

Human impacts on marine ecosystems

Keith Brander, Louis W. Botsford, Lorenzo Ciannelli, Michael J. Fogarty, Michael Heath, Benjamin Planque, Lynne J. Shannon, and Kai Wieland

3.1 Introduction

Apart from the sea surface, the oceans are the most remote and least visited part of the planet by humans, yet marine ecosystems are under increasing threat from a range of human activities including pollution, mineral extraction, climate change, fishing, habitat modification, and shipping (which generates noise and transports introduced species). It is relatively easy to list these factors and to map their likely impacts (Halpern *et al.* 2008), but it is more difficult to assemble evidence of impacts 'in situ' (the terms 'on the ground' or 'in the field' are incongruous in an aquatic context) and to be confident that observed impacts are correctly attributed to specified causes. Among the reasons for this are our lack of familiarity with marine ecosystems, lack of data, high natural variability, and the fact that most of the life in the sea is microscopic and almost unknown.

The aim of the GLOBEC programme was to advance our understanding of the structure and functioning of marine ecosystems and their response to physical forcing. Although human impact was not in itself a topic of the programme, the effects of fishing in particular are so great, especially on higher trophic levels, that they must be taken into account when evaluating responses to physical forcing. Furthermore, some of the best information which we have on changes in marine ecosystems comes from monitoring fish catches. Other marine biota from phytoplankton to benthos to seabirds and whales have also been affected by anthropogenic factors, sometimes to the point of extinction, but these are

not the main subject of the GLOBEC programme (Gifford *et al.*, Chapter 4, this volume), whose principal taxonomic subject was zooplankton. Only some of the work described in this chapter was carried out as part of the GLOBEC programme.

Following the Introduction, Section 3.2 presents some of the ethical and utilitarian ideas which underlie our relationship with marine ecosystems; it gives a brief overview of historic evidence concerning past states of marine ecosystems and of the intensification of human impacts. Section 3.3 describes direct impacts of fishing on the demography and biomass of exploited species and on loss of vulnerable species and habitats. Section 3.4 looks at the interaction between fishing and environment in causing observed ecosystem changes; it deals with changes in trophic structure and consequences for resilience and productivity. In Section 3.5, a short summary is followed by emerging conclusions about human impacts, future human stewardship, and utilization of marine ecosystems. Five case studies are embedded within the chapter to illustrate some of the issues raised.

3.2 Human interaction with the natural world and evidence of impact on marine ecosystems

3.2.1 Stewardship and sustainability

Interaction with the natural world is fundamental to our existence as individuals, communities, and societies. We depend on nature for our atmosphere,

food, fuel, shelter, recycling of waste, medicines, and recreation. Human attitudes to nature differ between communities and societies, depending on economic, cultural, and religious circumstances and attitudes change over time (Thomas 1983). What we judge to be acceptable or unacceptable behaviour has profound consequences for our use, exploitation, and often extermination of plants and animals. Such judgements form part of our spiritual and ethical values and inform our economic activities, diet, laws, regulations, and management.

The view that nature exists to serve man's interests has ancient roots in many cultures. Taming wild nature and domesticating plants and animals have been regarded as part of the advance of civilization although, as with most human actions, it is difficult to tell whether ethical justification precedes economic benefit or vice versa. Some cultures and religions take a more reverent view of nature than others, but it is evident that societies on all continents are capable of destroying their natural environment, with or without the aid of colonialism, industrialization, or religious conversion (Carrion *et al.* 2007). The doctrine of human stewardship and responsibility for nature has coexisted uneasily with the right to exploit 'inferior species' in most religions and cultures.

The terrestrial biosphere has now been transformed to a large extent for agriculture, urbanization, pastoralism, forestry, water management, and roads. Pests, weeds, predators, and competitors are exterminated and selected crops and animals are reared in enclosed, controlled conditions. The pressures of human population needs, food supply, and economic development dominate the landscape, although there is much concern over transformations which are taking place, such as loss of biodiversity, genetic engineering, and changes in land use (e.g. deforestation and loss of wetlands). Of the remaining natural world, some has been preserved by establishing areas which are protected to varying degrees from being transformed.

Coastal and shallow sea marine ecosystems have also been transformed by human pressures, and concerns about the depletion of fish stocks have been expressed for several centuries (Bolster 2008). However, it is only recently that historical awareness of such changes has acquired any prominence in marine science and fisheries management (Lotze

et al. 2006). This lack of information and historical awareness has given rise to what has been called the 'shifting baseline' syndrome, in which successive generations of scientists accept as the baseline the state of marine ecosystems at the start of their careers (Pauly 1995). In this way, the potential abundance, productivity, and diversity of marine species may be consistently underestimated (Rosenberg *et al.* 2005).

Our relationship with marine life is entirely different from our relationship with life on land. On land, we farm large herbivores (cows and sheep), but in the sea most herbivores are very small (zooplankton) and we capture only the larger herbivores (small pelagic fish) and carnivores (large pelagic and demersal fish). We do not live in the sea and have no direct experience of it. The vast majority of marine plants and animals can only be seen under strong magnification and have lifespans of a few hours, days, or weeks. Apart from coastal grasses and macroalgae, marine plants are motile and do not provide structure and shelter as terrestrial plants do. There is almost no cultivation of phytoplankton, although some investigation into their potential as biofuel is taking place (Haag 2007), as is the possibility of a role in mitigation of climate change by ocean iron fertilization (Browman and Boyd 2008). Over the past 3 decades the demand for protected areas in the sea has grown in order to preserve biodiversity and ecosystem functions, and to provide areas of refuge from overfishing and natural beauty for recreation.

There is a rapidly developing framework of national and international declarations, conventions, guidelines, and regulations on stewardship and sustainability of marine systems, which is discussed by Barange *et al.* (Chapter 9, this volume). The impulse for these developments comes from individuals, scientific and environmental organizations, and political leaders who express concern for the restoration of damaged ecosystems, preservation of biodiversity, and prevention of overfishing. The ecological pillar of the ecosystem approach to fisheries (EAF) aims to ensure sustainable yields of exploited species, while conserving stocks and maintaining the integrity of ecosystems and habitats on which they depend. There can be little disagreement that these are laudable aims and yet we have to ask whether they are compatible with other social and economic aims (the other two pillars of the EAF), in particular maximizing food production from the sea? Here the contrast

with attitudes to terrestrial food production is stark. If agriculture were forced to reverse the trends of the past few hundred years, to restore ecosystems and preserve predators and pests, then food production would rapidly decline below the level needed to sustain the human population. The UN Food and Agriculture Organization (FAO) advocates an EAF, but not to agriculture (although there are many initiatives to make land use less ecologically damaging).

Many unresolved questions and dilemmas arise, which require an understanding of how marine ecosystems function. Could we stabilize and maximize food production from the sea, while preserving as much of the ecosystem as possible, by transforming those areas which are not protected into managed production zones, like terrestrial agricultural systems? Do we know how to carry out such a transformation (Walker *et al.* 2004)?

3.2.2 Evidence of past states of marine ecosystems

Evidence for large amplitude fluctuations in the state of marine populations and ecosystems has accumulated at nearly all accessible spatial and temporal scales. Recent records based on direct observations of marine systems provide the basis for understanding contemporary interannual fluctuations. Historic records (based on the fishing trade), diaries, and public records, provide information about the state of marine systems over several centuries (Quéro 1998; Jackson *et al.* 2001; Ojaveer and MacKenzie 2007; see Box 3.1). Further back in time, historic records are often lacking but palaeo-oceanographic studies have revealed patterns of fluctuations in marine systems over thousands of years (Lotze *et al.* 2006). In this section, we present some of the evidence for variations in the state of marine systems at time scales ranging from a few decades to millennia.

Fisheries statistics, including information on numbers and sizes of fish caught at different ages, are collected routinely for many stocks by sampling of commercial catches and special research surveys. Some of these time series, which may also include information on maturity, fecundity, liver weight, fat content, and other measures of condition, go back nearly a century (e.g. Fig. 3.1-upper panel). In contrast there are few consistent, geographically exten-

sive time series for other components of marine biota. The variability of global fish catches has been increasing over time (Halley and Stergiou 2005).

In the Mediterranean Sea, the bluefin tuna (*Thunnus thynnus*) population has been harvested with passive nets for several centuries and catches have been precisely recorded by trading companies. Ravier and Fromentin (2001) examined 54 individual time series of trap catches from the western Mediterranean and the Atlantic coast of Portugal, Spain, and Morocco. They were able to reconstruct a composite time series of the relative abundance of the bluefin tuna population for more than 3 centuries, which displays pseudocycles of 20 and 100 years, with amplitudes of a factor of 20 (Fig. 3.1-middle panel). The development of the bluefin tuna fishery in northern Europe shows that it was an important part of the ecosystem in the early 1900s (MacKenzie and Myers 2007).

Catch data for the Baltic Sea show fluctuations in cod (MacKenzie *et al.* 2007a), herring, eel, and whitefish fisheries as far back as the sixteenth century (Poulsen *et al.* 2007). Mid-nineteenth-century New England fishing logs provide geographically specific daily catch records which can be used to estimate the biomass of cod on the Scotian Shelf at that time (Rosenberg *et al.* 2005). The estimate of nineteenth-century cod biomass of 1.2 million t is very close to the estimated carrying capacity from twentieth-century data (Myers *et al.* 2001) and four times higher than the peak total biomass estimated in the 1980s (Mohn *et al.* 1998).

Major losses of marine mammal, sea turtle, and seabird populations through harvesting and incidental catch in fishing operations over the last 3 centuries have led to radical reorganization of many marine ecosystems (e.g. Jackson *et al.* 2001; Estes *et al.* 2007) resulting in fundamental changes in energy flow and utilization. These impacts and resulting changes in abundance levels have been chronicled in historical accounts and a diverse array of fishery-related records (Starkey *et al.* 2008).

Palaeo-oceanographic investigations show variations in marine ecosystems over longer time scales. Baumgartner *et al.* (1992) analysed multiple sediment cores sampled from anoxic sediment in the eastern north Pacific and were able to reconstruct the history of sardine and anchovy populations for nearly 2 millennia (Fig. 3.1-lower panel). They found large amplitude, multidecadal fluctuations in the abundance of

both species. Fish bones from Mesolithic Stone Age excavations in Denmark record the catching of a number of warm water species during the Atlantic period (ca. 7000–3900 BC), when mean summer water temperature was 1.5–2.0°C higher than at present (Engelhoff *et al.* 2007). Several of the species (anchovy-*Engraulis encrasicolus*, European sea bass-*Dicentrarchus labrax*) caught then have been increasing in abundance again during the warming period over the past 20 years (MacKenzie *et al.* 2007b). In the north Pacific, Finney (1998) reconstructed the history of sockeye salmon abundance in the Kodiak Islands for 300 years by measuring changes in sedimentary $\delta^{15}\text{N}$. Again, the reconstructed history displays large changes in population abundance over time. When Finney *et al.* (2002) extended their analysis further back in time, they found that the variations over the last 2 millennia were of even greater amplitude.

For plankton we have two excellent time series which cover the California coast (1949-present: www.calcofi.org) and much of the North Atlantic (1946-present: www.sahfos.org). The latter uses the Continuous Plankton Recorder (CPR) on regular shipping routes to generate spatially and taxonomically detailed monthly time series of zooplankton (and some phytoplankton) (Planque and Reid 2002). The plankton community structure in the North Sea and adjacent areas has undergone large amplitude variations, with a general northward movement of mesozooplankton species (Beaugrand *et al.* 2002b), change in the balance of diatoms versus dinoflagellates (Leterme *et al.* 2006), and shifts in the phenology of major plankton species (Edwards and Richardson 2004).

Ecosystem changes in the past decades, in the North Sea and elsewhere, have been contemporary with

Box 3.1 Bassin d’Arcachon—historic records of 300 years of harvesting

The Bassin d’Arcachon is a tidal bay on the southern Bay of Biscay, French Atlantic coast, with an area of 155 km² at high tide. It is the principal area of oyster culture in Europe, with annual production of 18,000 t plus export of spat to many other areas. Fish have historically been plentiful in the Bassin, and in the eighteenth century about 500 people fished there during the summer. About half of the fishermen followed the fish out into the open sea in winter, when it became too cold for them in shallow water, returning in April. A fuller account of the fisheries and of the impacts of climate is provided by Quérou (1998).

