

## Status, trends and the future of the marine pelagic ecosystem

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Date submitted: 3 May 2001 Date accepted: 22 March 2002

### SUMMARY

Globally, humans impact environments and ecosystems faster than they become aware of their effects. The marine pelagic ecosystem includes a tremendously large and diverse environment, which might accordingly be considered to be resilient to externally forced changes, whether from humans or climate. This review considers that general hypothesis by pursuing two objectives. The first is to document the current status of and recent anthropogenic impacts on the marine pelagic ecosystem, with emphasis on the epipelagic zone (0–200 m) where organisms are concentrated and human impacts have been greatest. It shows that humans have proven capable of assuming the role of top carnivore in pelagic ecosystems where living resources are attractive and financially amenable to exploitation, and that overexploitation is the rule under such circumstances. Other anthropogenic activities associated with changes in various marine pelagic ecosystems, such as increased diseases, mortalities, extinctions, habitat invasions, and species replacements, function as sentinels and indicate that portions of the pelagic ecosystem are under considerable stress. It is argued that, without attention, these problems can be expected to worsen up to the year 2025 and beyond. In addition to a comprehensive evaluation of status and trends relating to conservation of the marine pelagic ecosystem, a second major objective is to evaluate whether current paradigms of ecosystem function are sufficient to improve the ability of the scientific community to predict future changes and to recommend relevant management strategies. This review differs from previous ones by proposing that current conceptual models have failed to provide the basis for accurately predicting patterns and features of pelagic communities, notably why specific organisms occur where and when they do. It is argued that predation pressure is shaped by natural selection in the sea as on land, and that it influences organism behaviour, life history strategy and morphology, all of which determine marine pelagic ecosystem structure, and therefore should be used to interpret function. From this perspective, attempting

to understand present patterns and predict the future of marine pelagic ecosystems, without understanding the intertwined roles of evolution and predation in forging contemporary pelagic communities, is a hopeless endeavour. It is proposed that both perspectives, resource availability and predation pressure, be incorporated into a revised paradigm of pelagic ecosystem structure and function, a necessity if policies are to predict anthropogenic impacts and environmental conservation is to be effective.

*Keywords:* marine, pelagic, ecosystem, pollution, extinction, invasions

‘But ritual feeds on itself and grows like a wild hedge, until it makes all movement impossible and clogs the streets of crumbling cities.’ *Red Earth and Pouring Rain*, Vikram Chandra (1995), p. 268.

### INTRODUCTION

Considered in its entirety, the marine pelagic ecosystem is perhaps the greatest in size of all ecosystems on earth. The oceans comprise 71% of the earth’s surface area of  $5.1 \times 10^8$  km<sup>2</sup> (Riley & Chester 1971), and if the marine pelagic environment is defined as comprising all ocean waters from the surface to the sediments with an average depth of 3.8 km, then its volume is very approximately 14 billion km<sup>3</sup>, or 99% of the earth’s biosphere volume (Norse 1994). Of course, ecosystem size is not necessarily equated with importance, diversity, or environmental complexity, but from the perspective of environmental conservation, it carries unique attributes. The size of the marine pelagic ecosystem is a source of both optimism and pessimism for the future. Thus the marine pelagic environment can potentially absorb tremendous impacts, an attitude towards use that has prevailed for centuries and still continues among marine scientists today (Roberts & Hawkins 1999). However, when an ecosystem this huge shows warning signs of adverse impacts, then the time for dramatic and immediate action has arrived. But like the canary whose narcosis warned miners of the presence of carbon monoxide (Peele 1941), the ecosystem can be revived if the symptoms are recognized, the diagnosis is accurate, and the relationships between organisms and their environments are understood.

Various aspects of the marine pelagic ecosystem have been previously reviewed. These can be classified into several

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generic categories: primary literature papers promoting revised or new conceptual models linking pelagic ecosystem structure and function (e.g. Pomeroy 1974; Margalef 1978; Smetacek & Pollehne 1986; Parsons 1988; Legendre 1990; Verity & Smetacek 1996); governmental and non-governmental reports on status and trends of particular important or endangered stocks or resources (e.g. IPCC [Intergovernmental Panel on Climate Change] 1996; HEED [Health, Ecological and Economic Dimensions of Global Change Program] 1998; Hilton-Taylor 2000); regional or water body-specific reviews, which typically address trophic linkages or ecosystem function (e.g. Steele 1974; Walsh 1977; Verity 1987; Smetacek *et al.* 1990; Cohen 1994; Rudstam *et al.* 1994); general reviews which summarize status and trends of anthropogenically impacted or ecologically important phenomena (e.g. Smayda 1990; Jackson *et al.* 2001); and primary literature papers relating the marine pelagic ecosystem to regulatory factors (Greve & Parsons 1977; Platt & Denman 1978; Cushing 1989; Kiorboe 1993) or global scale issues (e.g. Longhurst 1991; Wassmann 1998). Computer simulations and modelling approaches have also provided the basis for pelagic ecosystem review (Steele & Frost 1977; Moloney *et al.* 1991; Legendre & Rassoulzadegan 1996). All of these synthesis papers, and others too numerous to list here, contain varying combinations of data reports, interpretations, and comparison to current paradigms. However, none simultaneously reviews the status and trends of organisms in, and environmental phenomena affecting the marine pelagic ecosystem, summarizes apparent global patterns, evaluates the state of knowledge within the context of strengths and weaknesses of contemporary paradigms, proposes revisions to those paradigms, and offers predictions about the ecosystem's future over a time horizon of 25 or so years.

This paper addresses the future of the marine pelagic ecosystem by focusing on two distinct but highly related issues. First, what are the status, trends and threats to this ecosystem? Second, what are the paradigms that guide research on the marine pelagic ecosystem, past, present, and future? Essentially, one represents the knowledge base and level of understanding, while the other represents the mechanism by which that understanding is achieved. In principle, there should be feedbacks between them, and one of the objectives of this review is to evaluate whether the feedbacks are adequate to guide the next century of research. Two guiding principles provide structure for this evaluation. One is the predictive value of bottom-up (resource availability) versus top-down (predation) models of ecosystem structure. The other is to consider, largely within the framework of these two conceptual models, whether lack of perception of the importance of particular issues impacting the marine pelagic ecosystem reflects scientific ignorance or their contemporary absence of significance. Recommendations are offered to expand our conceptual understanding of the marine pelagic ecosystem, with the goal of better predicting system behaviour and responses to climatic and anthro-

pogenic activities. Where appropriate, comparisons are made with freshwater pelagic and terrestrial ecosystems in order to identify mechanisms behind the patterns, and to evaluate the extent to which conceptual models from these better-studied systems are appropriate for the marine pelagic ecosystem.

## PARADIGMS PAST AND PRESENT

The original conceptual basis for quantitative marine ecology is attributable to Victor Hensen (1887), who proposed that food supply controlled variations in adult fish stocks and that quantitative studies of plant and animal production in the sea would permit predictions of annual fish yields. Hensen (1887) envisaged a simple linear relationship between hydrography, plankton, and fish, and suggested that the apparent spatial homogeneity of marine waters compared to terrestrial systems would allow extrapolation from smaller to larger scales. Since fish were being 'harvested' by man, Hensen (1887) argued that relationships similar to agriculture existed between primary production and fish yield. Thus was born the notion that pelagic ecosystems were structured from the bottom up, or were resource-limited (Smetacek & Pollehne 1986).

This bottom-up thinking became dogma for several coincidental reasons. First, the general perception during the next 50 years was that phytoplankton dynamics reflected regulation primarily by environmental variables, such as light, temperature, and nutrients. This notion was supported by the early development of quantitative analytical methods in nutrient chemistry, which showed direct relationships between nutrient availability and phytoplankton growth (see Valiela 1995). Second, zooplankton studies were simultaneously not quantitative. Lohmann's (1908) demonstration that small colourless and thus zooplanktonic single-celled organisms were abundant and likely to be significant herbivores was ignored, and his method of concentrating plankton by centrifugation was not adopted. The combination of nets, preservatives which did not permit distinction between plant and animal cells, and low magnification microscopy, led to 50 years of focus on larger, multicellular herbivores (see Banse 1992, for additional discussion).

