and depletions aggravated by multispecies

fisheries, and unfavourable climatic regimes will always be difficult to reverse (Piet and Rice 2004; Brander 2007).

We are now catching up with the terrestrial preoccupation with captive rearing, as numerous forms of aquaculture are growing rapidly while global yields from wild-capture fisheries have been stalled for the past 15 years (FAO 2007). The current transition to aquaculture co-occurs with a period of uncertainty for the future of marine biodiversity. Whereas the transition to farming on land eventually led to the elimination of hunting of wild animals for food in most developed countries, there is little sign yet that the growth of aquaculture is relieving fishing pressure on wild stocks. Furthermore, fish farming often involves high-trophic-level carnivores, such as salmon, sea bass, and tuna. These farming operations create their own markets for wild-caught fishes to be converted to fish meal (Naylor *et al.* 2000). Thus, the challenges facing biodiversity in the sea show no signs of abating in the near future, and as with all environmental problems, our best hopes lie with a concerted global focus on the core underlying drivers of change: human population growth and increasing per-capita demands for resources.

While a major extinction wave driven by exploitation and habitat loss occurred on land during the Late Pleistocene and prehistoric Holocene, a similar process may now be unfolding in the oceans. The challenge will be to limit the scale of any impending marine extinction wave. The opportunity to forestall a major loss of ocean biodiversity has never been greater. Society, scientists, and managers are acutely aware of these problems and legislation and institutions are strengthening in response. However, several 'ratchet-like' processes, including a growing global population and international markets for marine products, make it very difficult to return to a more 'natural' state (see discussion in Pinnegar and Engelhard 2008).

Acknowledgements