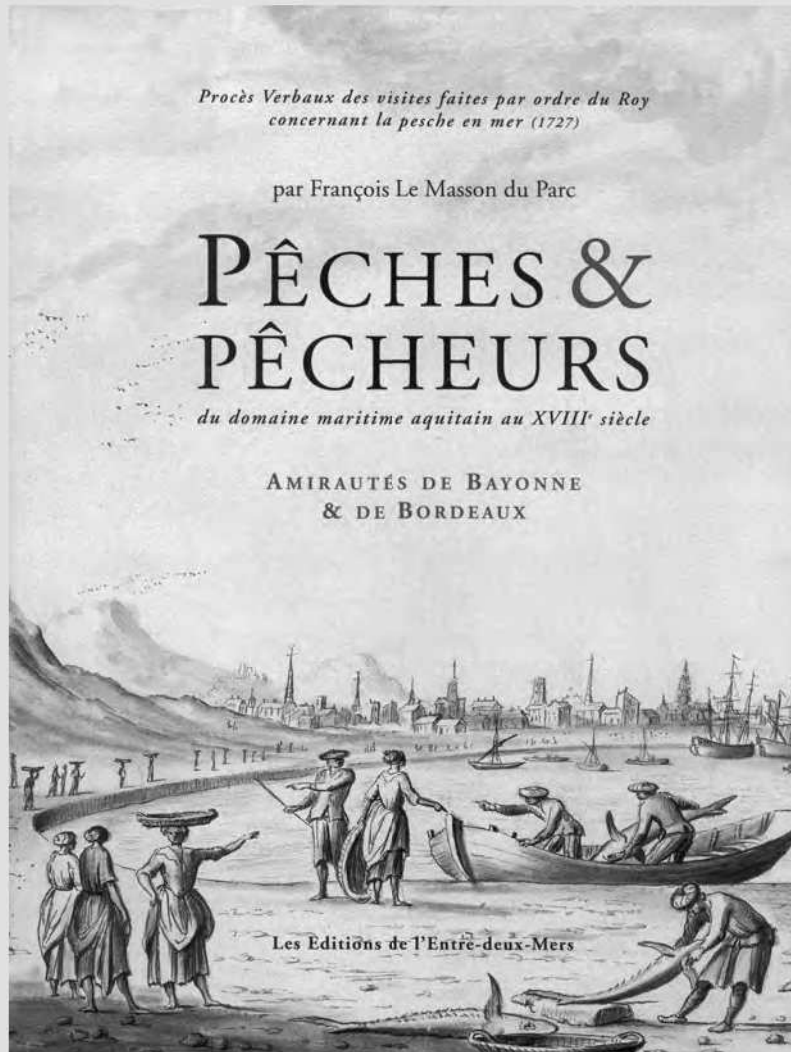
Two authors, Le Masson du Parc (1727) and Duhamel du Monceau (1771) wrote accounts of the fisheries in the Bassin and identified the principal species in the catch (Box 3.1, Fig. 1), which included harbour porpoise (*Phocoena phocoena*), bramble shark (*Echinorhinus brucus*), and angel shark (*Squatina squatina*). The latter was fished with a special net and the fishermen roped the tails with string to a wooden buoy, to bring them back alive.

Harbour porpoise are now a rare species in France and have disappeared from the southern Bay of Biscay; however globally they are still common. Only six specimens of bramble shark were recorded in the Bay of Biscay during the twentieth century and the species may be threatened, but data are deficient. In the mid-1800s, the annual catch of angel shark at Arcachon was around 25 t per year, but in 1996 the catch was 144 kg from the Bassin and 147 kg from the sea. This species is listed as critically endangered.

About 18 species of skates and rays were caught at the beginning of commercial fishing by steam trawlers between 1869 and 1891. The maximum catch of skates and rays at Arcachon was 1881 t in 1922, which was 23.8% of the total landings. Between 1975 and 1989 the catches of skates and rays had dropped to less than 9 t, which was 0.45% of the total landings. Most of these species, such as the ‘common’ or blue skate (*Raia batis* L.) are now very rare. This is one of the largest (2–3 m), late maturing (>age 11) species of ray, which is now critically endangered, mainly due to fishing (Brander 1981).

continues

Box 3.1 continued



Box 3.1, Figure 1 Cover illustration of the new edition of Le Masson du Parc (1727).

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rapid evolution in fishing practices and major climatic variations (human induced or not). It is, therefore, still a challenge to attribute causes to the observed variations in populations or ecosystem structure. One way of gaining information on ecosystem fluctuations which are not influenced by intensive fishing and

other anthropogenic drivers is by mining data on periods before fishing began.

Variability seems to be the rule rather than the exception, even in unexploited marine populations and ecosystems; the longer the time series, the greater are the variations (Vasseur and Yodzis 2004). Whether

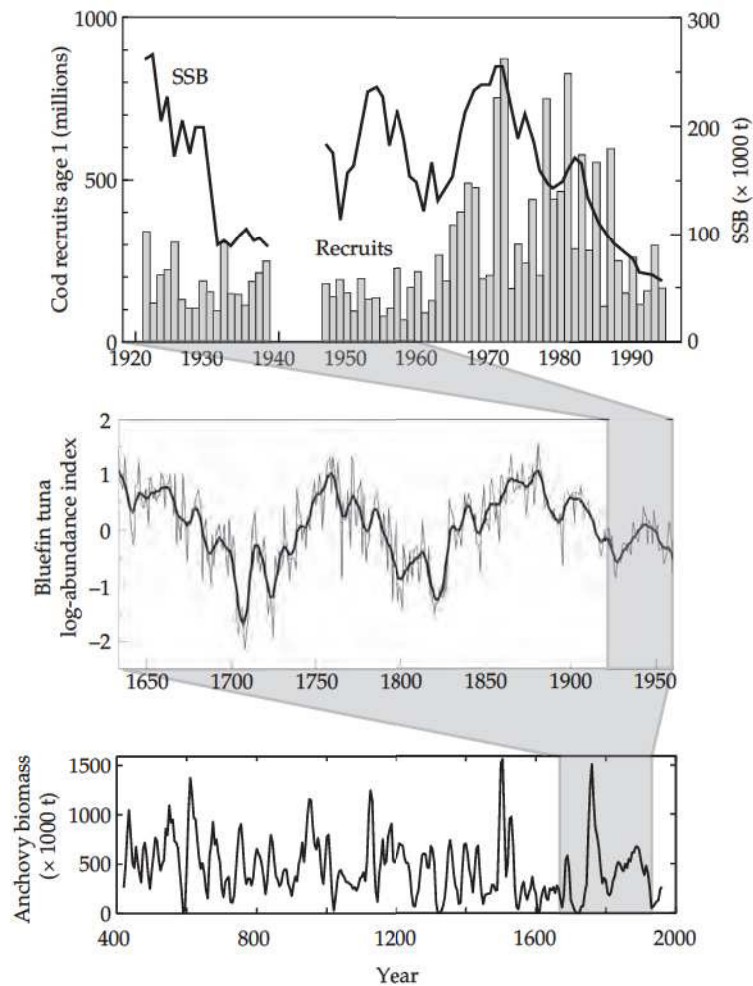


Figure 3.1 Evidence of fluctuations in fish populations over different overlapping time scales (indicated by grey shapes). Top panel-spawning stock biomass and recruitment of North Sea cod from contemporary sampling of fish catches and age structure for 1921 to 1993 (see Section 3.5.1). Middle panel-composite time series of relative abundance of bluefin tuna from the western Mediterranean and Atlantic for 1650 to 1960 (see details in text). Bottom panel-relative abundance of northern anchovy off California from 1700 BP (see details in text). (Baumgartner, personal communication.)

marine ecosystems are becoming less complex, and have lower mean trophic levels (Pauly *et al.* 1998) and simplified food webs is difficult to judge and certainly depend upon the timescale at which such observations are made. However, recent intensification of human impacts (Section 3.2.3) and the particular effects of fishing (Section 3.3) impose a change in the nature of the forces driving variations in marine ecosystems and the speed at which these variations may occur. Understanding the interplay between ‘natural’ modes of fluctuations and the effect of human distur-

bances will require intensified efforts in monitoring and modelling the state and dynamics of marine ecosystems.

3.2.3 Intensification of human impacts during the twentieth century: from local to global impacts

Human population growth has resulted in greatly intensified pressure on marine systems over the last century, affecting a broad spectrum of ecosystem

services including provision of food, shoreline protection, and water quality. Over 40% of the human population now resides within 100 km of the coast; if current rates of population growth are maintained, the number of humans living near the coast will increase from 2.3 billion in 2000 to 3.1 billion in 2025 (cited in Duxbury and Dickinsen 2007). A recent global map of human impacts on marine ecosystems (Fig. 3.2) aggregates the effects of 17 anthropogenic drivers of ecological change, which can be grouped into pollution, climate change, fishing, shipping, and seabed structures. The areas of greatest impact are, not surprisingly, the busy shelf seas of north-east Europe and Japan, but even the Arctic and Antarctic are affected.

Overexploitation of marine resources has been identified as the dominant factor affecting biodiversity and abundance levels of marine organisms

(Millennium Ecosystem Assessment 2005; Lotze *et al.* 2006). Patterns of overall fish utilization and supply, including marine and freshwater capture fisheries and aquaculture, closely parallel the growth in the overall human population (FAO 2007; Fig. 3.3). Approximately 90% of the global capture fishery yield is from marine systems. The escalating demand for seafood resulted in nearly a tripling of global fleet capacity (gross registered tons-GRT) during the period 1970 to 1995 (<http://www.fao.org/figis>). Reducing fleet overcapacity remains the major impediment to controlling fishing mortality. Globally, 3% of the stocks for which information is available are classified as under-exploited, 20% are moderately exploited, 52% are considered fully exploited, 17% as overexploited, 7% are depleted, and 1% are listed as recovering (Fig. 3.3; FAO 2007). Excluding production by China, the capture production of fish, crustaceans, and molluscs

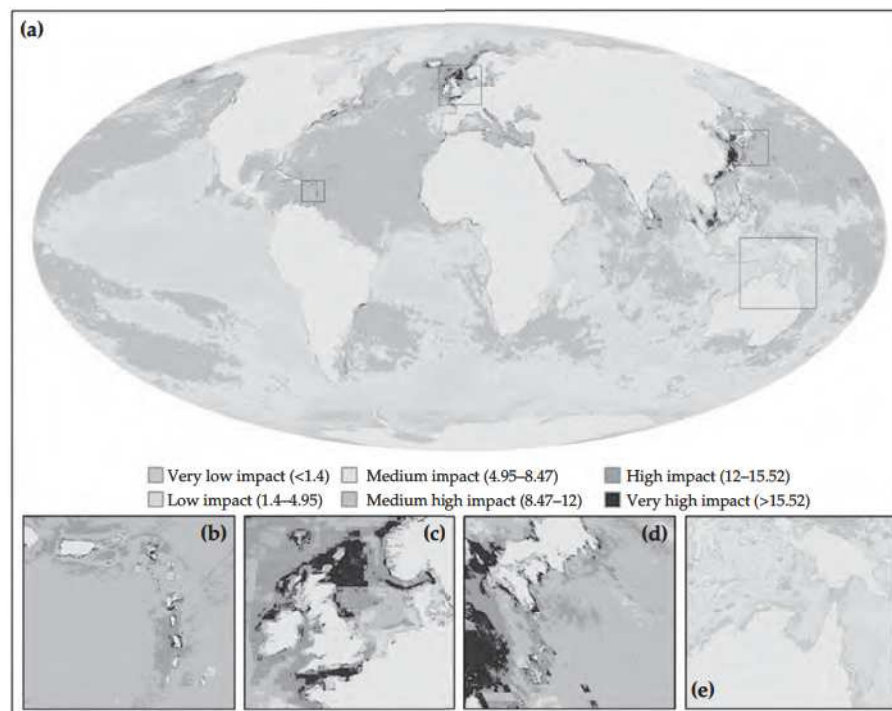


Figure 3.2 Global map from Halpern *et al.* 2008 reprinted with permission from AAAS showing (a) cumulative human impact on marine ecosystems. Insets show highly impacted regions including (b) the Eastern Caribbean, (c) the North Sea, (d) Japanese waters, (e) one of the least impacted regions, in northern Australia, and (f) the Torres Strait. The methodology uses expert judgement, standardization, and weighting to combine the 17 anthropogenic drivers. Terms describing degree of impact correspond to the 'per cent degraded' scheme of Lotze *et al.* (2006). (See Plate 8).

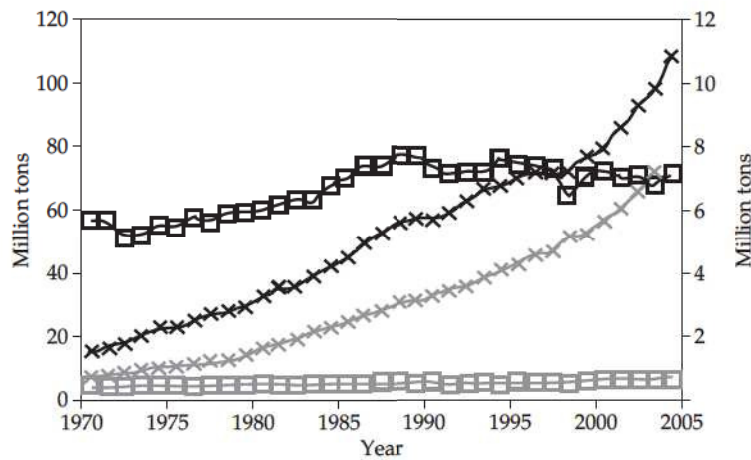


Figure 3.3 Trends in world capture fisheries (squares—left axis) plus aquaculture production (crosses—right axis) excluding problematic data from China. Black is marine and grey is fresh water. (Modified from Food and Agricultural Organization of the United Nations 2007).

has been declining annually by 233,000 t since 1989 (Brander 2007a).

Coastal development has also resulted in widespread loss of wetlands, mangrove forests, and rooted aquatic vegetation, which collectively serve as nursery areas for commercially and recreationally important species and as important buffers against storm damage in nearshore areas. Lotze *et al.* (2006) report declines of 50% or more of wetlands, seagrasses, and other submerged aquatic vegetation in estuarine and coastal areas. The Millenium Ecosystem Assessment (2005) cites habitat loss as a major determinant of loss of biodiversity in the coastal zone over the last century. It has been suggested that the impact of events such as Hurricane Katrina and the 2004 Asian tsunami was exacerbated by loss of protective vegetation (Lotze *et al.* 2006).

While enhanced environmental protection has resulted in recent declines in the incidence of some forms of pollution (e.g. heavy metal contamination), nutrient enrichment has continued unabated, resulting in eutrophication of coastal waters and growing incidence of anoxic and hypoxic conditions (Lotze *et al.* 2006). The effect of nutrient enrichment on coastal systems has been amplified by loss of the filtration capacity of aquatic vegetation and overexploitation of suspension feeders such as oysters.