Beginning in the 1970s, there were several major discoveries or conceptual revelations that together revised our understanding of pelagic food webs. The role of aquatic bacteria was seen to be substantially more complex than previously appreciated; bacteria used the dissolved organic matter produced by phytoplankton and zooplankton as carbon sources for growth and made an alternative microbial food web provided for protozoan grazers (Pomeroy 1974). Medical fluorescence microscopy showed that there were substantial numbers of tiny phytoplankton also being eaten by protozoan zooplankton, all contributing to the dissolved organic matter pathway back to bacteria (Azam *et al.* 1983). With further research, the linkages within the microbial food web and connections to the 'classical' food web involving diatoms, copepods and fish have been explored.

This revised paradigm has not led to the predictive capability required for effective environmental stewardship. Whereas, the mainstream approach to studying terrestrial ecology is based upon the species unit (Wilson 1992), pelagic systems have been largely studied on the basis of generic variables such as pigment concentrations, size-fractionated biomass, or rate processes within specific trophic levels. On such a basis, general features of ecosystems and how these influence trophic structure and energy flow are now broadly understood (Cohen 1994). Many properties of species in marine pelagic ecosystems can be determined with great precision; for example morphology, life cycle stages and certain aspects of physiology, and there is promise of increased specificity using molecular genetics. Nevertheless, appreciation of the nature of the properties that gear a given species to a specific pelagic environment, and which are responsible for its occurrence or persistence in a given water mass is, at best, poor. Knowledge of the temporal and spatial distribution patterns of many species is now fairly sound, yet it is unknown why these organisms occur when and where they do. Therefore, little can be predicted.

Predictive ability does exist. For example, correlations suggest that yields of marine fisheries increase linearly with annual rates of primary production (Nixon 1988; Iverson 1990). The high efficiency of conversion of solar energy into marine fish via photosynthesis (Nixon 1988) indicates that availability of adequate resources is a significant force in the overall structure and function of marine pelagic ecosystems. In one sense, these data seem to validate the view that, from basic knowledge of how vertical mixing regulates primary production and assuming certain features of food chain length and efficiency, fish yield can be estimated (Hensen 1887; Ryther 1969). However, while Hensen (1887) wanted to predict annual variability in fish yield within a given region from variations in plankton production, Ryther (1969) proposed that variability in food chain length among regions, which also vary in long-term averaged primary production, could be used to make generic predictions of fish yield among these disparate regions. Annually-averaged phytoplankton production and fish yield from various regions appear positively correlated (Nixon 1988; Iverson 1990) but the causal connection depends strongly upon diverse assumptions regarding conversion factors and transfer efficiencies. However, variability within one region over many years has scarcely been studied, nor have documented variations in food chain length or trophic complexity among regions been incorporated. It is well known that fish recruitment and fishery yield can vary 10-fold from one year to another (Cushing 1982), whereas interannual variation in primary production rarely exceeds a factor of 2 (Lindahl 1995; Hubel *et al.* 1998). Thus, while it is comforting to find predictable relationships between the base of the food web and fisheries yield or production when averaged over large scales, the equations may be less accurate in a specific environment for a given year.

To summarize, the bottom-up perspective has not been successful in predicting many patterns and features of pelagic

communities, nor why specific organisms, morphologies, and life histories occur where and when they do. 'Current knowledge and paradigms of ecosystem function are provisional, incomplete, and subject to change' (Christensen *et al.* 1996). The lack of such a fundamental understanding might potentially result in a poor ability to understand ecosystem response to perturbations, whether naturally or anthropogenically induced. The next section will investigate the status and trends of some salient indicators of ecosystem function.

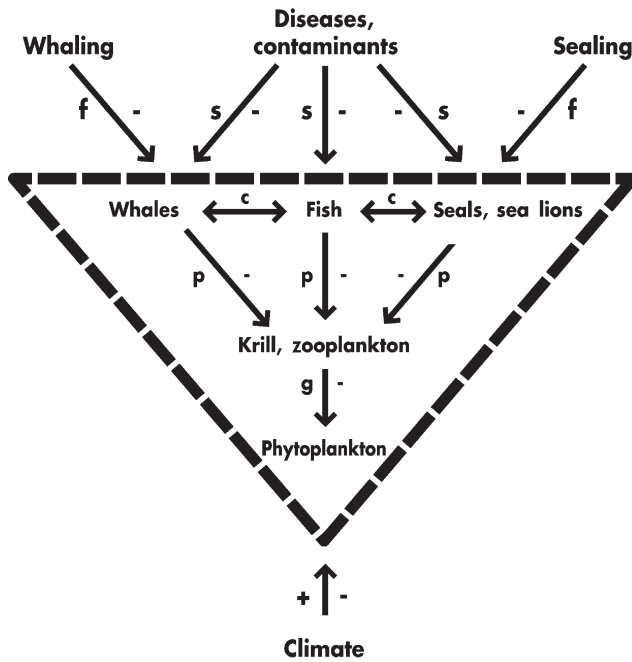
## CONTEMPORARY ENVIRONMENTAL CONCERNS

Historically, the main human interest in marine pelagic ecosystems was their yield in natural resources, notably those of fisheries. Unfortunately, these resources typically became overexploited as the growing human population and technological advancements yielded increased demand and capture efficiency (Sahrhage & Lundbeck 1992). Despite early evidence that pelagic resources might collapse under the combined weight of overharvesting and/or natural variability, there was little interest in learning the origins of resources and what factors regulated resource yield, until major stocks were devastated (e.g. Roberts & Hawkins 1999). It is becoming increasingly apparent that the structure and function of pelagic ecosystems changes significantly due to exploitation (Parsons 1992).

### Marine mammals

By whaling and sealing, humans early assumed the role of top carnivore in the marine pelagic ecosystem (e.g. Gaskin 1987). In the North Atlantic, whaling extended back to at least Roman times, but did not become an ecosystem threat until the period of Arctic whaling around Spitsbergen (Svalbard) in the 1600s (De Smet 1981). In the Antarctic, sealing was the first lucrative business in the late 1700s, and after extermination of the resource sealers switched eventually to whales in the late 1800s.

Prior to commercial harvesting, stock sizes of whales were estimated to have been  $42 \times 10^6$  tonnes (Valiela 1995). By the time a near-global moratorium was placed upon whaling in the 1960s, stocks were estimated at only  $7 \times 10^6$  tonnes, a reduction of *c.* 80%, with most of the removal accomplished in just the last 30 years. The reduction of whales and seals in the Antarctic may have caused a trophic cascade (*sensu* Carpenter *et al.* 1987) and other changes in ecosystem dynamics (Katona & Whitehead 1988; Fig. 1). Before commercial exploitation, whale and seal stocks were thought to be at environmental carrying capacities, thus limiting their prey, i.e. krill and copepods (Valiela 1995). Heavy whaling then released krill from predation, and krill stocks are now thought to be considerably larger: their biomass may exceed that of *Homo sapiens* despite living in a geographic area only twice the size of the USA. In contrast, dominant copepods



**Figure 1** A conceptual model of a highly simplified three trophic level pelagic ecosystem, and some of the major types of natural and anthropogenic forces which determine ecosystem structure and function. Whaling and sealing are classic examples of human activities (fishing = f) that typically cause negative (-) impacts on resources. Diseases and contaminants are natural and human-induced stresses (s), which generically are associated with negative impacts on recipient or target populations. Climatic effects can be positive or negative. Within an ecosystem, organisms compete (c) for resources and prey (p) or graze (g) on one another, typically with negative consequences for prey stock size.

have not shown long-term patterns consistent with a large-scale trophic cascade, perhaps because of interannual variability, long-term temperature changes, decadal fluctuations, and compensatory feeding by other carnivores (Vuorinen *et al.* 1997). However, most whale, penguin, and seal populations are now responding to the large-scale cessation of whaling as though their food supply has increased: they are maturing earlier, growing faster, with higher pregnancy rates, and living longer than before whaling began (Gambell 1968; Croxall *et al.* 1988; Parsons 1992; but see also

Jennings & Kaiser 1998; Smith *et al.* 1999), although not all whale species responded positively (Kraus 1990; Hamilton *et al.* 1998). The direct effects of overharvesting may be exacerbated by other stresses (Fig. 1), particularly in larger pelagic organisms and those that feed at higher trophic levels, a possibility that is discussed later in the context of diseases. Also, many smaller cetacean species have been declining in abundance (Brownell *et al.* 1989).