The extraction of marine mineral resources represents a growing industry which includes sand, coral, gravel, and shell for aggregate; beach replenishment and cement manufacture; and magnesium, salt, sulphur, diamonds, tin, gold, and heavy minerals (Wiltshire 2001). The extraction of deep sea deposits such as manganese nodules and crusts and methane hydrates continues to attract interest. These extractive activities could affect critical marine habitats and marine organisms dependent on them. The magnitude of impact on marine ecosystems related to these activities is difficult to assess, but a substantial body of knowledge has built up concerning the impacts of oil exploration, extraction, and oil spills (e.g. Hjermann *et al.* 2007). The issue is of renewed concern as the Arctic Ocean is being opened for oil exploration and may have particularly vulnerable ecosystems (Thorne and Thomas 2008).

3.3 Fisheries-induced changes

Collectively, the many effects of fishing on populations not only reduce the population abundance, but also make them more sensitive to additional fishing pressure, additional mortality, and environmental variability (Ottersen *et al.* 2006; Anderson *et al.* 2008; Perry *et al.* 2010a; Planque *et al.* 2010). Environmental effects are generally

observed on younger stages (typically eggs and larvae), while fishing primarily affects larger and older individuals. The combination of the two results in increased variability in abundance and greater risk of collapse. Fishing acts through well-recognized effects on population dynamics, but also causes subtler changes in the behavioural and geographic structure of populations. Some of the effects are irreversible or slowly reversible; in order to reverse the effects of fishing and to halt a negative trend of population abundance, individuals may need to get older, memories of preferential migratory pathways may have to be rebuilt, genetic diversity may have to be restored, and new habitats may need to be recolonized. All of these take time, and may slow down the recovery of highly depleted stocks. The sensitivity of fisheries and marine ecosystems to human impacts is discussed further in Section 3.4. The history of the fisheries at Greenland over the past century (Box 3.2) illustrates some of the consequences of rising levels of exploitation and their interaction with environmental changes.

3.3.1 Demographic change

The fundamental effects of fishing and other human impacts on marine population dynamics are associated with changes in the population age structure. Fishing changes age structure by removing individuals over a range of ages each year. Since fish of older ages will have been fished for more years than younger individuals, the effect is to skew the age structure from its natural form to one with relatively fewer older individuals. The effect of this truncation of the age structure, if recruitment remained constant, would be to reduce population biomass. However, some populations may compensate for the reduction in biomass when fishing begins by increasing their recruitment. Eventually, however, as fishing increases further, recruitment will begin to decline, raising the possibility of population collapse through recruitment overfishing.

To understand how truncation of the age structure can lead to overfishing, we first note that it reduces the total amount of reproduction in the lifetime of the average individual in the population. We know from discussions of human populations

that lifetime reproduction is an important indicator of whether individuals in the population will replace themselves in the next generation. If every couple has two offspring, which survive to reproduce there will be zero population growth, while if they produce more than two the population will increase, and vice versa. Fish in natural, unfished populations typically produce up to several million eggs per year of which only a tiny fraction need survive to reproductive age for replacement. What makes the prediction and management of marine fisheries, as well as the assessment of other human impacts on fish populations, extremely difficult is that we know little about how the survival from egg to reproductive age is governed, or what minimum number of eggs must be produced in a fish lifetime for the population to persist.

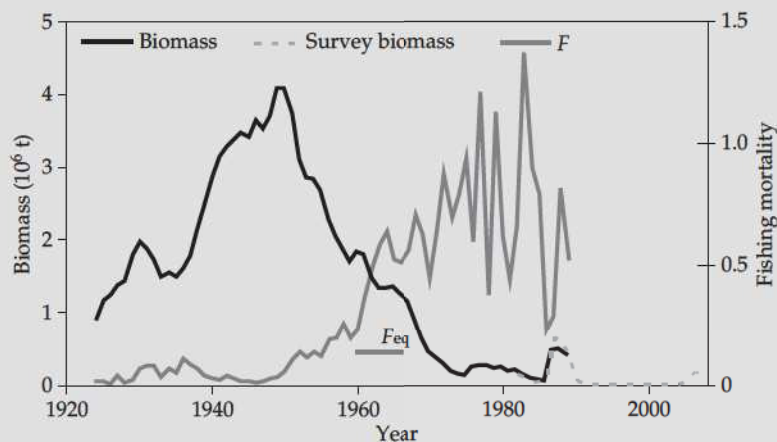
The dynamics underlying this qualitative description can be seen in a graphical representation of the equilibrium condition of a model of an age-structured population with density-dependent recruitment (Sissenwine and Shepherd 1987; Botsford 1997). The population is represented by an assumed density-dependent relationship between the number of eggs produced each year, and the number of young individuals (recruits) they produce (Fig. 3.4). The equilibrium level of recruitment of a natural, unfished population will be at the intersection of the egg-recruit relationship and a line through the origin with slope $1/LEP$, where LEP is lifetime egg production. As the amount of fishing or other mortality increases, LEP declines, moving the equilibrium to the left. Recruitment will remain constant until it reaches the knee of the curve where it will begin to decline. The equilibrium recruitment will be zero when the slope of the straight line (i.e. $1/LEP$) becomes greater than the slope of the egg-recruit relationship at the origin. The value of LEP at which this happens is the critical replacement threshold. Fishery biologists have examined the value of this threshold for a number of species for which the necessary egg-recruit data exist. They express the critical replacement threshold as a fraction of natural, unfished lifetime egg production (FLEP) and have found it to be in the range of 30–50% (the critical replacement threshold is also known as the ‘spawning potential ratio’ or ‘eggs per recruit’) (Goodyear 1993; Mace and Sissenwine 1993; Myers *et al.* 1999).

Box 3.2 Greenland—effects of fishing and climate change

The cod fishery gradually developed during the 1920s and was dominated in its early days by a foreign offshore hook and line fishery before bottom trawls became more prominent (Horsted 2000). After the Second World War, the fishery expanded rapidly in the West Greenland offshore areas and annual catches rose to about 460,000 t in the early 1960s and then fell steeply. Following a brief increase in catch at the end of the 1980s, the fishery collapsed completely in the 1990s with no signs of recovery since then. Fishing mortality increased to about 0.8 at the beginning of the 1960s and fluctuated around this level until the stock collapsed (Box 3.2, Fig. 1). Hovgård and Wieland (2008) estimated that the equilibrium fishing mortality at this time was about 0.14 and they concluded that the collapse of the stock was primarily due to high fishing mortality, given the low productivity of the stock (in terms of recruitment per unit of spawning stock biomass). Mesh-size and minimum landing size regulations were introduced in the late 1960s, but the major stock decline occurred while the fishery was only restricted by modest access limitations (Horsted 1991). Subsequently, Total Allowable Catch (TAC)

regulations were introduced in 1974, but did not provide effective protection because they were typically set above the recommended level and ineffectively enforced (Horsted 2000). The drop in fishing mortality which occurred in the 1980s was probably too late due to the combined effects of low ocean temperatures and low spawning stock in Greenland waters.

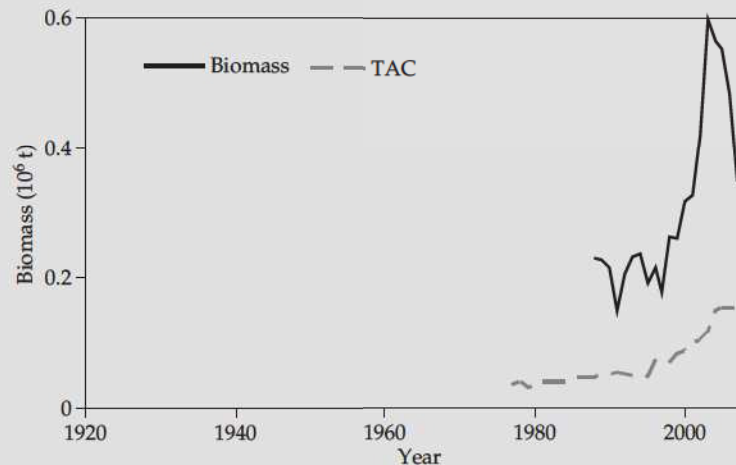
The fishery for northern shrimp (*Pandalus borealis*) began in inshore areas in 1935. In 1970, a multinational offshore bottom trawl fishery started to develop and landings increased gradually to ~155,000 t in 2005 (NAFO 2007). Annual effort in the West Greenland shrimp fishery increased from about 80,000 h in the late 1970s to more than 200,000 h in the early 1990s and remained relatively high thereafter (Kingsley 2007). Considerable by-catch of juvenile cod and redfish has occasionally been observed (Sünksen 2007), but no quantitative studies on the impact of the shrimp fishery on the recruitment of commercially important fish species or benthic organisms are available to date. Catch restrictions were first imposed in 1977 and the fishery has since been managed by TAC. Survey indices



Box 3.2, Figure 1 Estimates of stock biomass (age 3+) and mean fishing mortality (1924–81: ages 5–12; 1982–9: ages 5–7) for Atlantic cod at West Greenland. F_{eq} the fishing mortality for equilibrium biomass per recruit is shown for the early 1960s (ages 5–12). (From Hovgård and Wieland 2008.)

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Box 3.2 continued



Box 3.2, Figure 2 Survey indices of stock biomass for northern shrimp (*Pandalus borealis*) and actual total allowable catch (TAC) for West Greenland.

showed a threefold increase in stock biomass of northern shrimp from 1997 to 2003 at relatively moderate TAC levels (Box 3.2, Fig. 2). Thereafter, the biomass indices from the survey began to decline, and concerns were raised that the current level of exploitation is no longer sustainable (NAFO 2007), in particular following the decline in recruitment since 2001 (Wieland *et al.* 2007). Sorting grids became mandatory in 2000,

which has likely contributed to an increase in biomass of juvenile Greenland halibut. In addition to high TACs, reasons for the decline in shrimp biomass may therefore also include predatory effects considering the strong negative relationship between Greenland halibut biomass and shrimp recruit survival found by Wieland *et al.* (2007).

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While for many fisheries we can calculate FLEP from information on survival and fecundity, the critical replacement threshold is highly uncertain.

One useful conceptual consequence of these relationships for the question of human impacts on populations is that sustainability imposes an upper limit on the sum total of all sources of mortality on a fish population, and that total can be assessed in terms of the effects on LEP. This zero-sum characteristic of 'surplus' mortality necessitates that an increase in mortality from one source must be offset by decreases from other sources. The common view that single causes of population change can be considered separately is mistaken and results in erroneous views about management issues, for example, we should not have to reduce fishing

because pollution is really the cause of population decline, or because climate change is the cause of the decline (Schiermeier 2004). Such 'finger pointing' in policy debates misses the true nature of population dynamics. The dynamics of salmon populations (see Box 3.3) provide good examples of both the interactions between different factors and the 'fixed sum' characteristic of the mortality required to achieve sustainability.

Another consequence relates to the question of why it is important to study the effects of environmental variability on fish populations when we cannot do anything about it? The abundance or catch we see each year is a consequence of all of the survival factors. We are often interested in measuring the effects of remedial actions such as reducing

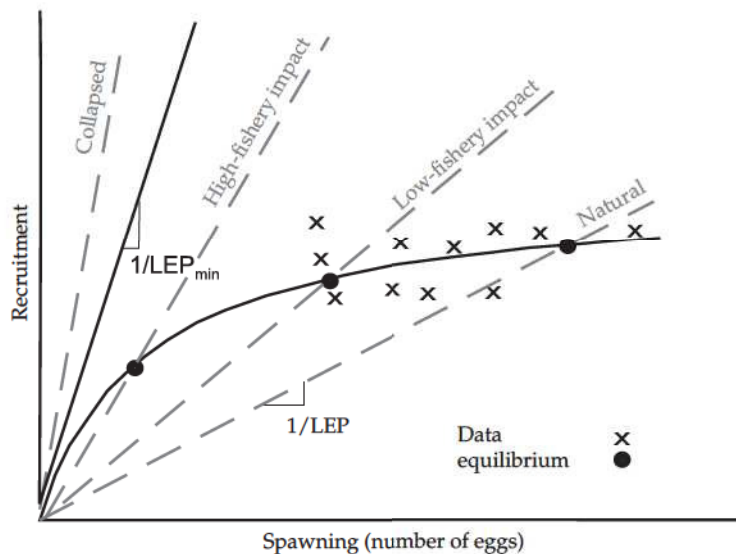


Figure 3.4 A simple schematic representation of how fishing reduces recruitment and may lead to overfishing: a plot of egg production versus the number of recruits that results from them, along with the lines through the origin with slope equal to $1/LEP$ under various conditions. The equilibrium is at the intersection of these. As fishing reduces LEP , the equilibrium moves to the left and recruitment declines, then eventually collapses. A fishery manager can observe the data points to the right ('x's), but does not know the egg-recruit relationship. Pressure to increase catches, profits, and employment pushes the equilibrium to the left, but the point at which the recruitment will collapse is unknown.

fishing or pollution, to determine their effectiveness through adaptive management. By studying the processes we aim to transform the environmental variability from noise to understandable signal and thus either factor them out or at least take into account their effects on populations and on management.

Specific fecundity (eggs produced per unit of female biomass) may change with the age and size of the fish (Marshall *et al.* 2006). Larger, older fish sometime have higher specific fecundity and their eggs and larvae may have higher survival rates due to having greater nutritional reserves (Berkeley *et al.* 2004; Trippel *et al.* 2005). Changes in age and size structure due to fishing can therefore have quite complex effects on reproductive output, and the calculation of LEP should take such demographic factors into account. However, when differential larval survival with female age was taken into account, the effects of reduced specific fecundity on population persistence and management were not substantial (O'Farrell and Botsford 2006). Higher nutritional reserves do not always translate into higher survival, as there is a trade-off between size

of the larvae (which reduces predation) and the energy provided by nutritional reserves (which reduces starvation; Fisher *et al.* 2007).

Removal of older or mature individuals from a population may alter the behavioural interactions among the remaining individuals. For example, older individuals consistently migrate towards the same spawning and feeding grounds. Transfer of knowledge among old and young individuals, through simple behavioural rules of schooling fish (e.g. Couzin *et al.* 2006), allows the population to maintain a 'conservatism' of migratory routes (Corten 2002). In contrast, the excessive removal of mature individuals and the consequent lack of guidance and transfer of knowledge may increase the percentage of the population that deviates from its established migratory routes. Searching for far and unexplored habitats (i.e. dispersal) does not always have a negative outcome on a population, as it opens up the possibility of colonizing new and perhaps more favourable habitats and to increase genetic diversity (Iles and Sinclair 1982). However, dispersal in fish is typically confined to early life stages, which are numerous and to a

Box 3.3 Coastal ecosystems and salmon in the north-east Pacific

Because salmon are anadromous, human impacts occur in freshwater ecosystems as well as marine ecosystems and provide greater opportunities to illustrate interactions among multiple impacts. Human impacts on salmon have conventionally been expressed as the four 'H's: harvest, hydro-power (dams), hatcheries, and habitat. Impacts on habitat, and through hydropower, are greater in the southern part of the range of Pacific salmon, the west coast of the contiguous United States, than in Alaska, where the freshwater environment is relatively pristine.

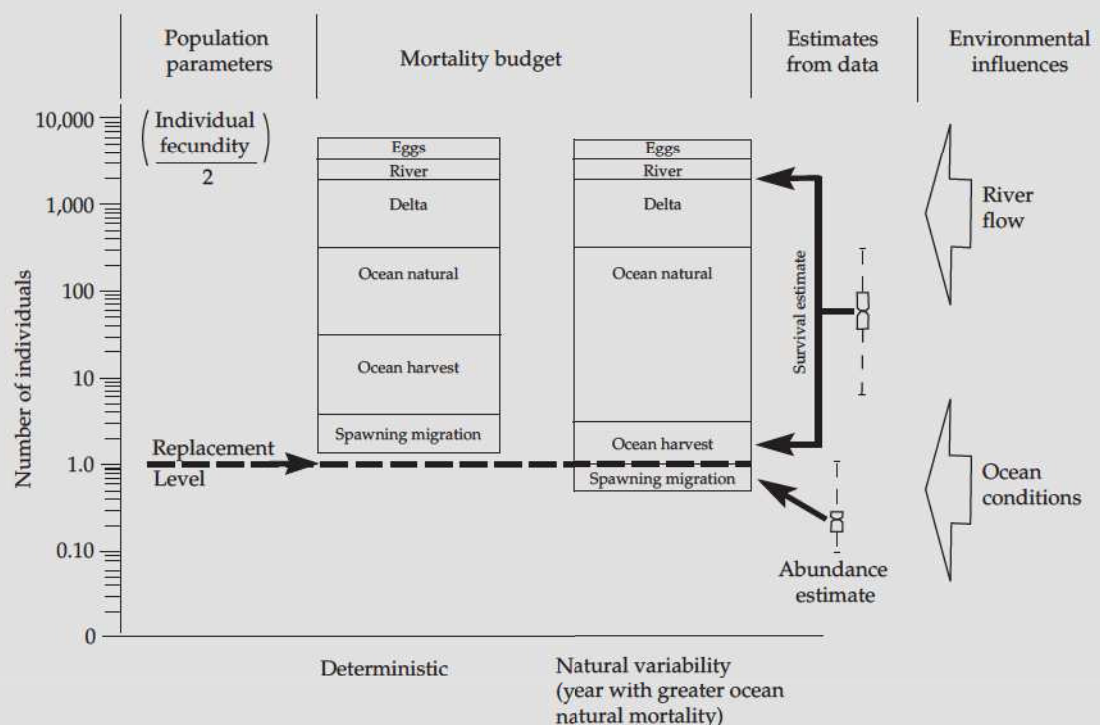
Salmon were harvested by Native Americans long before the European presence and even then, society required an explanation for the tremendous variability in salmon runs (Taylor 1999; Finney *et al.* 2002). Catch records began being kept with the advent of salmon canneries in the late 1800s (Taylor 1999), and there is no doubt that there were more salmon then than now. The current status of Pacific salmon is that stocks of all five species are abundant and sustainably harvested in Alaska, but less abundant and less clearly sustainable in Canada and the contiguous United States. Reasons for this difference include: (1) a more pristine freshwater environment in Alaska and (2) different oceanographic conditions, with most Alaskan populations in the Alaska Coastal Current and the more southern populations in the California Current System (CCS). In the CCS, off the west coast of the contiguous United States, salmon are dominated by two species, coho salmon (*Oncorhynchus kisutch*) and chinook salmon (*Oncorhynchus tshawytscha*). Coho salmon fisheries management in the CCS began to reduce allowable catch because of low abundance in the 1990s. In addition, at that time nine Evolutionary Sustainable Units (ESUs) of chinook salmon and four ESUs of coho salmon were listed under the US Endangered Species Act (<http://www.nmfs.noaa.gov/pr/species/esa/fish.htm>).

Management of human impacts on Pacific salmon requires an assessment of the complex combination of the four Hs and recently appreciated unpredictable oceanographic influences, to determine their combined effect on sustainability. Because these species are semelparous, evaluation of the effects of LEP on population persistence (Fig. 3.4) is much simpler. Since reproduction occurs only once in a Pacific salmon's lifetime, twice the inverse of individual fecundity is the survival necessary to sustain the population. Since this is a single number, we can express lifetime mortality as the sum of the logarithms of mortality due to causes in each stage (Box 3.3, Fig. 1). This allows a clear view of how human and natural impacts combine in some years to produce a total mortality that reduces the reproduction in each individual's lifetime to less than its replacement value. The valuable insight from this figure as regards human impacts is that it is the sum of mortalities, not a single factor, that leads to populations being lower than the replacement level (i.e. unsustainable). Both the farmer withdrawing water from a river for irrigation of agriculture and the fisherman removing his catch contribute to mortality and the overall level of survival being less than sustainable. There is rarely a single cause of a decline in abundance, as is often proposed. Freshwater management and harvest levels that are sustainable under some ocean mortality conditions may not be sustainable under other ocean conditions. This is particularly problematic because ocean conditions are not predictable. For example, ESA recovery plans require management actions that are predicted to return populations to a recovered state, raising the question of what the assumed ocean mortality should be in those predictions?

We are gaining an increasing understanding of the ways in which ocean conditions affect salmon as we observe continuing unprecedented changes in environmental conditions. The US GLOBEC Northeast Pacific programme was founded in the

continues

Box 3.3 continued



Box 3.3, Figure 1 The autumn run of Sacramento River chinook salmon as an example of how the sum of logarithms of mortality illustrates the way in which multiple factors, including water diversions in the Sacramento-San Joaquin Delta, harvest in the ocean, and variable survival due to ocean conditions, can lead to a lack of adequate individual replacement. Two examples of the mortality budget are shown, with the one on the right falling below the replacement level because of higher ocean mortality. The long-term estimates available, spawning abundance through spawning counts and survival estimates from coded wire tags, are indicated. Fishery catch is also known. Both ocean conditions and river flow are subject to environmental variability.

mid-1990s on the precepts that: (1) salmon populations covaried inversely between Alaska and the California Current, (2) salmon ocean survival was determined soon after ocean entry as juveniles, and (3) mesoscale physical variability was important to coastal ocean productivity and salmon survival. Interest was focused on the regime shift in ocean conditions in the mid-1970s, in which coho salmon in the CCS covaried inversely with coho in Alaska (i.e. decreasing in the CCS, increasing in Alaska), but chinook salmon did not covary (Botsford and Lawrence 2002). Coho and chinook salmon abundance were found to vary with interannual *El Niño* Southern Oscillation (ENSO) conditions in the CCS (Botsford and Lawrence 2002), and on decadal,

semi-basin scales, salmon abundance appeared to vary with the Pacific Decadal Oscillation (PDO; Mantua *et al.* 1997). Analysis of coded wire tag data from coho salmon for 1980–2004 indicates a lack of inverse covariability between the CCS and Alaska (Teo *et al.* (2009)).

During the last decade there have been big shifts in ocean conditions in the CCS, which have affected salmon populations and the public's awareness of the impacts of climate on the marine ecosystem. In 1997–8 there was an intense *El Niño* followed by a strong *La Niña* (Chavez *et al.* 2002; Schwing *et al.* 2002). The *La Niña* in 1999 led to a cooling along the coast, which appeared to signal a shift in the PDO to a different state (Bond *et al.*

continues

Box 3.3 *continued*

2003). These cool conditions lasted 4 years and were accompanied by a more productive CCS. The coastal zooplankton and pelagic fish communities shifted to being dominated by more northern species, and biomass anomalies of three cold water (i.e. northern) copepods were found to be positively correlated with the survival of coho salmon over the previous 14 years (Peterson and Schwing 2003).

These years were followed in 2005 by a warming event that was apparently driven by the unusually late initiation of sustained upwelling winds (Schwing *et al.* 2006; Barth *et al.* 2007). This led to lower primary and secondary productivity in the CCS during the spring and early summer, a shift in zooplankton community structure with less dominance by northern species, and changes in the nekton. A particularly remarkable example was the impact of reduced prey (krill) levels on a planktivorous bird, Cassin's auklet (*Ptychoramphus aleuticus*), which led to complete abandonment of their breeding site on the Farallon Islands (just west of San Francisco, California) for the first time in 35 years of observations (Sydeman *et al.* 2006). In 2006, there were again periods of low upwelling winds early in the season, and there was again no reproduction by Cassin's auklet.

In 2008, as this is being written, the projected return of spawners to the autumn run of chinook salmon on the Sacramento River (which enters the ocean at San Francisco) is the lowest on record, and the associated fishery has been closed for the first time in recorded history. These spawners are from the cohorts that would have entered the ocean in

the springs of 2005 and 2006, the years of unusual upwelling winds and low reproduction by Cassin's auklet. The closing of the fishery has fueled extensive speculation by the public regarding the cause of the decline. These responses are mostly the single cause 'finger pointing' mentioned in the text. For example, a non-governmental conservation organization has teamed with fishermen in a critique of water diversion for agriculture in California's central valley as being 'one of the most significant and reversible' factors contributing to the decline of chinook salmon (NRDC 2008). The explanation by the National Marine Fisheries Service that the decline in the Sacramento River salmon run in 2008 is due to adverse ocean conditions in 2005 and 2006 is viewed with considerable public scepticism.

In summary, research on ocean influences on salmon has identified modes of variability that appear to be without historical precedent, but has not produced predictive results. However, it is providing a context which aids in understanding past (and present) variability. In some cases, just having the experience of dealing with interactions between population dynamics and environmental variability can aid in dealing with contentious issues such as the former range of ESA-listed species (Adams *et al.* 2007). It seems likely that the primary benefits of GLOBEC research will be more of this nature than of predicting the future.

Acknowledgement: Louis W. Botsford thanks H. Batchelder and W.T. Peterson for comments on the salmon box.

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certain degree expendable, while mature individuals are scarce and precious. Increased random dispersal of adults is unlikely to be beneficial to the population.

Another important aspect of the dynamics associated with overfishing is that trajectories of decline may not be reversible or the rate of reversal may be much slower than expected from the population rates (recruitment, growth, and natural

mortality) which prevailed before the collapse occurred (Hutchings 2000). Although stock-recruitment models predict higher growth rates and fast recovery times of population at low abundance (due to density-dependent effects), in nature the recovery of severely depleted stocks occurs at much slower rates or sometimes does not occur at all (e.g. Labrador and Newfoundland cod; Shelton *et al.* 2006). For some stocks that

experienced protracted declines, that is, Pacific sardine in the California Current, Dungeness crab in central California, and the Eurasian perch in Lake Windermere in the United Kingdom, modelling results showed that an increase in individual growth rate may have locked populations into a lower stable state (Botsford 1981). The asymmetry between the rise and fall of fish stocks can be due to the more subtle and long-lasting changes that fishing induces on fish populations, particularly if such changes were an undetected contributory factor in the stock decline (Drinkwater 2002; Brander 2007b).

Finally, another effect of the truncation of age structure through fishing is the fundamental change in population dynamics on short time scales. For example, populations that are dominated by young individuals are more unstable because the buffering effect of strong year classes is confined to shorter periods, making the population more dependent on recruitment rather than on the existing stock (Hsieh *et al.* 2006). Furthermore, the effect of fishing on the spawning age structure can change the relative sensitivity of populations to fluctuations on different time scales (Botsford 1986; Bjornstad *et al.* 1999,

2004), and lead to cyclic behaviour (Botsford and Wickham 1978).

On a longer timescale, the indirect effects of fishing act as a selective pressure that counters those imposed by nature (Fig. 3.5). The selective pressure in exploited populations is generally to mature at younger ages and to grow slower in order to reproduce before being caught, and to escape the size-selective gears. In contrast, the selective pressure from the natural environment is to grow fast and large in order to escape size-selective mortality (Conover 2007; Edeline *et al.* 2007; Fig. 3.5). Which of these two contrasting forces prevails depends on their intensity. Clearly, under regimes dominated by high harvest rates the selective forces imposed by fishing become dominant. Consequently, age and size of maturity may get progressively smaller, causing a reduction in natality and possibly also survival during early life stages (Heino and Godø 2002; Olsen *et al.* 2004; Jørgensen *et al.* 2007).