**Fish, fisheries and climate**

Although pelagic ecosystem productivity, and to a certain extent function, reflect physical controls on resource availability (Nixon 1988; Iverson 1990) predators and prey have co-evolved, and hence widespread removal of predators (Parsons 1992; Pauly 1995; FAO 1997; Buckworth 1998; Table 1) may be expected to induce salient alterations in ecosystem structure and function (Aronson 1990, 1994; Steneck 1997). Several categories of ecosystem changes are induced by massive fish removal (Table 2), including the replacement of one species by another typically non-commercial fish, the expansion of organisms one trophic level lower if compensation does not occur, and the loss of organic matter from the food web to the benthos (Parsons 1992; Jennings & Kaiser 1998). Indirect effects on marine ecosystem structure and dynamics induced by fishery removals can be as important (Botsford *et al.* 1997; Trites *et al.* 1999). Cascading effects of harvesting can fundamentally alter community structure at trophic levels beneath that of the overexploited species (Steneck 1997). For example, the recovery of northern right whales (so named because they were the ‘right’ ones to kill) from whaling may be inhibited by competition for zooplankton prey with the planktivorous sand lance (*Ammodytes* spp.), which evidently exploded in abundance in response to human overexploitation of the traditional planktivorous fish, herring (*Clupea harengus*) and mackerel (*Scomber* spp.) (Payne *et al.* 1990). But examples also exist where fishery removal of predators apparently did not affect the abundance of prey or competing species (Jennings & Kaiser 1998).

Moreover, changes in ecosystem structure occur independent of fisheries effects (Mann 1993). Large fluctuations in sardine and anchovy stocks have occurred over thousands of

**Table 1** Examples of fish species and ecosystems where fishing mortality is thought to have significantly reduced target stocks.

Scientific name	Common name	Location	Reference
<i>Clupea harengus</i>	Herring	North Sea	Hempel 1978
<i>Ammodytes</i> spp.	Sand Lance	North Atlantic	Sherman <i>et al.</i> 1981
<i>Theragra chalcogramma</i>	Walleye Pollack	Bering Sea	Springer 1992
<i>Engraulis ringens</i>	Anchovy	Peru upwelling	Beverton 1990
(Several taxa)	Sharks	South Africa coast	van der Elst 1979
<i>Sardinops sagax caerulea</i>	Sardine	California coast	MacCall & Prager 1988
<i>Gadus morhua</i>	Cod	Baltic Sea	Jonzen <i>et al.</i> 2000
		North Sea	Cook <i>et al.</i> 1997
		North Atlantic	Hutchings & Myers 1994
		North Atlantic	Myers <i>et al.</i> 1996

**Table 2** Examples of ecosystem changes potentially induced by overfishing.

<i>Impact</i>	<i>Location</i>	<i>Prior Dominant</i>	<i>Effect afterwards</i>	<i>Reference</i>
Species replacement	North Sea	Herring, mackerel	Sand lance, sprat, pout increase	Hempel (1978)
	Southern Ocean	Large whales	Small whales, penguins increase	Laws (1984, 1985)
	Bering Sea	Walleye pollock	Plankton-feeding birds increase	Springer (1992)
	California Current	Anchovy	Sardines increase	Botsford <i>et al.</i> (1997)
	Adriatic Sea	Mackerel, sardines	Jellyfish increase	Avian & Sandrini (1988)
	Black Sea	Mackerel	Jellyfish increase	Zaitsev (1992)
Prey expansion	Eastern Canada	Cod, groundfish	Seals, shrimp, crabs increase	Bundy (2001)
	North Sea	Bluefin tuna	Herring, mackerel increase	Tiews (1978); Daan (1978)
	Barents Sea	Herring	Capelin increase	Blindheim & Skjoldal (1993)
	NW Atlantic	Herring, mackerel	Sand lance increase	Sherman <i>et al.</i> (1981)
Sedimentation	Gulf of Maine	Cod, haddock	Small fish, lobster increase	Steneck (1997)
	Peru upwelling	Anchovy	Organic content increase	Rowe (1981)
Indirect trophic effects	Peru upwelling	Anchovy	Birds, guano decrease	Parsons (1992)
	Gulf of Maine	Cod	Whales, sand lance compete	Payne <i>et al.</i> (1990)
	Gulf of Alaska	Shrimp, capelin	Seals, sea lions decrease	Hansen (1997)
	Barents Sea	Capelin	Cod seals, birds starve	Dragesund & Gjosaeter (1988)
			Seal migration altered	Haug <i>et al.</i> (1991)
		Whale distribution shifts	Christiansen (1990)	

years during periods when fisheries could not have been responsible (Baumgartner *et al.* 1992; Jennings & Kaiser 1998). While the causes of those fluctuations are not yet fully understood, there is substantial evidence elsewhere that climate influences long-term fluctuations in fish stocks that are also exploited commercially (Cushing 1982, 1990; Southward *et al.* 1988; Corten 1990; Alheit & Hagen 1997; but see also Dragesund *et al.* 1997), including correlations between decadal weather patterns, plankton and herring in the North Sea (Aebischer *et al.* 1990), the interaction between long-term patterns in Pacific salmon (*Oncorhynchus* spp.) and the Pacific Decadal Oscillation (Boesch *et al.* 2000), alteration of Southern Ocean food web structure by climate-induced changes in sea-ice cover (Loeb *et al.* 1997), and basin-wide similarity in abundance patterns of widely-separated sardine stocks (*Sardinops* spp.) (Kawasaki 1991). The North Pacific example is particularly intriguing, as phytoplankton biomass (estimated as chlorophyll *a*) approximately doubled between 1968 and 1985 (Venrick *et al.* 1987), during a period when the Aleutian low-pressure system intensified. The latter process is thought to mix more nutrients up from depth into the euphotic zone, which could then support more phytoplankton growth. Positive correlations were also reported between the Aleutian strengthening and zooplankton abundance (MacFarlane & Beamish 1992), and also fishery catch data for Pacific salmon (Beamish 1993; Beamish & Bouillon 1993).

The notion that climate changes and fisheries exploitation interact to cause more persistent changes in ecosystem structure and function than either would induce alone (Parsons

1992; Fig. 1) derives from evidence that climate and exploitation together accelerate species replacements (Skud 1982), and that changes in fish stocks can occur relatively quickly during periods of elevated environmental variability (Steele & Henderson 1984). Even when changes occur relatively quickly, there is invariably a long lag before scientists and managers recognize these events (IPCC 1996). In fact, one of the very reasons that it is so difficult to discriminate direct human impacts on fisheries from climate-induced changes is that the two may often be synergistic (see IPCC 1996 and Stromberg 1997 for examples).

The Peruvian anchovy fishery is a classical example of the interaction between climatic influences on fish recruitment through physical regulation of resource availability, and exploitation of spawning stock by commercial fishery. The Peruvian upwelling system is driven by local winds, but warm, nutrient-poor waters periodically cap the resulting cold, nutrient-rich productive waters (Bohle-Carbonell 1989). The latter are ultimately derived from large-scale changes in atmospheric circulation that reduce or even reverse the typical westerly trade winds (El Niño-Southern Ocean [ENSO] events), allowing subtropical surface waters to be transported east along the equator and then north and south upon encountering the Americas (Enfield 1989). The Peru anchovy fishery increased dramatically from near-zero landings in the late 1950s to being the largest in the world in the early 1970s, after which it vacillated greatly and frequently during the next two decades (Cushing 1982; Bohle-Carbonell 1989). It is now generally understood that upwelling intensity, fishing, and natural predation mortality

determine anchovy stocks in normal (non-ENSO) years (Mathisen 1989). ENSO years impact anchovies directly by reducing habitat size, which increases exposure to commercial purse seiners, and indirectly by favouring higher natural predation mortality. Other biological mechanisms that impact anchovies during ENSO years include increased density-dependent cannibalism, food scarcity, and increased metabolic costs (Valiela 1995). If the fishery harvest does not compensate for these enhanced natural losses during ENSO years, then anchovy stocks are reduced to levels that require long recovery periods (Muck 1989).