3.3.2 Spatial dynamics

Spatial aspects of population dynamics of marine fish and invertebrate populations have seldom

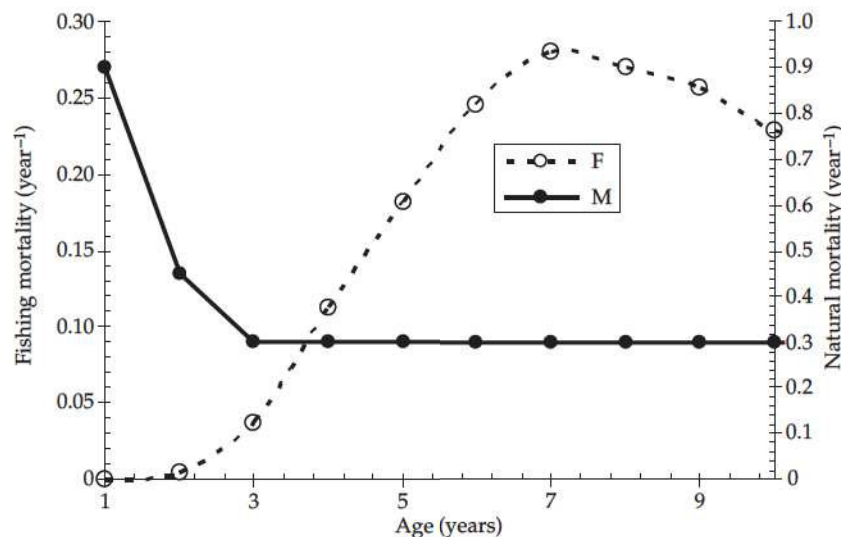


Figure 3.5 Fishing (F) and natural (M) mortality for different age classes of walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea (Ianelli *et al.* 2007). The contrasting trends of F and M illustrate the opposing selective pressure of natural and fishing mortality.

been accounted for in fishery management, but are beginning to receive more attention. With the rise in interest in spatial management through marine protected areas, spatial variability will be increasingly important. Most fish populations of interest in fisheries are metapopulations, that is, more or less distinct subpopulations linked by a dispersing larval stage, in addition to adult movement (Botsford *et al.* 1994).

The conceptual change in population persistence when one explicitly accounts for the distribution of a population over space is simply that the replacement concept must be expanded to include all possible replacement paths over space (Hastings and Botsford 2006). This means that it is the distribution of LEP over space that is important, and that linkages over space through larval dispersal and adult swimming are also important. Fishing probably changes the spatial distribution of LEP, even though that is currently rarely accounted for in management. Fishing could change dispersal paths, and it is quite likely that climate change will alter coastal circulation and thus exchange rates through larval transport. If that were to increase alongshore advection, as it could likely do in upwelling regions, it could have the effect of reducing local replacement and populations therefore failing to persist (Gaylord and Gaines 2000), an effect that would be more likely if the populations were heavily fished.

Fishing exerts spatial effects by reducing the geographic and genetic diversity of a population. For example, harvest typically peaks in feeding and spawning grounds and during times in which fish are concentrated and thus more easily captured. Particularly during spawning, fish may be isolated by genetic origin, which could result from behavioural interactions (Corten 2002) or imprinted mechanisms (Iles and Sinclair 1982) enabling them to conserve a memory for their spawning locations. Selective removal of these genetically homogeneous individuals will reduce the overall geographic and genetic diversity of the entire pool of stocks. The outcome of such loss is lower persistence. An example is the sockeye salmon in Bristol Bay whose resilience against major events of climate change has been attributed to the complex population structure of the entire pool of

stocks inhabiting the regions (Hilborn *et al.* 2003). Another example is the recent restructuring of walleye pollock spawning aggregations in the western Gulf of Alaska. The historically dominant spawning ground in Shelikof Strait (between Kodiak Island and the Alaska Peninsula) is no longer dominant (Ciannelli *et al.* 2007). Co-occurring with these geographic changes, the entire abundance of pollock in the region has reached an historical minimum, placing a threat on the viability of what once used to be a very active fishery. Shrinkage in the geographic extent of a stock is an early warning that the population is losing its genetic or social structure, and that it may be heading for a rapid decline. For example, the collapse of the north-west Atlantic cod (Newfoundland and Labrador Seas) was preceded by shrinkage of their spatial distribution (Atkinson *et al.* 1997; Warren 1997). The California sardine population has also been described to significantly shrink its distribution range during low abundance periods (Lluch-Belda *et al.* 1989; MacCall 1990; McFarlane *et al.* 2002).

3.3.3 Effects of fishing on species composition and biodiversity

Fishing increases the mortality rate and reduces the life expectancy of fish within the size and age range of the gear being used. Life expectancy (in years) is the inverse of the total annual mortality rate. In heavily exploited areas, such as the North Sea, the mortality due to fishing is many times greater than the mortality due to natural causes and life expectancy is correspondingly reduced (Fig. 3.6).

The relationship between life expectancy and LEP was explained in Section 3.3.1. Species which are vulnerable to fishing prior to becoming mature (because they are large and mature at a late age) are particularly sensitive to being overexploited, because many of them will be caught before reproduction begins. Fishing can be expected to remove such sensitive species first (whose recruitment trajectory has almost no harvestable surplus, i.e. close to the 'natural' sloping line in Fig. 3.4). This has been observed in many cases (Brander 1981; Quero

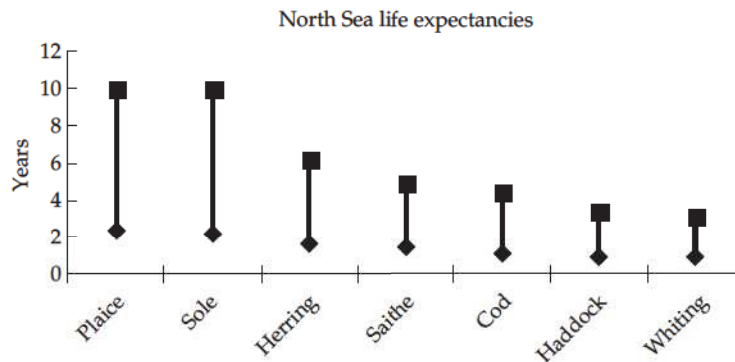


Figure 3.6 Change in life expectancy ($1/\text{total instantaneous mortality}$) at fishable age for a selection of North Sea species. The squares represent the unfished and the diamonds the fished life expectancy. (Data from table 1 of Brander 2003b.)

1998; Jackson *et al.* 2001; Lotze 2007), but often occurred during previous centuries, when records were poor (see Box 3.1). Such disappearances therefore often happen gradually and almost unnoticed. Dulvy *et al.* (2003) estimated that on average 53 years elapse between the last sighting of a marine species and the scientific acknowledgement of its disappearance.

The small number (18 to 21) of marine species which have become globally extinct over the past 300 years, compared to on land (829 species), probably reflects lack of monitoring as well as greater remoteness and resilience of marine ecosystems. The life history characteristics (e.g. high fecundity and highly dispersive early life stages) of many marine organisms may confer greater resilience relative to terrestrial species. It is estimated that more than 133 marine species (including 32 bony fish, 19 cartilaginous fish, 14 marine mammal, and 12 bird species) have undergone local, regional, or global extinction. Most of the extinctions (55%) were ascribed to exploitation and 37% to habitat loss (Dulvy *et al.* 2003).

A recent meta-analysis concluded that the oceans' capacity to provide food, maintain water quality, and recover from perturbation has been impaired through loss of biodiversity (Worm *et al.* 2006), but other studies of the relationship between biodiversity and ecosystem functioning and services produce a more nuanced picture (Balvanera *et al.* 2006). The relationship between biodiversity and resilience is not well

established. The structure of ecosystems and in particular the organization of species interactions may be more important to system stability (May *et al.* 2008).

Size and species-selective harvesting can result in marked changes in relative species composition in exploited systems (see Box 3.4). Resulting changes in trophic structure may affect fundamental patterns of energy flow and utilization in marine ecosystems. Such changes may represent alternate stable states that may be difficult to reverse with direct intervention designed to restore previous community structures.

Some of the issues are discussed further in Section 3.4.1. In addition to the potential loss of species, the consequences of loss of local sub-populations have also become a source of concern, including effects on level of sustainable production, risk of progressive stock collapse as successive sub-populations are extirpated, loss of resilience to other pressures such as climate change, and compromised ability to recover from periods of stock decline (e.g. Hilborn *et al.* 2003; Heath *et al.* 2008a).

3.3.4 Damage to or loss of habitats

Efforts to understand the direct and indirect effects of fishing on marine ecosystems have assumed increasing importance as we move towards developing ecosystem-based approaches to fishery management.

Box 3.4 Georges Bank—fishery depletion and management

Georges Bank, a highly productive submarine plateau located off the New England coast, has supported important commercial fisheries for over 3 centuries (German 1987). The strong rotary tidal forces on the bank coupled with topographic rectification results in the establishment of an anticyclonic gyre during the stratified season, resulting in the retention of planktonic organisms (although advective processes remain important at all times of the year). Upwelling of nutrient-rich water onto the bank and mechanisms of cross-front exchange and mixing result in high levels of primary production on the bank, historically fueling high levels of fish production.

A pattern of sequential depletion of fishery resources and large-scale changes in the relative abundance of different ecosystem components as a result of species-selective harvesting strategies has dominated the dynamics of the Georges Bank ecosystem (Fogarty and Murawski 1998). These changes include the depletion of marine mammal populations in the eighteenth century (Waring *et al.* 2004; Clapham and Link 2006), collapse of major fisheries such as that for Atlantic halibut by the mid-nineteenth century, and a series of fishery declines initiated by the arrival of distant water fleets on Georges Bank in 1961 (Clark and Brown 1977). The rapid escalation in fishing effort by these fleets resulted in an initial increase in landings due to a 'fishing up' effect. Groundfish stocks subsequently declined under heavy exploitation and the sequence was repeated for small pelagic fish (principally Atlantic herring and mackerel) and 'other' fish stocks (including elasmobranchs, large pelagics) throughout the next 2 decades (Fogarty and Murawski 1998; Overholtz 2002).

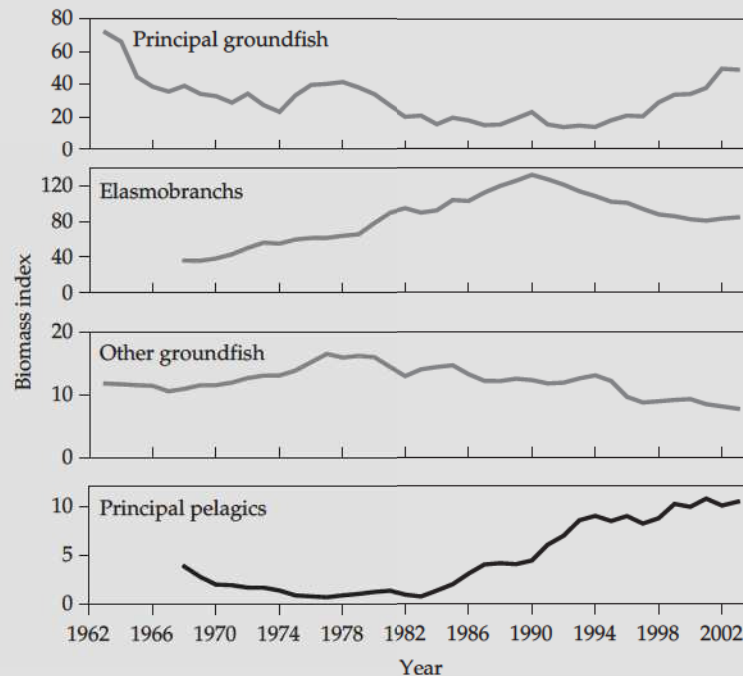
With the exception of some gear restrictions, the fisheries on Georges Bank were effectively unregulated prior to the 1950s. With the advent

of fishing activities by the distant water fleet and subsequent decimation of fishery resources, the need for direct controls on fishing was evident. The establishment of a quota management system in 1973 by the International Commission for Northwest Atlantic Fisheries (ICNAF; Hennemuth and Rockwell 1987) based on ecosystem principles provided the nucleus for recovery of depleted stocks (see also Barange *et al.*, Chapter 9, this volume). A quota-based management system was maintained following the establishment of extended jurisdiction in 1977 but was replaced by constraints on mesh size, legal size limits for fish, and seasonal area closures in 1982 under widespread violation and lack of effective enforcement of the quota limits. When these qualitative measures failed to adequately protect fishery resources, court-ordered restrictions (including the use of large-scale year-round closures and limits to days-at-sea) were added in 1994 (Murawski *et al.* 1997; Fogarty and Murawski 1998).

The direct and indirect effects of fishing and regulatory actions are reflected in fishery-independent abundance estimates for major fish groups (Box 3.4, Fig. 1). As principal groundfish populations (primarily gadoid and flatfish stocks) declined under heavy exploitation, small elasmobranch (skates and spiny dogfish) populations initially increased, possibly reflecting a form of competitive release. However, a redirection of fishing effort on these species as groundfish continued to decline resulted in reduced elasmobranch populations by the mid-1990s. Sharp reductions in fishing pressure resulted in increases in herring and mackerel populations through the mid-1990s (Overholtz 2002). With the imposition of more restrictive management starting in 1994, gadoid and flatfish populations have also recovered although the magnitude of the response has varied substantially among species.

continues

Box 3.4 continued



Box 3.4, Figure 1 Figure 1 Trends in biomass of major fish species groups on the north-east continental shelf of the United States based on fishery-independent research vessel surveys for principal groundfish, elasmobranchs, and other groundfish (smoothed mean kg/tow) and for principal pelagic fishes (predominately herring and mackerel; million tons) based on sequential population analysis. Georges Bank accounts for a dominant proportion of overall biomass of the demersal fish indices. (Figure courtesy of Northeast Fisheries Science Center, Woods Hole, Massachusetts, USA.)