Nevertheless, although climate changes impact fish stocks, the impact of fisheries on targeted stocks is unequivocal: the pattern of peak yields followed by declines has occurred repeatedly and globally. Small pelagic fish, especially clupeoids, are particularly vulnerable due to their shoaling habit and consequent detectability and catchability (Beverton 1990), but given a respite from fishing mortality, they are also the most resilient (Hutchings 2000). Particularly devastating are fisheries which expose fish to harvest for years before they reach sexual maturity, as in the case of cod (*Gadus morhua*) (Myers *et al.* 1996; Cook *et al.* 1997), and fisheries which target species with large body size, slow growth, and slow reproduction, like sharks and rays. Total fish harvest has remained relatively constant for several years but the mean trophic level of fisheries landings declined from 1950 to 1994 (Pauly *et al.* 1998, 2000), which strongly indicates that fisheries are switching to smaller species lower in the food web. By itself this trend does not portend disaster; it only implies that harvested species are becoming closer to the plankton at the base of the food web. Coupled with long-term declines in those very stocks of low trophic level fish, however, it implies that more and more regions are likely to experience collapses of their current fisheries in the future and also major changes in pelagic food web structure. Aquaculture is considered by some to eventually mitigate global overfishing (e.g. Isaksson 1994), yet those cultured fish which require more meal derived from wild fish per unit mass of aquaculture fish produced place even further pressure on already over-exploited wild populations (Naylor *et al.* 2000). Fishing may even alter evolution of target species (Policansky 1993; Rijnsdorp 1993) and their competitors, which may have evolved to fill available niches prior to excessive harvesting (Trites *et al.* 1997).

### Diseases

Chronic and acute diseases additionally affect pelagic organisms (Fig. 1). In the endangered green turtle fibropapilloma tumours grow primarily on the skin, but they can also appear between scales and scutes, in the mouth, on the eyes, and on internal organs; they appear to be associated with a chelonian herpesvirus (Lackovitch *et al.* 1999). These tumours generally increase in size and number over time, causing debilitation and eventually death. There were sporadic reports of fibropapillomatosis in turtles as early as the 1930s,

but in the 1980s it began infecting large numbers of green turtles concurrently in several discrete geographic regions, such as Hawaii, Florida and Australia (Gamache & Horrocks 1991). Within a decade, fibropapillomatosis became the single greatest perceived threat to the green turtle, and tumours have begun to show up on other sea turtle species in increasing numbers. Globally, marine turtle populations are in decline (Eckert 1995; Limpus 1995).

A mass mortality of the endangered Mediterranean monk seal occurred off the coast of Mauritania in spring 1997, killing two-thirds of the monk seals living there, with especially heavy mortality of breeding adults (Forcada *et al.* 1999). Two causes were proposed, namely intoxication by ingestion of fish contaminated with paralytic shellfish poisoning (Hernandez *et al.* 1998; Reyero *et al.* 1999), and transmission from a dolphin morbillivirus (Osterhaus *et al.* 1997) associated with mass mortalities of bottlenose dolphins (*Tursiops truncatus*) off the USA east coast and in the Gulf of Mexico, harbour seals (*Phoca vitulina*) in the North Sea, and striped dolphins (*Stenella coeruleoalba*) in the Mediterranean Sea (Osterhaus *et al.* 1997; Harvell *et al.* 1999).

Diseases are not limited to marine mammals and turtles. Numbers of wild Atlantic salmon (*Salmo salar*) in Maine rivers (USA) are at an all-time low, and the US Fish and Wildlife Service and the National Marine Fisheries Service recently listed the species as endangered under the Endangered Species Act (NOAA [US National Oceanic and Atmospheric Administration] 1999). Three fish diseases threaten recovery efforts. The salmon swim-bladder sarcoma virus was found in hatchery-raised Atlantic salmon, and broodstock destroyed to stop the potential spread of the disease to native fish. Infectious salmon anaemia found in Canadian salmon could potentially spread to the Maine population. Additionally, a bacterial infection called coldwater disease was recently found to be a potentially serious problem for these fish. It is likely that penned fish introduce exotic pathogens into wild stocks, although the extent is currently uncertain (McVicar 1997). The potential significance of diseases to conservation of pelagic species can be inferred from such events as the epizootic infection and accompanying mass mortality of Swedish herring stocks in the fall of 1991 due to ichthyophonosis, which was estimated to have killed 300 million fish, or 10% of the population (Rahimian & Thulin 1996). Diseases introduced to wild populations by exogenous fishes are particularly virulent (Utter 1998). Moreover, the development of antibiotic resistance by farmed fish pathogens is widespread, and this drug resistance has proven transferable (e.g. Sorum 2000). The prevalence of a wide variety of fish diseases including skin lesions, hepatomas, carcinomas and papillomas, is known to be stimulated by environmental contaminants such as polynuclear aromatic hydrocarbons (PAHs: Lower & Kendall 1990; Weeks *et al.* 1990). Whales, too, suffer from a host of endemic diseases, especially parasitic infections, but there is no strong evidence that susceptibility to

pathogens is enhanced by pollution-driven immunosuppression (Lambertsen 1990).

### Chemical contaminants

Common synthetic pollutants in marine pelagic ecosystems include: organochlorine (OC) pesticides such as DDT, dieldrin and chlordanes; their metabolites such as DDE and DDD; and industrial pollutants such as polychlorinated biphenyls (PCBs) and hexachlorobenzene (HCB) (Ronald *et al.* 1984). Despite their ban in most developed nations and dramatic reductions in global production, their resistance to degradation and lipophilic properties have resulted in continuing biomagnification in food webs (Becker 2000). Cetaceans show poor metabolism of PCBs (Tanabe *et al.* 1988), and PCBs and DDT in particular have been associated with reproductive problems in marine mammals and therefore pose a potential risk (Reijnders 1980; Aguilar & Jover 1982; but see O'Shea & Brownell 1994), including in the endangered northern right whale (Woodley *et al.* 1991). OC concentrations are positively correlated with trophic level and inversely related to cetacean body size (Borrell 1993). Marine turtles, including the green turtle (*Chelonia mydas*), show elevated body burdens of OC pesticides and heavy metals, in some locations at concentrations sufficient to cause toxic effects in other vertebrates (Godley *et al.* 1999; McKenzie *et al.* 1999). However, attempts to document cause-effect relationships may be confounded by other anthropogenic effects (Addison 1989). PAHs also exert toxic effects on marine organisms at very low tissue concentrations. For example, PAHs cause reproductive failure, deformed larvae and precocious maturation among fish (Manahan 1990; Johnson *et al.* 1993; Collier *et al.* 1998), and occur in some coastal waters at concentrations sufficient to be of toxicological concern to ecosystem and human health (Deb *et al.* 2000). Moreover, contamination of open ocean waters by various marine pollutants may be just as severe as in coastal waters (Davis 1993).

Numerous chemical pollutants are thought to elicit their effects by disrupting normal hormone pathways, and large numbers and amounts of these endocrine disruptors have been released into the environment since World War II (Colborn *et al.* 1993). They act by either enhancing or interfering with the actions of natural hormone, endocrine, or immune systems within an organism. Since hormones are particularly important in regulating reproduction, and pre- and/or post-natal development, the effects of endocrine disruptors may be greatest on these processes (Palmer *et al.* 1998). Effects of exposure during development are permanent and irreversible, and risks can also occur after birth or hatching, or transgenerational exposure can produce susceptible offspring (Colborn *et al.* 1993). In fish, this may cause decreased fertility and egg production in females, and reduced gonad size or feminization of males (Arcand-Hoy & Benson 1998). Exposure to endocrine disrupting chemicals has also been associated with reduced fertility in seals (Reijnders 1986) and alteration of immune function in beluga whales (Martineua *et al.* 1988).

### Hydrocarbon exploration

Oil spills represent another category of concern for local marine pelagic ecosystems. The very few large spills (>600 tonnes) account for a high percentage of total oil spilled and therefore have the biggest pelagic ecosystem impact. For example, during 1990–1999, just 1% of the spills accounted for 75% of the spilled oil (ITOPF [International Tanker Owners Pollution Federation] 2001). Fortunately, these large events, on average, have been decreasing for the past 30 years. The *Exxon Valdez* spill, while only the 34th largest in recorded history, is widely considered to be the most environmentally and ecologically damaging spill ever. Approximately 250 000 sea birds, 2800 sea otters, 300 harbour seals, 22 killer whales, and untold billions of eggs and larvae belonging to salmon, herring and other fishes died (EVOSRP [*Exxon Valdez* Oil Spill Recovery Plan] 1999; Peterson 2001). Clearly such events can be locally devastating to all components of the ecosystem, both immediately and long-term: of the 23 species injured by the *Exxon Valdez* spill, only two had recovered 10 years later.

Offshore oil and gas mining poses a serious threat to marine turtles as exploration activities can destroy or seriously disrupt foraging and nesting habitats. Dredging not only destroys habitat, it also results in the incidental injuring or killing of sea turtles. Oil on the skin and shell of a marine turtle can affect respiration and salt gland functions, as well as the turtle's blood chemistry. Ingestion of tar pellets is also a major concern, as tar balls are the second most common type of ingested debris (e.g. NMFS/FWS [US Marine Fisheries Service/US Fish and Wildlife Service] 1992, 1998).

Among marine mammals, cetaceans appear most tolerant of oil exposure, and reports of kills from oil spills are rare and equivocal (Geraci 1990; Geraci & St Aubin 1990). In contrast, sea otters (*Enhydra lutris*) are very vulnerable because their life history and behaviour facilitate their exposure to spilled oil (Geraci & Williams 1990; Ralls & Siniff 1990). Polar bears (*Ursus maritimus*) and pinnipeds have intermediate vulnerability, especially seals when spills occur adjacent to breeding colonies (McLaren 1990; St Aubin 1990). Local extinction is possible in such cases, especially for already-endangered species with reduced abundances or isolated populations, e.g. Hawaiian (*Monachus schauinslandi*) and Mediterranean (*Monachus monachus*) monk seals, and Steller's sea lions (*Eumetopias jubatus*). However, it seems that current dangers of toxic contamination from OCs, heavy metals and oil are relatively small for pelagic open-water cetaceans, especially those that regularly migrate away from more contaminated sites and also feed low in the food web (O'Shea & Brownell 1994).

### Harmful algal blooms

Episodic harmful algal blooms (HABs) are natural events, but once considered to be rogue blooms, they are now commonplace (Smayda 1997a,b). What is new is their global spread,

raising considerable alarm and concern within the scientific community, commercial fisheries and aquacultural industries, and among public health officials (Smayda 1989, 1990; Hallegraeff 1993). Regions previously free from HABs now suffer such blooms, species previously benign have become toxic or nuisances, and in many regions, the frequency and intensity of HABs have been increasing (Smayda 1990; Hallegraeff 1993; Anderson 1995a). A significant global increase in die-offs of commercially and ecologically important finfish, shellfish, and mammals has accompanied the global surge of HABs (Brusle 1995; Reyero *et al.* 1999; Scholin *et al.* 2000; Table 3). Financial losses to commercial fisheries and associated industries sometimes exceed US\$ 100 million per bloom event. Diarrhetic shellfish poisoning (DSP) has now been found to occur in Japan, Europe, Chile, Thailand, Nova Scotia, and possibly Tasmania and New Zealand (Hallegraeff 1993). HABs and the phycotoxin responsible for paralytical shellfish poisoning (PSP) historically have been primarily phenomena of colder water, and their current proliferation in tropical and sub-tropical waters and increased outbreaks in temperate and boreal seas is ecologically profound. Increased toxic bloom frequency has also been reported from the Baltic Sea, North Sea, Adriatic Sea, Black Sea, South Africa, Hong Kong, Korea, and the Seto Inland Sea (Smayda 1989, 1990). HABs accompanied by human illness and death have apparently spread to regions previously devoid of such blooms, including Spain, Central and South America, Tasmania, New Guinea, Philippines, Indonesia and Thailand.

The habitat conditions driving the apparent global HAB expansion remain obscure, but six primary explanations have been advanced: (1) increased scientific awareness; (2) natural variation accompanying unusual climatological conditions; (3) a response to global warming; (4) stimulation by increased nutrient enrichment of coastal waters; (5) increased aquacultural and fish farm activities in coastal waters; and (6) dispersal of harmful species into new regions by ships' ballast water, or regional transplantation of shellfish stocks. All of these explanations are applicable to some degree, but none has been definitively established for a given region or bloom species. Different combinations of climatic and habitat conditions can induce HAB events, but two putative causative factors have received special attention, namely eutrophication of coastal waters and ballasted introductions of novel species. These are discussed further below.

### Eutrophication

There is experimental and circumstantial field evidence that dinoflagellates, which constitute the principal HAB species, have an ecophysiological requirement for nutrient-enriched water masses in order to bloom (Smayda 1997b), but many HAB events fall outside of this paradigm. This is not surprising, since at least nine different HAB life-form types with three different adaptive strategies have been identified (Smayda & Reynolds 2001). This variety may also reflect habitat modifications, such as through fishing and local

**Table 3** Some exceptional mortalities of natural populations associated with harmful algal blooms.

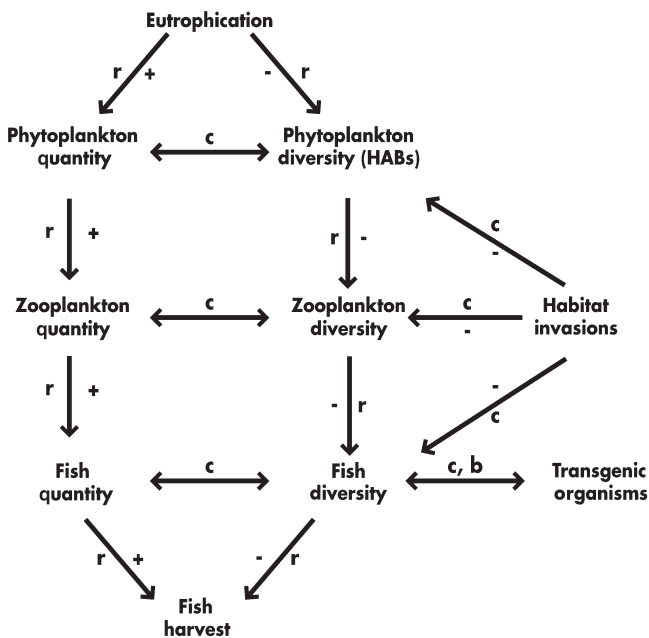
Community	Date	Location	Die-off magnitude	Harmful species	Source
Reef community	1971	Gulf of Mexico	'nearly complete extirpation'	<i>Karenia brevis</i>	Smith (1975)
Benthic community	1971	Tampa Bay	'17 of 22 most abundant species'	<i>Karenia brevis</i>	Roberts <i>et al.</i> (1979)
Surf clam ( <i>Spisula solidissima</i> )	1976	New York Bight	143 000 tonnes	<i>Ceratium tripos</i>	Mahoney & Steimle (1979)
Fish	1946–1947	Gulf of Mexico	$5 \times 10^8$ fish	<i>Karenia brevis</i>	Gunter <i>et al.</i> (1948)
	1986	Gulf of Mexico	$2 \times 10^7$ fish	<i>Karenia brevis</i>	White (1988)
	1991–1993	Pamlico Sound	$10^3$ – $10^9$ fish	<i>Pfiesteria piscicida</i>	Burkholder & Glasgow (1997)
Cod ( <i>Gadus morhua</i> )	1988	Skagerrak	1988 year-class eradicated	<i>Chrysochromulina polylepis</i>	Dahl <i>et al.</i> (1989)
Herring ( <i>Clupea harengus</i> )	1976; 1979	Bay of Fundy	'hundreds of tonnes'	<i>Alexandrium tamarense</i>	White (1988)
Black duck ( <i>Anas rubripes</i> )	1972	Massachusetts	1600	<i>Alexandrium tamarense</i>	Sasner <i>et al.</i> (1975)
Lesser scaup duck ( <i>Aythya affinis</i> )	1973–1974	Gulf of Mexico	12 000–20 000	<i>Karenia brevis</i>	Quick & Henderson (1974)
Eider duck ( <i>Somateria mollissima</i> )	1981	Kattegat	10 000	<i>Prorocentrum minimum</i>	Granéli <i>et al.</i> (1989)
Brandt's cormorant ( <i>Phalacrocorax penicillatus</i> ); brown pelican ( <i>Pelecanus occidentalis</i> )	1991	Monterey Bay	300	<i>Pseudo-nitzschia australis</i>	Work <i>et al.</i> (1993a, b)
Hawaiian monk seal ( <i>Monachus schauinslandi</i> )	1980	Laysan Island	'mass die-off'	ciguatoxic fish	Gilmartin (1987)
West Indian manatee ( <i>Trichechus manatus latirostris</i> )	1996	Florida	149 animals	<i>Karenia brevis</i>	Landsberg & Steidinger (1998)
Humpback whale ( <i>Megaptera noveangliae</i> )	1987	Cape Cod Bay	14 animals	PSP toxin	Geraci <i>et al.</i> (1989)
Sea lion ( <i>Zalophus californianus</i> )	1998	Monterey Bay region	>400 animals	<i>Pseudo-nitzschia australis</i>	Scholin <i>et al.</i> (2000)

edaphic and other provincial effects, particularly in nearshore habitats. The following, brief comparative ecological analysis of nutrient-enrichment effects in two major, eutrophicated inland seas reveals some general characteristics of excessive nutrient enrichment observed in more open coastal systems (Fig. 2).