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An emerging focus on habitat-related considerations is evident in the now extensive literature on this topic (Barange *et al.*, Chapter 9, this volume; Kaiser and deGroot 2000) and in legislative mandates such as the essential fish habitat provisions of the Sustainable Fisheries Act of 1996 in the United States (Benaka 1999).

Harvesting can affect habitat-related productivity in several ways ranging from reduction in structural complexity to effects on benthic production and prey availability (Hall and Harding 1997; Jennings and Kaiser 1998; Jennings *et al.* 2001; Kaiser *et al.* 2003). The former includes consideration of loss of shelter-providing structures and its effects on survivorship of sheltering species while the latter concerns patterns of

energy flow and availability to higher trophic levels. Sainsbury (1988, 1991) directly incorporated the effects of habitat availability in production models for fish assemblages on the north-west continental shelf of Australia. In his basin model, MacCall (1990) considered mechanisms of habitat selection and the implications for the development of spatially explicit harvesting strategies. Walters and Juanes (1993) developed models of predation risk in relation to habitat complexity and availability. Destructive fishing practices were shown to exert dramatic effects on productivity and biodiversity of coral reef systems (Saila *et al.* 1993), although this may not be immediate (Sano 2004). Hayes *et al.* (1996) explored the linkages between habitat, recruitment processes, and the implications

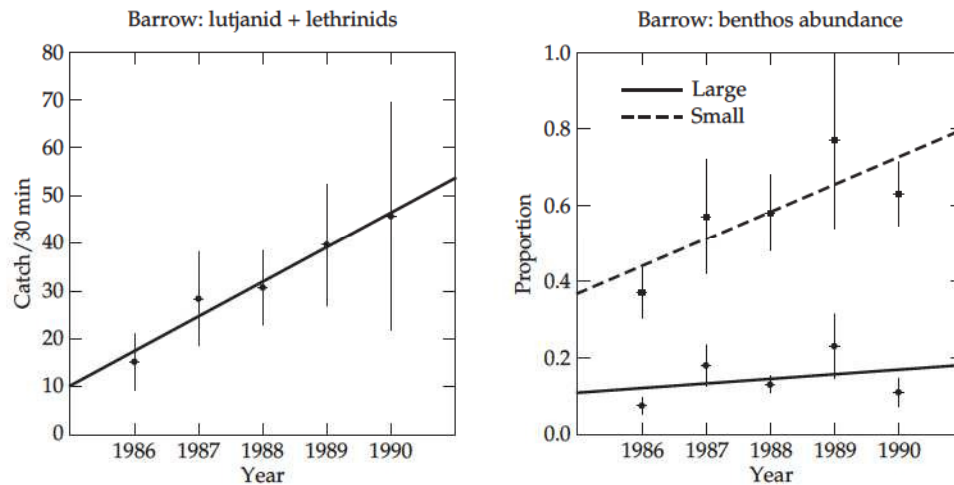


Figure 3.7 Abundance of two fish taxa (lutjanids and lethrinids) in a fishery closed area (left panel) and the proportion cover for two size classes (<20 cm and >20 cm height) of shelter-providing sponges (right panel) on the north-east continental shelf of Australia during 1986–90. (Courtesy K. Sainsbury.)

for management. Habitat-related considerations have now also been directly incorporated in models of marine-protected areas (e.g. Mangel 2000; Rodwell *et al.* 2003; Kaplan *et al.* 2009). A risk analysis framework was used by Fogarty 2005 to explore the effects of fishing-induced loss in habitat and carrying capacity on the shape of the production function and the recovery dynamics of overexploited resources.

Sainsbury (1988, 1991) provided the most extensive empirical evidence for the effects of habitat availability on fish abundance. Recovery of shelter-providing sponges was tracked following cessation of fishing in areas closed to fishing on the north-east continental shelf of Australia and linked to the abundance of commercially important fish species. Concomitant increases in abundance of two fish taxa and in the abundance (proportion bottom-area covered) of sponges were observed (Fig. 3.7). A habitat-impact model was found to be more consistent with the observed population trajectories than a standard production model (see also Sainsbury *et al.* 1997).

3.3.5 Consequences for ecosystem turnover rates and carrying capacity

Indicators derived from available catch and abundance time series, and various kinds of ecosystem

models, have been used to examine the ecosystem effects of fishing (e.g. Rochet and Trenkel 2003; Cury *et al.* 2005; Shin *et al.* 2005). For example, there is much effort being directed at selecting indicators that can be used as a means for quantifying ecosystem changes, especially those induced by fishing (Garia and Staples 2000; Degnbol and Jarre 2004; Link 2005; O'Boyle *et al.* 2005). Trophic models have been constructed for the Benguela and Humboldt ecosystems for static periods before human intervention, and compared to models for several periods along the gradient of fishing pressures through time (Neira 2008; Watermeyer *et al.* 2008a,b; Neira *et al.*, in preparation). Dynamic trophic models of the southern Benguela, southern Humboldt, and South Catalan Sea were used to simulate the closure of fisheries on small pelagic fish and the collapse of small pelagic fish stocks (Shannon *et al.* 2009).

Fishing has been shown to have some severe effects on the structure and functioning of marine ecosystems by disturbing the trophic interactions underlying the food web. Fishing changes community structure, often with long-term consequences. For example, fishing reduces the mean size of individuals comprising stocks (e.g. Bianchi *et al.* 2000; Sibert *et al.* 2006), thereby resulting in

communities that are dominated by species of small body size and which reproduce fairly rapidly. This phenomenon has been termed 'fishing down the marine food web' (Pauly *et al.* 1998). Collapses in small pelagic and other fisheries in recent years have also altered the mean trophic level of the catch, with large declines and/or fluctuations in recent decades in the northern Benguela (Cury *et al.* 2005), southern Humboldt (Neira 2008; Neira *et al.*, in preparation), and Mediterranean Sea ecosystems (e.g. Coll *et al.* 2006a).

Stocks of certain non-fished groups, usually those at low trophic levels and/or having high turnover rates, may proliferate under heavy fishing. In some instances, such as off Morocco, the negative effects of overfishing some species can be outweighed to a certain extent by the benefits from the proliferating species, in this case octopus (Gulland and Garcia 1984). However, in other cases fisheries may suffer, for example, where the proliferating species competes with other commercially important species for prey. Model simulations carried out by Shannon *et al.* (2009) suggest that in systems dominated by small pelagic fish, jellyfish may become more abundant when small pelagic stocks are heavily fished and thus when competition for zooplankton prey is lessened. It appears that jellyfish may alter the energy pathways of a food web (e.g. the Namibian case; Heymans *et al.* 2004). A model fitted to time series data available for the South Catalan Sea suggests that certain species not targeted by fisheries, such as benthopelagic fish, may have proliferated in response to declining stocks of competitors such as small pelagic fish and predators such as demersal fish, and a simultaneous increase in planktonic prey availability (Coll *et al.* 2006a; Shannon *et al.* 2009). The proliferation of species such as these may alter the food web substantially and divert the flow of energy to higher trophic levels, with detrimental consequences for production of fish species harvested by man. The Black Sea ecosystem has undergone a regime shift, reportedly due to over-exploitation (resulting in trophic cascades through the food web) and eutrophication, which has led to the demise of small pelagic fish and

the proliferation of jellyfish (Daskalov 2002; Gücü 2002).

Thus, because marine ecosystems are complex webs of trophic and other interactions, fishing has effects on the ecosystem that are much wider than the target species themselves. For example, small planktivorous fish play a key role in the pelagic ecosystems of major upwelling regions (e.g. Benguela, Peru). Higher trophic levels are subject to bottom-up control by the abundance of planktivorous fish prey, while zooplankton are subject to top-down control, also by planktivorous fish but acting as predators. The control in such systems has been termed 'wasp-waist' (Rice 1995; Bakun 2006; Hunt and McKinnell 2006), and changes in abundance of small pelagic fish have large implications for species at both higher and lower trophic levels of the food web. Trophic models of several upwelling ecosystems at different (static) time periods suggest that flows to detritus may increase when the abundance of small pelagic fish decreases (Shannon *et al.* 2009), and that systems may shift from being driven by pelagically dominated processes to being dominated by benthic communities. Such appears to be the case off Namibia (van der Lingen *et al.* 2006b). Changes in the flows between benthic and pelagic components of food webs have been proposed as a means of assessing the impacts of fishing (Shannon *et al.* 2009).

We have touched on just a few of the proposed indicators for tracking ecosystem changes over time and particularly, fishing-induced changes. However, it is not a simple matter to disentangle fisheries-induced changes from environmentally induced changes, and in fact these two drivers act synergistically or antagonistically to produce the ecosystem changes we ultimately observe (van der Lingen *et al.* 2006b). For example, in the northern Benguela, anchovy and sardine stocks have collapsed while jellyfish *Chrysaora hysoscella* and *Aequorea aequorea* appear to have increased since the 1980s, reportedly due to sequential unfavourable environmental events, the effects of which were exacerbated by fishing more heavily than was sustainable at the low-stock biomass levels that prevailed (Bakun and Weeks 2004).

3.4 Sensitivity of marine ecosystems

3.4.1 Interactions between fishing and environment in driving observed ecosystem changes

Sensitivity is used here in a fairly broad sense to include both how direct the response to human impact is and also how resilient the marine ecosystem is to perturbation. Human impacts may alter the sensitivity of individuals, populations, or ecosystems and there may be interactions between several simultaneous factors (e.g. fishing and climate; Perry *et al.* 2010a; Planque *et al.* 2010). Some of the underlying population processes have already been introduced in Section 3.3.

Species richness, that is, the number of species present, is an important element of ecosystem structure, which in turn affects food-web complexity and ecosystem function. Latitudinal gradients in species richness are well documented across terrestrial, freshwater, and marine systems with fewer species present at higher latitudes, but the causes remain unclear (Townsend *et al.* 2000). Gradients in primary production, seasonality, specialization of predators, environmental harshness, and evolutionary age of the system have all been examined in the ecological literature, but none provide unambiguous explanations (Begon *et al.* 2005). In the ocean basins, species richness of fish communities has been noted to decline with poleward distance from the tropics in both hemispheres (Cheung *et al.* 2005), with covarying effects due to depth (Macpherson and Duarte 1994; Macpherson 2003). In the North Atlantic, there is a correlation between richness and temperature, such that for a given latitude both richness and temperature are greater in the eastern Atlantic than the western (Frank *et al.* 2007). Latitudinal species diversity gradients for groundfish on the north-west Atlantic continental shelf respond to interannual changes in bottom temperature, which is in turn linked to a dominant climate signal, the North Atlantic Oscillation (NAO) (Fisher *et al.* 2008). Species diversity may therefore be sensitive to climate change.

Semi-enclosed seas such as the Baltic and Mediterranean tend to be outliers in the latitudinal pattern of richness. The former is colder and younger in a geological and evolutionary sense

than the North Atlantic at large, and exhibits lower species richness than expected for the latitude, while the Mediterranean is warm for its latitude and provides habitat for both temperate and subtropical species.

Production at successive levels in the food web can be considered as a function of primary production and represented as the product of trophic level and efficiency of transfer between trophic levels (Ryther 1969; Aebischer *et al.* 1990; Schwartzlose *et al.* 1999; Chavez *et al.* 2003). Regions which are poor in nutrients and the necessary trace elements required for phytoplankton growth, such as tropical gyres, can support only small fishery yields. In contrast, regions where oceanographic processes or major river inputs deliver large quantities of nutrient to the surface waters typically support substantial fisheries. Comparing across ecosystems in the north-west Atlantic, Frank *et al.* (2005) found a positive correlation between long-term average primary production and fishery yield. However, within individual ecosystems the relationship over time between primary and higher trophic level production was clearly positive in some, and clearly negative in others. Positive relationships between prey and predator time series are indicative of resource-driven or 'bottom-up' control of the food-web components, while inverse relationships indicate predation-driven or 'top-down' control. The latter has long been recognized in some lake systems and in nearshore or intertidal marine communities where species richness is low and the system is dominated by a small number of predators (Chapin *et al.* 1997). Recently, it has become clear that both bottom-up and top-down control may also pertain in open-shelf ecosystems, and that fluctuation between these states is an important signal of pressure due to fishing and/or climate changes. Frank *et al.* (2006) concluded that the species poor, lower primary production systems which predominate at higher latitudes and lower temperatures in the north-west Atlantic shelf region are fundamentally top-down controlled, while the lower latitude, species rich, higher primary production systems are fundamentally bottom-up controlled.

Ecosystems are rarely driven entirely by only one type of control (bottom-up, top-down, or wasp-waist); they are driven 'by a subtle and changing combination of control types that might depend on the ecosystem state, diversity and integrity' (Cury *et al.* 2003). Fishing, and climatic factors which affect the productivity of individual species, also have the capacity to shift a system between bottom-up and top-down control. For example, Hunt *et al.* (2002) showed a pattern of reversibly alternating control in the Bering Sea pelagic ecosystem between bottom-up in cold regimes and top-down control in warm regimes. Similarly, Litzow and Ciannelli (2007) describe changes in the trophic control of the ecosystem along the shelf south of the Alaska Peninsula (North Pacific). The system was initially bottom-up controlled in the early 1970s (as indicated by positive correlations between prey (mainly shrimp and capelin) and predators (mainly Pacific cod), shifted to top-down control during the late 1970s coincident with a rise in temperature, and then reverted to bottom-up control. The oscillation between control processes was coincident with a change in state of the system from one in which shrimp and capelin abundance, measured by catch per unit effort in surveys and commercial landings, was high and Pacific cod were scarce, to one in which cod abundance was ~50 times greater and shrimp and capelin had declined by a factor of ~100. The mechanism of the state change was hypothesized to be warming mediated shifts in the survival of Pacific cod larvae related to the timing of zooplankton production, and temperature dependent migration patterns of cod. As previously mentioned, the removal of larger, predatory fish by fishing leaves ecosystems that are often dominated by small pelagic fish- 'fishing down the food web' (Pauly *et al.* 1998; Pauly and Palomares 2005)-and, given that small pelagic fish are more sensitive to environmental effects than larger fish at higher trophic levels, it is possible that bottom-up effects may become more pronounced as a result of fishing (Cury and Shannon 2004; Shannon *et al.* 2009).

The sensitivity of 'wasp-waist' controlled systems to fishing and environment has already been discussed in Section 3.3.5. Changes in the marine

ecosystem of the North Sea can be used to illustrate many of the issues concerning the interaction between fishing and environment (see Box 3.5).

In contrast to the North Sea, the planktivorous fish guild at high latitudes in the North Atlantic (e.g. Barents Sea) is dominated by capelin and herring with few other fungible species present (for a definition of fungibility see Box 3.5). Capelin dynamics show more evidence of top-down control by piscivory, than bottom-up control by zooplankton (Hjermann *et al.* 2004). In the context of the latitudinal gradient in species richness and trophic control noted by Frank *et al.* (2006, 2007), the scope for species fungibility is presumably reduced in species-poor systems, making them more prone to top-down control. Thus, in the species-poor Baltic Sea, cod and sprat abundances show strong inverse correlation indicating top-down control of sprat by cod, with cod dynamics being impacted by a combination of fishing and climatic factors (Köster *et al.* 2003a,b; Alheit *et al.* 2005). Similarly, Worm *et al.* (2006) noted that the proportion of fisheries in a collapsed or extinct state (indicating top-down control by fishing), declines monotonically with species richness.

In summary, with the possible exception of the major upwelling systems, the natural state of warm low latitude, species-rich ecosystems containing many fungible species is for bottom-up control of production processes, with natural variability in primary production driving variability in the production of higher trophic levels. With increasing distance poleward and lower mean temperature, decreasing species richness and fungibility makes food webs more prone to top-down control in which the dynamics of low trophic levels are strongly regulated by predation. Bottom-up controlled systems are more resilient to the undesirable large-scale restructuring of food webs associated with the trophic cascades which may be precipitated by the disruption of predator-species dynamics in top-down controlled systems. In the short term, it appears therefore that high latitude, species-poor systems may be more vulnerable to reorganization by climate change and/or fishing. However, in the long term, we might hypothesize that the poleward expansion of species ranges might increase species richness in high latitude systems making them less prone to top-down control and more resistant to trophic cascades, although perhaps more susceptible to bottom-up

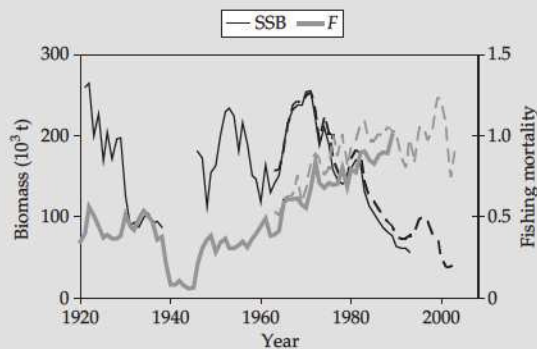
Box 3.5 North Sea-changes in pelagic versus demersal energy flow

Fishing activity and catches of species of commercial interest have been monitored and recorded in the North Sea for several centuries. Changes in population abundance can be inferred from catch rates. For example, fishing mortality on cod (*Gadus morhua*) in the North Sea was moderately high from 1920 to the late 1930s, dropped during the war years and then climbed steadily from the late 1950s to the end of the twentieth century (Box 3.5, Fig. 1). The spawning biomass fluctuated considerably during the twentieth century. From the late 1950s to 1970 spawning biomass doubled, probably due to improved planktonic conditions for early life survival (Beaugrand *et al.* 2003a) and in spite of a concurrent doubling of fishing mortality. The declining trend in spawning biomass since 1971 is due to a combination of fishing pressure and adverse changes in plankton production, composition, and phenology.

In addition to changes in biomass of individual fish species, such as cod, interannual changes also occurred at the level of fish communities. Heath (2005) and Jennings *et al.* (2002) highlighted the decline of the demersal piscivorous fish commu-

nity due to fishing. In the case of pelagic, planktivorous species, individual populations may have been impacted by fishing, but other functionally similar species expanded to fill the vacant niches, thus maintaining the planktivore role in the system. Differential responses of the pelagic and demersal communities resulted in multidecadal changes in the trophic structure of the North Sea ecosystem.

Several studies have claimed to show that the pelagic food web in the North Sea has underlying bottom-up control. Aebischer *et al.* (1990) reported parallel trends in phytoplankton, zooplankton and herring biomass, kittiwake breeding success, and weather indices as evidence of bottom-up forcing. However, it is clear that herring biomass cannot be considered purely as a product of trophic forcing. More likely, fishing combined with environmental (including trophic) factors were involved in the temporal changes which, coincidentally, were correlated with zooplankton and phytoplankton abundance. Similarly, Richardson and Schoeman (2004) cited spatially coherent temporal correlations between phytoplankton abundance and zooplankton herbivores, and between herbivorous and carnivorous zooplankton as evidence of bottom-up food-web control in the north-east Atlantic and North Sea in particular. Frederiksen *et al.* (2006) showed that off the Scottish east coast in the north-western North Sea, diatom, zooplankton, and sandeel abundance, and the breeding success of some seabirds, were all positively correlated implying bottom-up controlled. Reid *et al.* (2001a) noted parallel changes in food-web components including plankton groups which indicated periods of rapid restructuring of the North Sea taxa in the late 1980s. However, Hunt and McKinnell (2006) considered the complexity of diagnosing the nature of trophic forcing within ecosystems and concluded that in fact the necessary data are rarely available, and that correlations between time series of selected species may not of themselves be sufficient



Box 3.5, Figure 1 Spawning stock biomass (black) and fishing mortality (blue) for North Sea cod. The series for 1920–90 (solid lines) are from Pope and Macer (1996). The series for 1963–2003 (dashed lines) are from the ICES Data Centre <http://www.ices.dk/datacentre/StockSummaryDatabase>.

continues

Box 3.5 *continued*

evidence. The authors suggested that fisheries removals are probably decreasing the strength of the couplings between fished species and their prey, thus diminishing the likelihood or demonstrating bottom-up effects of climate change. A solution may be to consider time series of production by functional groups of species which encompass the total flux through the food web, rather than time series of biomass of individual species. Along these lines, Heath (2005) found significant positive correlations during the period 1973–99, between omnivorous zooplankton and planktivorous fish guild production, and between the productions of planktivorous and pelagic piscivorous fish guilds, giving added weight to the case for bottom-up control of the North Sea pelagic food web. Frank *et al.* (2007) found that, given the species richness in the North Sea, these correlations were consistent with the emergent pattern of bottom-up versus top-down control for shelf ecosystems around the North Atlantic.

A key factor in the bottom-up response of planktivorous fish production in the North Sea seems to be the extent of species redundancy, or the fungibility of species, that is, the degree to which species are interchangeable with others of the same functional type within the ecosystem. In the relatively species rich North Sea, Heath (2005) noted that sprat, herring, sandeels, and Norway pout appeared to be functionally interchangeable within the planktivorous fish guild, and that while the production of the guild as a whole was

bottom-up driven by zooplankton production, the constituent species had undergone boom and bust phases in response to fishing and climatic factors which bore little or no relation to underlying plankton production. For example, as herring production declined during the 1970s partly through overfishing, sprat production expanded to fill the food-web niche vacated by herring, reversing in the 1980s as herring stocks recovered.

Species fungibility may be less effective in buffering the effects of fluctuations in individual species in the North Sea demersal food web. Several studies have noted that species richness and diversity of the groundfish community have declined over time, and the growth and maturity characteristics of species changed, in the most heavily fished parts of the North Sea (Greenstreet *et al.* 1999; Jennings *et al.* 1999; Greenstreet and Rogers 2006). Heath (2005) estimated that production of demersal piscivorous fish as a guild had decline since 1973 due to reductions in the major commercial species by fishing and lack of sufficient replacement by non-target species to maintain the guild-level production. Also, there was a highly significant negative time-series correlation between the consumption of macrobenthos by demersal fish and the production of macrobenthos carnivores, which was symptomatic of top-down control. Thus, within the North Sea, different branches of the food web displayed fundamentally different control mechanisms.

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effects of climate change. Indeed, recent evidence, that fish species diversity gradients respond to interannual variability in bottom temperature, suggests that the effect may be quite rapid (Fisher *et al.* 2008).

From a management point of view, identifying top-down controlled systems which may be vulnerable to reorganization by climate change and/or fishing, based on species richness, primary production characteristics, and temperature, would seem to be an important step to devising

more holistic schemes for ecosystem harvesting. Another development indicated by such considerations is a move towards fisheries management targets based on functional groups, in addition to those based on target species, with the aim of conserving ecosystem stability as well as individual species (Hughes *et al.* 2005).

Trophic models fitted to time series of catch and abundance data have been used to explore the contributions of fishing, the environment, and

internal trophic flow controls towards driving observed ecosystem fluctuations/changes. In the southern Benguela, (Shannon *et al.* 2004b, 2008), model simulations suggest that the environment was more important than fishing in changing the ecosystem dynamics in the second part of the twentieth century. These studies suggested that availability of mesozooplankton prey to anchovy and sardine, driven by environmental conditions, and the availability of anchovy and sardine as prey to their predators, could be key processes in this ecosystem, although the underlying mechanisms require further analyses and investigation. By comparison, a trophic model fitted to time series data for the southern Humboldt upwelling system (Neira 2008; Neira *et al.*, in preparation) found that fishing may explain nearly a third of the observed variability in the time series examined and that the dynamics of this ecosystem may have been further affected by a long-term change in primary production. In the case of the northern Humboldt Current, fishing accounted for only about one-fifth of observed variability in the time series used to fit a trophic model, and environmental forcing was important. Environmental forcing which acts in the traditional bottom-up way was found to be more important than environmental forcing acting directly on the interactions between meso- and macrozooplankton (prey) consumptions by anchovy and sardine, or between anchovy and common sardine consumption by their respective predators (Taylor *et al.* 2009). A comparable model of the South Catalan Sea (Coll *et al.* 2006a) suggested that fishing and the environment played equally important roles in driving the observed changes in that ecosystem. These studies highlight the importance of considering synergistic effects of fishing, internal flow controls (predator-prey interactions), and environmental forcing acting at different levels within the food web.

3.4.2 Coastal versus open ocean

Open ocean and coastal or inner-shelf ecosystems may differ in their responses to human activity. The

exposure of coastal ecosystems to impacts generated by land-based human populations such as nutrient input, waste disposal, and engineering activity is greater. Coastal and open ocean ecosystems differ in energy inputs and finally in species richness.

In the open ocean, aggregates formed of dead phytoplankton cells and faecal pellets in the surface waters, referred to as marine snow, are progressively digested and respired by microbial activity during their sedimentation into the mesopelagic and bathypelagic zones (Lampitt and Antia 1997; Lampitt *et al.* 2001). As a consequence, the material reaching the sea floor is denuded of carbon and nutrients, and only a small fraction of annual primary production in the euphotic zone is available to support deep ocean benthic food webs. Deep sea taxa have evolved to survive in this impoverished environment by slow growth rates, late maturation, extreme longevity, and low fecundity compared to shallow sea taxa inhabiting equivalent temperature ranges. Species richness typically declines with depth below ~1,000 m in the deep ocean, and with increasing latitude (Macpherson and Duarte 1994; Rex *et al.* 2000; Macpherson 2003; Kendall and Haedrich 2006). This combination of life history characteristics and poverty of species makes deep sea fish and communities exceptionally vulnerable to fishing (Devine *et al.* 2006) and recovery times will be correspondingly long. Given the paucity of species, it is expected that the deep ocean benthopelagic food web would be controlled by top-down predation, and that the removal of fish from such a system would lead to growth in abundance of invertebrates and other taxa in the more heavily fished areas, but it is not known whether this is the case.

In contrast to the deep ocean, the sea floor in shallow-shelf seas and coastal regions receives high nutritional quality phytodetritus, and in areas where the seabed is within the photic zone filter-feeding benthos may graze directly on live phytoplankton. Whereas the sensitivity of deep sea benthic communities to human intervention is a product of their impoverished nutritional state, the sensitivity of shallow sea communities arises from their relatively highly enriched nutritional state. Eutrophication of shallow-shelf seas

adjacent to major centres of human population by nitrogen and phosphorus from agricultural, industrial, and sewage discharges is an endemic phenomenon. The excess organic matter resulting from nutrient enrichment leads to hypoxia and anoxia especially in areas subject to water column stratification. Diaz (2001) reviewed global patterns in the incidence of oxygen deficiency and revealed a clear trend of increasing hypoxia. The early stages of eutrophication may increase food-web production and fishery yields, but as nutrient emissions increase the damaging effects of over-enrichment with organic matter become manifest first as seasonal benthic mortality events (e.g. Elmgren 1989; Diaz and Solow 1999; Nilsson and Rosenberg 2000; HELCOM 2002) and ultimately reduced species richness and declining fishery yields (e.g. as in the Black Sea; Mee 1992). The natural trophic state of shallow sea and coastal marine ecosystems is probably slightly net autotrophic (i.e. a small net sink for carbon dioxide and phosphorus), but systems disrupted by enrichment become net heterotrophic (i.e. net sources of carbon dioxide and phosphorus) due to the increasing predominance of organic degradation processes over primary production (Heath 1995).