The Black Sea, the largest eutrophicated ecosystem in the Mediterranean basin, has become progressively nutrient-enriched over several decades, fertilized by discharge of the heavily polluted Danube River, which delivers 70% of the total run-off into this sea (Cociasu *et al.* 1997). During this time, inorganic nitrogen concentrations have significantly increased and phosphorus and silicon have decreased. These conditions are thought to inhibit diatom-based fish food webs and to enhance flagellate-based jellyfish food webs (Officer & Ryther 1980; Ryther & Officer 1981). A diverse set of inter-linked ecosystem and habitat changes has accompanied this nutrient enrichment (Zaitsev & Alexandrov 1997). Between the 1960s and 1980s, phytoplankton abundance and the areal extent of blooms increased 10-fold, important changes in species composition occurred, water transparency decreased

by about half, the hypoxic (low oxygen) zone increased dramatically causing similarly dramatic die-offs of benthic animals, and populations of nuisance seaweed species increased; meanwhile herbivorous zooplankton populations became sparse and less biodiverse, and jellyfish abundance soared (Zaitsev 1992; Mutlu *et al.* 1994; Zaitsev & Alexandrov 1997; Gordina *et al.* 2001). These changes, which continue, were accompanied by the successful bioinvasion of non-indigenous species (Kovalev & Piontkovski 1998; Kideys *et al.* 2000). Other stresses including pollution, industrial wastes, oil spills and overfishing have significantly altered the ecology of the Black Sea, which may be a microcosm of changes to be expected in marine pelagic ecosystems elsewhere (Woodard 2000).

Many of the nutrient-stimulated responses reported for the Black Sea have also been found in the eastern North Sea, particularly in the German Bight and Dutch Wadden Sea (see Smayda 1989). Long-term increases in nutrient delivery and altered nutrient ratios induced by discharge of the Rhine, Weser and Elbe Rivers have been accompanied by increases in phytoplankton abundance and primary production, a shift from diatom to flagellate and jellyfish predominance, enhancement of the nuisance species *Phaeocystis*, and aperiodic hypoxic and anoxic events in the German Bight (Cadée 1986; Cadée & Hegeman 1986; Radach *et al.* 1990; Riegman *et al.* 1992).



**Figure 2** Two generic responses of a pelagic ecosystem to increased nutrient loading. In response to additional resources (r), the quantity of phytoplankton may change, typically increasing (+) in numbers and/or biomass, or the community composition may change often with negative (-) effects such as reduced diversity, e.g. development of harmful algal blooms (HABs). Shifts in abundance/biomass and diversity may alter competition (c) within the trophic level for resources with consequences for higher trophic levels. Similarly, zooplankton and fish may change in quantity or quality, altering resource distributions within and among trophic levels. Habitat invasions by novel taxa occur in all trophic levels and alter the balance of competition for resources and energy flows. Transgenic organisms represent a special case of habitat invasion through competition and breeding (b) with wild stocks.

### Habitat invasions

Hallegraeff and Bolch (1991, 1992) have championed the importance of ballast water introductions of novel species leading to subsequent HAB outbreaks and contributing to the global spreading of toxic species. Much of the supporting evidence rests on the behaviour of the PSP-producing dinoflagellate, *Gymnodinium catenatum*, the precipitous blooms of which in Tasmanian waters beginning in early 1970 prompted surveys of its resting cysts in dated sediment cores. The absence of fossil specimens in local strata deposited prior to 1970 prompted Hallegraeff and Fraga (1998) to speculate that ballast water was the source of inoculum triggering the observed blooms and persistence of *Gymnodinium catenatum*. While the ballast water theory as an explanation of the global expansion of HAB remains unproven, there is compelling evidence that invasions of alien species of pathogens, parasites, phyto- and zooplankton, macroalgae, benthic invertebrates, and vertebrates are now commonplace (Fig. 2), and often the result of rapid and repetitive trans-oceanic or regional dispersal via transit in ballast water or by shellfish transplantation (Ribera & Boudouresque 1995; Carlton 1996; Ruiz *et al.* 2000). Fish species accidentally or deliberately introduced by man, a process known since at least Roman times (Moyle 1986), represent another form of habitat invasion. Unlike freshwater and estuarine assemblages, marine fish communities rarely contain introduced species, although the striped bass and American shad are notable exceptions, one reason presum-

ably being the greater diversity of natural marine fish assemblages (Moyle 1986).

### Extinctions

In the absence of fortuitous circumstances or successful environmental conservation activities, the ultimate fate of threatened or endangered species is extinction. The sheer magnitude of the pelagic ecosystem and the incredible fecundity of fishes (often millions of eggs per female per spawning event) convinced early scientists and writers that man could not possibly exhaust such resources, much less cause extinctions (Lamarck 1809; Byron 1812; Huxley 1883). This argument even survived into the 20th century, albeit rather from the perspective of economics as much as catchability (Graham 1935; see discussion in Radovitch 1981; Woodard 2000).

However, a surprisingly large number of pelagic species are extinct or may imminently become so (Diamond 1984; Roberts & Hawkins 1999). The World Conservation Union (IUCN) Red List of species that are in varying degrees of imminent or future risk of extinction includes marine pelagic representatives in four groups. These are defined here as those animals which spend significant portions of their life cycle within pelagic waters either feeding on pelagic prey or on prey that are themselves pelagic feeders. Surface feeding and diving feathered seabirds are excluded. Among marine mammals (Table 4), three species are recognized as being extinct, four taxa are critically endangered, 14 taxa are endangered, and another 23 taxa are vulnerable to extinction (vulnerable species are not listed for brevity). Carlton *et al.* (1999) also consider the sea mink, *Mustela macrodan*, extinct. Amongst marine birds (Table 5), there are no known extinct or critically endangered species; three penguin species are

**Table 4** Marine mammals on the 2000 World Conservation Union Red List of extinct, critically endangered, or endangered organisms, with cause of extinction or current major threat(s). Definitions of threat types and listings of additional species or populations that are vulnerable to extinction are given in Hilton-Taylor (2000). Major categories of threats include: current or historic effects of direct exploitation (Exploit); declines in extent of occurrence, area of occupancy, or quality of habitat (Habitat Q/Q); declines in the number of locations or subpopulations (Subpop #s); decreases in the number of mature individuals (Mature #s); and the effects of introduced taxa, hybridization, pathogens, pollutants, parasites, or competitors (I/H/PPP/C).

Common name	Scientific name	Cause or threats				
		Exploit	Habitat Q/Q	Subpop #s	Mature #s	I/H/PPP/C
<i>Extinct</i>						
Caribbean monk seal	<i>Monachus tropicalis</i>	•				
Japanese sea lion	<i>Zalophus californianus</i> ssp. <i>japonicus</i>	•				
Steller's sea cow	<i>Hydrodamalis gigas</i>	•				
<i>Critically endangered</i>						
Bowhead whale	<i>Balaena mysticetus</i> (Svalbard-Barents Sea stock)				•	
Gray whale	<i>Eschrichtius robustus</i> (Asian or Northwest Pacific stock)				•	
Gulf of California porpoise	<i>Phocoena sinus</i>			•		
Mediterranean monk seal	<i>Monachus monachus</i>			•		•
<i>Endangered</i>						
Blue whale	<i>Balaenoptera musculus</i>	•				
Bowhead whale	<i>Balaena mysticetus</i> (Baffin Bay, Davis Strait stock)				•	
Bowhead whale	<i>Balaena mysticetus</i> (Okhotsk Sea subpopulation)				•	
Finless porpoise	<i>Neophocaena phocaenoides</i> (Yangtze River subpopulation)			•		
Grey seal	<i>Halichoerus grypus</i> (Northeast Atlantic subpopulation)				•	
Hawaiian monk seal	<i>Monachus schauinslandi</i>			•		
Hector's dolphin	<i>Cephalorhynchus hectori</i>	•			•	
Herring whale	<i>Balaenoptera physalus</i>	•				
Marine otter	<i>Lutra felina</i>	•	•			
Northern right whale	<i>Eubalaena glacialis</i>				•	
Pollack whale	<i>Balaenoptera borealis</i>	•				
Saimaa ringed seal	<i>Phoca hispida</i> ssp. <i>saimensis</i>		•		•	
Sea otter	<i>Enhydra lutris</i>		•			•
Steller's sea lion	<i>Eumetopias jubatus</i>	•				

endangered and seven others are vulnerable. Among marine reptiles (Table 6), none are known to be extinct, four taxa are critically endangered, three more species are endangered, and one iguana and two other turtles are vulnerable. Among coastal and pelagic marine fish (Table 7), three are extinct, 16 taxa are critically endangered, 24 more taxa are endangered, and up to 120 further taxa are vulnerable to extinction. In addition to the IUCN, other organizations and legislative acts address various categories of risk, e.g. for fish (Musick *et al.* 2000).