3.4.3 Introduced/non-native species

Invasive species have exerted profound effects on aquatic ecosystems, resulting in fundamental restructuring through changes in habitat, predation impacts, and competition with native species. Aquatic nuisance species are 'organisms introduced into new habitats...that produce harmful impacts on aquatic natural resources in these ecosystems and on the human use of these resources (<http://www.anstaskforce.gov/>)'. Freshwater systems, such as the Great Lakes of North America, provide some of the best-known examples of the effects of introduced species, through direct mortality (e.g. lamprey effects on lake trout) or habitat disturbance (zebra mussels). A good source of information on introductions of non-indigenous marine species in the North Atlantic (including viruses, bacteria, fungi, plants, invertebrates, and

fish) and their impacts is provided by International Council for the Exploration of the Sea (ICES) (2007f). An up-to-date collection of papers on marine bioinvasions was edited by Pederson and Blakeslee (2008). Ballast water discharge, escape of aquaculture species, intentional or accidental release of aquarium species, live release of fishing bait, and the loss of live marine organisms transported for human food all potentially serve as vectors for the introduction of invasive marine species (e.g. Carlton 1989; Carlton and Geller 1993). Introduced species may undergo dramatic increases in abundance if their natural predators, diseases, and parasites are not present in the new environment.

In the Black Sea, a population explosion of the introduced gelatinous species *Mnemeopsis leidyi* occurred in the mid-1980s (Grishin *et al.* 1994), and it became a major competitor with the indigenous pelagic fish stocks for zooplankton production (Grishin *et al.* 1994; Shiganova 1998). This compounded the effects of overfishing (Daskalov 2003), leading to a trophic cascade which was manifest as extreme phytoplankton blooms (Yuney *et al.* 2002).

The introduced colonial tunicate *Didemnum* sp. has rapidly increased in abundance off the north-eastern United States, in coastal waters, and on the continental shelf. *Didemnum* was first detected there in 1988 (Bullard *et al.* 2007) and is now a dominant species in nearshore and continental waters off New England. Since 2002, it has been found on gravel beds on Georges Bank (Fig. 3.8), which are an important substrate for settlement and growth of sea scallops and provide shelter for juvenile cod and haddock. The tunicate carpeting the gravel could impair these habitat functions. As of summer 2007, *Didemnum* was abundant in two gravel areas totaling over 230 km² (88 square miles) (Fig. 3.8). Its offshore spread may continue, or it may be limited by the mobile sands that border the gravel, or (to the north and east) by temperatures too cold to reproduce.

Introduction of lionfish *Pterois volitans*, a venomous coral reef species native to the Indo-Pacific region, has recently been documented off the east coast of the United States (Whitfield *et al.* 2002, 2006; Hare and Whitfield 2003). Adult lionfish have been observed



Figure 3.8 Invasive *Didemnum* (tunicate) mat on gravel substrate on Georges Bank. (From <http://woodshole.er.usgs.gov/project-pages/stellwagen/didemnum>. Photographed by Page Valentine and Dan Blackwood, U. S. Geological Survey.)

from southern Florida to Cape Hatteras, North Carolina. Juvenile lionfish have now been observed off North Carolina and Bermuda and as far north as New York (Fig. 3.9). Available information on juvenile and adult distributions suggests reproductive populations of lionfish exist off the south-eastern United States. Overwintering mortality of juveniles may account for the current lack of evidence for adults north of Cape Hatteras. However, under projected climate warming scenarios, the potential range of adult lionfish may extend northwards (Kimball *et al.* 2004). Potential fishery-related impacts of the lionfish introduction are currently unknown but this species may compete with economically important grouper species for habitat and food resources (Hare and Whitfield 2003). Grouper populations are currently overfished, possibly freeing resources for lionfish to exploit.

3.4.4 Human activities as triggers or amplifiers of abrupt ecosystem changes

Large-scale changes in marine ecosystems over relatively short time frames have been recorded in a number of systems. The interplay of harvesting and underlying ecosystem processes has been implicated in many of these cases. Lluich-Belda *et al.* (1989) coined the term 'regime shift' to describe alternating global patterns of sardine and anchovy abundance. Collie

et al. (2004) define a regime shift as a low-frequency, high-amplitude change in oceanic conditions that may propagate through several trophic levels; they distinguish between smooth, abrupt and discontinuous ecosystem responses. Smooth regime shifts occur when an ecosystem state variable exhibits a linear response to a forcing function, while abrupt and discontinuous regime shifts arise as a result of underlying non-linear system dynamics. The latter category gives rise to the possibility of alternate stable states in which forcing by oceanographic and/or anthropogenic factors results in rapid shifts between ecosystem configurations. The characteristically reddened spectrum of marine processes (Steele 1985) coupled with harvesting pressure can result in synergistic effects which increase the likelihood of persistent shifts in ecosystem states (Collie and Spencer 1994).

The interaction between temperature and harvesting pressure has been recognized as a contributing factor in the collapse of sardine populations on the west coast of the United States and the specification of sustainable harvesting levels for this species is now tied to changes in temperature (Jacobson *et al.* 1995). Hare and Mantua (2000) identified a regime shift in the North Pacific starting in 1976/7 that resulted in dramatic changes in Pacific salmon populations and other ecosystem components. Choi *et al.* (2004) noted that decadal-scale changes in temperature and stratification affecting benthic-pelagic coupling, combined with overharvesting of cod and other species led to a restructuring of the Scotian Shelf ecosystem to one dominated by small pelagic fish and characterized by sharply reduced productivity of the groundfish assemblage.

In systems dominated by top-down controls (see Section 3.4.1), rapid changes in ecosystem configuration can be triggered by human activities, resulting in indirect effects at two or more trophic levels removed from the level directly affected by anthropogenic forcing (e.g. Frank *et al.* 2005). This effect is termed a trophic cascade. Frank *et al.* (2007) further noted that ecosystem susceptibility to top-down control and resiliency to exploitation are related to species richness and to temperature. Top-down controlled systems are sensitive to overfishing and depletion of predator species (Christensen *et al.* 2003) and the resulting changes may not be reversible with

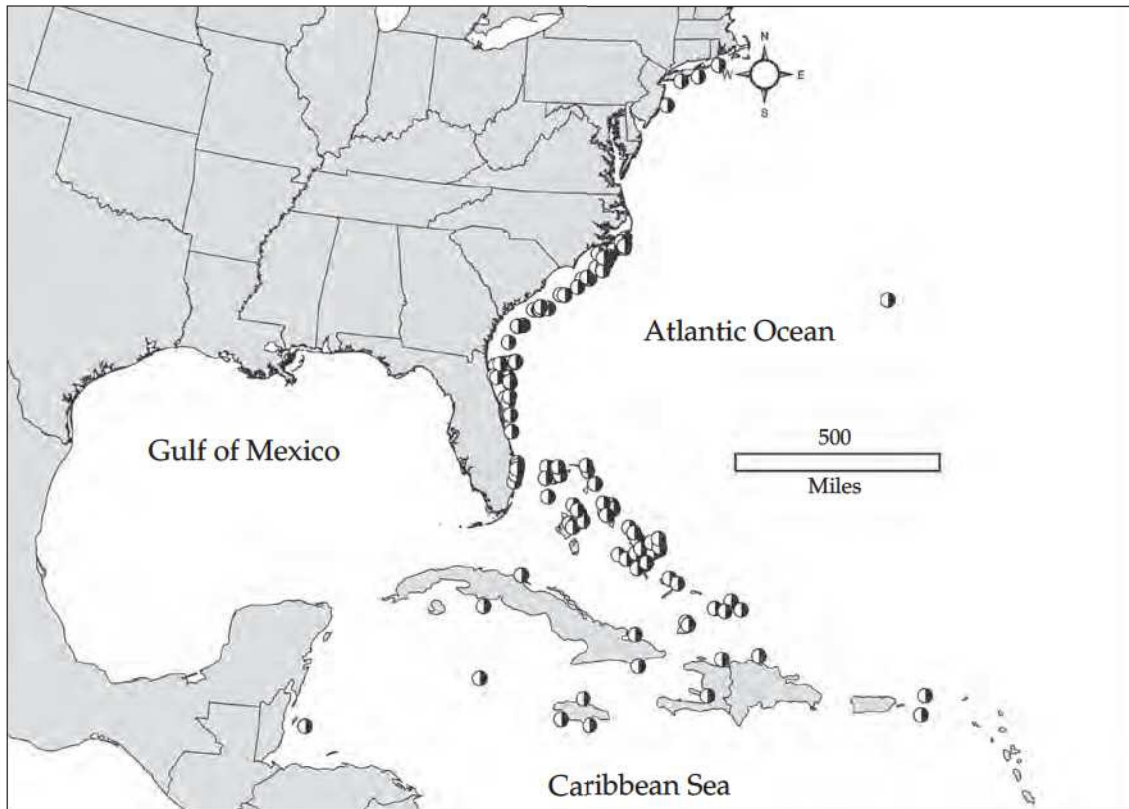


Figure 3.9 East coast of the United States and the Atlantic Ocean, showing locations of lionfish sightings from August 2000 to January 2005 (Whitfield *et al.* 2006).

the reduction or elimination of fishing mortality. Examples are the increase in shrimp production and fisheries in high-latitude ecosystem where cod has been depleted by fishing (Worm and Myers 2003; Frank *et al.* 2005). In the Black Sea, overfishing of marine predators provoked cascading changes, resulting in increases in abundance of planktivorous fish and jellyfish, and a corresponding decrease in zooplankton and increase in phytoplankton (Daskalov 2002) and decrease of the mean trophic level in the ecosystem (Daskalov 2000). Knowlton (1992) noted that in coral reef ecosystems, removal of herbivores through harvesting and/or an increase in eutrophication related to human activities can result in a shift to an algae-dominated system.

Species loss through environmental events may also precipitate trophic cascades in top-down control sys-

tems. For example, unusually warm conditions during summer 1999 caused mass-mortality of invertebrate species in the north-western Mediterranean (Cerrano *et al.* 2000; Perez *et al.* 2000) allowing other species, pre-adapted to the new conditions, to replace them and potentially precipitating food-web restructuring.

3.5 Summary and conclusions

We reviewed studies showing that human impacts on marine ecosystems due to fishing, habitat degradation, and other factors have intensified with time and that evidence of alteration of marine populations and ecosystems goes back many centuries, particularly in coastal areas. Awareness of such long-term changes due to both natural causes and human impacts has

increased, as historical and archaeological studies have reconstructed information on the species composition, relative abundance, and age composition of exploited fish. Prior to the recording of fish catches and biological characteristics in order to track and control fisheries for sustainable harvesting, some detailed records were kept for purposes of taxation and trade. Greater attention to the effects of climate and lengthening time series provided by monitoring programmes now give us clear evidence of past changes in marine ecosystems, but the evidence comes mainly from the fish component of the ecosystems and from a few well-studied areas of the world oceans.

The accumulation of more complete and detailed information about what marine ecosystems used to be like, not only over the past century, but over many centuries of human impact, may in principle provide a clearer target for efforts at conservation and restoration. However the evidence of past variability, even in the absence of human impacts, shows that there is no static, historically pristine state to aim at; change is the norm. Overexploitation of fish stocks is the main cause of loss of biodiversity and decline in abundance of marine organisms. This has stimulated great public concern and political pressure to protect fish stocks and the ecosystems of which they are a part. It is imperative to act in order to prevent further degradation of marine habitats and loss of biodiversity and to restore sustainable fisheries.

We describe the effects of fishing on population age structure and resilience in some detail, using the concept of LEP to explain the dynamics of replacement. Because replacement depends on all sources of mortality it is their collective effect which determines whether exploitation is sustainable. Resilience and the rate at which stocks recover depend on details of behaviour, internal dynamics, alternate stable states,

metapopulation structure, and ecosystem changes. Population recovery may therefore take much longer than estimated from models based on pre-decline vital rates especially if they do not include relevant processes, such as those itemized above. Furthermore, since we know that future environmental conditions will be different from those in the past, because of climate change, this means that the recovered state of a population or ecosystem may be different from the past state.

Fishing causes damage to habitats and alters the trophic structure of ecosystems in a variety of ways, with effects which go far beyond the species targeted by the fisheries. Although most of the changes which have been observed have been detrimental (e.g. loss of production of desirable species), there could in principle also be desirable changes, resulting in cultivation of desirable species, or using spatial planning to achieve desired objectives in different areas. Turning principle into practice however requires much greater understanding of the processes governing such ecosystem changes than we presently possess.

The EAF is being developed to ensure sustainable yields of exploited species, while conserving stocks and maintaining the integrity of ecosystems and habitats on which they depend, but considerable difficulties remain in making this fully operational. One issue concerns objectives, for example the extent to which high food production from the sea is compatible with the maintenance (or restoration) of ecosystems and habitats. Conflicting objectives need to be resolved, trade-offs evaluated, priorities established, and effective control measures agreed between different interest groups and countries—quite a tall order, but one with which we will grow increasingly familiar as we come to terms with the need to take responsibility for management of a small planet.