These data illustrate that the abundance of endangered marine mammals reflects a broad array of problems, but principally the effects of prior exploitation, which has left fragmented populations with relatively few mature individuals to maintain genetic diversity. Endangered penguins are also exposed to a broad array of problems. Turtles ubiquitously suffer from exploitation and loss of habitat quality and quantity, principally nesting beaches. The direct impact of human activities is clearly evident in the total of 180 species or populations of fish that are endangered or vulnerable, of which the vast majority have been overexploited and/or suffer from loss of habitat. It is becoming evident that the number of species of marine mammals, turtles, and fish in

which abundances are now severely depressed appears to be unprecedented in human history (Carlton *et al.* 1999).

**The open north-east Atlantic Ocean: a case study**

Open ocean waters far from shore are typically less affected by human activities, although important exceptions do occur, such as the global scale of historical whaling activities and the current global distributions of recalcitrant synthetic chemical contaminants. However, the human population is expected to continue expanding, thereby placing increased burdens on living and non-living resources further away from land, which will increase impacts associated with commerce, trade, and transportation. Situated between the industrialized USA and Western Europe, the open waters of the north-east Atlantic are likely to be the first to be more heavily impacted (OSPAR [Commission for the Protection of the Marine Environment of the North-east Atlantic] 2000).

Of 19 specific types of anthropogenic impacts, only six require any substantive degree of current concern (OSPAR 2000). Fisheries (high level of concern) show clear evidence of impacts on some but not all targeted species, and special attention was recommended for deepwater fishes, which have

**Table 5** Marine birds on the 2000 World Conservation Union Red List of endangered organisms, with current major threat(s). There are no extinct or critically endangered species on the Red List. Definitions of threat types and listings of additional species or populations that are vulnerable to extinction are given in Hilton-Taylor (2000). Major categories of threats include: current or historic effects of direct exploitation (Exploit); declines in extent of occurrence, area of occupancy, or quality of habitat (Habitat Q/Q); declines in the number of locations or subpopulations (Subpop #s); decreases in the number of mature individuals (Mature #s); and the effects of introduced taxa, hybridization, pathogens, pollutants, parasites, or competitors (I/H/PPP/C).

Common name	Scientific name	Cause or threats				
		Exploit	Habitat Q/Q	Subpop #s	Mature #s	I/H/PPP/C
<i>Endangered</i>						
Erect-crested penguin	<i>Eudyptes sclateri</i>		•	•	•	
Galápagos penguin	<i>Spheniscus mendiculus</i>	•		•	•	•
Yellow-eyed penguin	<i>Megadyptes antipodes</i>		•		•	

**Table 6** Marine reptiles on the 2000 World Conservation Union Red List of critically endangered, or endangered organisms, with current major threat(s). There are no extinct species on the Red List. Definitions of threat types and listings of additional species or populations that are vulnerable to extinction are given in Hilton-Taylor (2000). Major categories of threats include: current or historic effects of direct exploitation (Exploit); declines in extent of occurrence, area of occupancy, or quality of habitat (Habitat Q/Q); declines in the number of locations or subpopulations (Subpop #s); decreases in the number of mature individuals (Mature #s); and the effects of introduced taxa, hybridization, pathogens, pollutants, parasites, or competitors (I/H/PPP/C).

Common name	Scientific name	Cause or threats				
		Exploit	Habitat Q/Q	Subpop #s	Mature #s	I/H/PPP/C
<i>Critically endangered</i>						
Green turtle	<i>Chelonia mydas</i> (Mediterranean subpopulation)	•	•		•	•
Hawksbill turtle	<i>Eretmochelys imbricata</i>	•	•			
Kemp's ridley turtle	<i>Lepidochelys kempfi</i>	•	•			
Leatherback turtle	<i>Dermochelys coriacea</i>	•	•			
<i>Endangered</i>						
Green turtle	<i>Chelonia mydas</i>	•	•			•
Loggerhead turtle	<i>Caretta caretta</i>	•	•			
Olive ridley turtle	<i>Lepidochelys olivacea</i>	•	•			

**Table 7** List of coastal and open sea fish on the 2000 World Conservation Union Red List of extinct, critically endangered, or endangered organisms, with cause of extinction or current major threat(s). Definitions of threat types and listings of additional species or populations that are vulnerable to extinction are given in Hilton-Taylor (2000). Major categories of threats include: current or historic effects of direct exploitation (Exploit); declines in extent of occurrence, area of occupancy, or quality of habitat (Habitat Q/Q); declines in the number of locations or subpopulations (Subpop #s); decreases in the number of mature individuals (Mature #s); and the effects of introduced taxa, hybridization, pathogens, pollutants, parasites, or competitors (I/H/PPP/C).

Common name	Scientific name	Cause or threats				
		Exploit	Habitat Q/Q	Subpop #s	Mature #s	I/H/PPP/C
<i>Extinct</i>						
Beluga	<i>Huso huso</i> (Adriatic Sea stock)	•				
New Zealand Grayling	<i>Prototroctes oxyrhynchus</i>	•				
Ship Sturgeon	<i>Acipenser nudiiventris</i> (Aral Sea stock)	•				
<i>Critically endangered</i>						
Albacore tuna	<i>Thunnus alalunga</i> (South Atlantic stock)	•				
Boccacio rockfish	<i>Sebastes paucispinus</i>	•		•		
Brazilian guitarfish	<i>Rhinobatos horkeli</i>	•				
Coelacanth	<i>Latimeria chalumnae</i>	•	•	•		
Giant sea bass	<i>Stereolepis gigas</i>	•				
Jewfish	<i>Epinephelus itajara</i>	•				
Largetooth sawfish	<i>Pristis perotteti</i>	•	•			
Northern bluefin tuna	<i>Thunnus thynnus</i> (Western Atlantic stock)	•				
Skulpin	<i>Physiculus helenaensis</i>			•		
Southern bluefin tuna	<i>Thunnus maccoyii</i>	•				
Speckled hind	<i>Epinephelus drummondhayi</i>	•				
Spotted handfish	<i>Brachionichthys hirsutus</i>		•			•
St Helena dragonet	<i>Callionymus sanctaehclenae</i>			•		
Totoaba	<i>Totoaba macdonaldi</i>	•	•		•	•
Warsaw grouper	<i>Epinephelus nigritus</i>	•				
Wide sawfish	<i>Pristis pectinata</i> (N and SW Atlantic subpopulation)	•	•			
<i>Endangered</i>						
Angular angel shark	<i>Squatina guggenheim</i> (Brazilian subpopulation)	•				
Atlantic halibut	<i>Hippoglossus hippoglossus</i>	•				
Basking shark	<i>Cetorhinus maximus</i> (North Pacific)	•				
Bigeye tuna	<i>Thunnus obesus</i> (Pacific stock)	•				
Borneo shark	<i>Carcharhinus borneensis</i>			•		
Brownstriped grunt	<i>Anisotremus moricandi</i>		•			
Common sawfish	<i>Pristis pristis</i>	•	•			
Common skate	<i>Dipturus batis</i>	•	•			
Delta smelt	<i>Hypomesus transpacificus</i>		•	•		
Green sawfish	<i>Pristis zijsron</i>	•	•			
Knifetooth sawfish	<i>Anoxypristis cuspidata</i>	•	•			•
Monterrey spanish mackerel	<i>Scomberomorus concolo</i>		•			
Nassau grouper	<i>Epinephelus striatus</i>	•				
New Grenada sea catfish	<i>Arius bonillai</i>		•	•		
Pincushion ray	<i>Urogymnus ukpam</i>		•	•		
Port Davey skate	<i>Raja</i> sp.		•			
Queensland sawfish	<i>Pristis clavata</i>	•	•			
Red porgy	<i>Pagrus pagrus</i>	•				
Redfish	<i>Sebastes fasciatus</i>	•				
Saint Lucia mullet	<i>Liza luciae</i>		•			
Shortspine thornyhead	<i>Sebastolobus alascanus</i>	•				
Smoothback angel shark	<i>Squatina occulta</i>	•				
Speartooth shark	<i>Glyphis glyphis</i>			•		
Swordfish	<i>Xiphias gladius</i> (North Atlantic stock)	•				
Whitefin topeshark	<i>Hemirhamphus leucoperiptera</i>		•	•	•	

slow growth, low fecundities, are at the end of long food webs, and therefore are especially vulnerable to overexploitation. Significant habitat changes (high/medium level of concern) are those induced by fishing activities and industrial exploitation, and are essentially benthic impacts. Hydrocarbons such as tarballs, which have important but limited ecological consequences, and radionuclides, which disperse within biota, are thought to be of moderate concern. Tributyltin is a problem in localized nearshore waters, while litter, especially discarded plastics, can negatively affect charismatic macrofauna; both are rated in OSPAR (2000) as medium/low concerns.

In general, ecosystem health in north-east Atlantic open waters has not yet been seriously compromised, although chemical contamination is widespread, albeit at lower levels than in nearshore waters (OSPAR 2000). There is no evidence that biological productivity has been altered, biodiversity reduced, or trophic function impaired. However, temporal and spatial scales of physical, chemical, and biological processes in open ocean waters are so variable that discrimination of trends due to anthropogenic impacts from natural variability is extremely challenging. Some of the uncertainties in data on physical processes which impact the status of the pelagic ecosystem include how circulation patterns will respond to climate change, how to predict those changes, and how those changes will impact chemical and biological processes. Uncertainties in ocean chemistry which affect ecosystem structure and function include poor baseline data needed to recognize long-term changes in contaminants, inadequate data concerning effects on biota of chronic exposure to low contaminant levels, poor knowledge of impacts of endocrine and hormonal disrupters, and insufficient understanding of links and transformations between chemical parameters and living organisms. Uncertainties in biological data include the life cycles and factors regulating most keystone species, how to discern anthropogenically-induced changes from natural trends, the structure and dynamics of deepwater food webs, the impacts of removing top predators, and conceptual and quantitative links between species composition, productivity, and ecosystem function. It is salient that many of the gaps in scientific understanding noted for the north-east Atlantic are broadly applicable to marine pelagic ecosystems globally.

## PERSPECTIVES AND REVISED PARADIGMS FOR THE FUTURE

### The need for expanded perspective

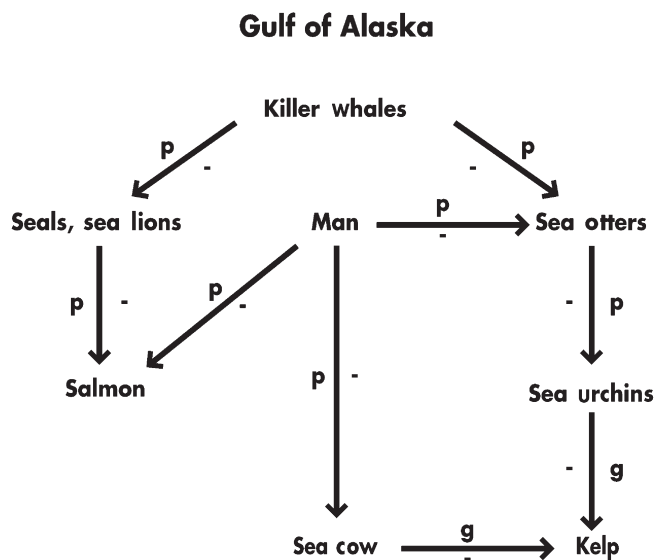
Why are there currently so many diverse ecological problems in the marine pelagic ecosystem? Why can science not advise before, or at least when, humanity begins to overexploit or otherwise challenge this ecosystem? It is proposed here that a new conceptual framework is required around which to organize future research, data interpretation, and diagnostic prediction. A central theme of the present argument is that it

is essential to distinguish on the one hand between factors affecting production and standing stocks, in which the nature, type, and amount of resources may be essential, and on the other hand factors affecting time/space distributions, diversity, community composition, and energy transfer, in which predation, morphology, and life cycles may be more influential. For example, Polis (1999) argued that the need for limiting resources is sufficiently stringent that it explains most of the variability in global patterns of food web structure and function. From this perspective, the oceans are 'blue' because of relatively severe nutrient limitation. However, it is significant that a century of interpreting marine pelagic food webs from this resource perspective alone has resulted in inadequate understanding and poor predictability.

### Predation as a selective principle

While predation is considered important in structuring benthic communities (Dayton 1985; Wootton 1994), comparatively little attention has been given to the possibility that predation (hereafter, one organism eating another, independent of trophic level) might be important in structuring pelagic ecosystems. Trophic cascades, in which predators regulate lower food web components, result in inverse patterns in abundance or biomass across more than one trophic link in a food web (Pace *et al.* 1999). Evidence is accumulating that consumer control of prey biomass does occur in marine pelagic ecosystems, whether as carnivores predating herbivores or herbivores grazing phytoplankton, or true multi-tier cascades (see Verity & Smetacek 1996). Examples of top-down control of marine pelagic community structure have been reported from the largest predators to the smallest plankton (van der Elst 1979; Parsons & Kessler 1987; Reckermann & Veldhuis 1997; Durbin & Durbin 1998). At regional scales, the spatial distributions of putative predators and prey have been shown to mirror one another, as observed between euphausiid and phytoplankton biomass in the Benguela upwelling system (Pillar *et al.* 1992), and anchovy and zooplankton biomass in the Peru upwelling ecosystem (Cushing 1971). At basin-wide scales, decadal patterns in pink salmon, macrozooplankton, and phytoplankton in the subarctic North Pacific suggest predatory control of plankton biomass in the form of a classic cascade (Shiomoto *et al.* 1997). Cascades are also commonplace in certain types of benthic marine ecosystems (Pinnegar *et al.* 2001).

With direct human intervention in pelagic food webs at an all-time high, it might not be surprising that human activities might indirectly interact with natural processes. For example, killer whales in the Gulf of Alaska have recently begun to prey significantly on sea otters, and the pattern of changes in otter, sea urchin and kelp abundance matches that predicted by cascade theory (Estes *et al.* 1998). It is proposed that killer whales switched their diet to otters, which have not previously been traditional prey, because of reductions in killer whales' typical prey, seals



**Figure 3** A flow chart of the direct and indirect effects of human fishing activities in the Gulf of Alaska. Killer whales typically prey (p) on seals and sea lions, which prey on salmon. Human overexploitation of salmon resources negatively impacts seal/sea lion populations, thereby reducing prey availability for killer whales, which switch to feeding on sea otters. Under normal ecosystem conditions, the latter keep sea urchin populations under control, thereby stimulating development of kelp beds. Killer whale removal of otters causes a trophic cascade whereby sea urchins are released from grazer control and subsequently denude kelp beds. In historical times, human hunting of sea otters may have caused a cascade similar to that currently induced by killer whales. The resulting removal of kelp by urchins eliminated the major food resource for sea cows, thus facilitating their extinction by human hunting. After Anderson (1995b) and Estes *et al.* (1998).

and sea lions, caused by fishery exploitation of their prey (salmon). Thus the indirect effects of one predation-structured food web, namely humans–salmon–seals/sea lions, may have induced a trophic cascade in another food web, namely killer whales–otters–urchins–kelp (Fig. 3). It may also be that human exploitation of a trophic cascade increased the rate of extinction of another member of the coastal North Pacific ecosystem, Steller's sea cow (Anderson 1995b). Sea cows, which long ago lost the ability to submerge, became dependent on shallow-water macrophytes that only occur in areas where sea otter predation limits urchin overgrazing of kelp. Historically, shorelines barren of kelps are correlated with aboriginal settlements around which they hunted otters (Simenstad *et al.* 1978). The theory is that aboriginal hunters decimated sea otters, which caused sea urchin population explosions and subsequent denuding of kelp forests, and thus destroyed sea cow foraging habitats (Anderson 1995b). Subsequent hunting of sea cows by Europeans then quickly exterminated the species.

Such data illustrate that the occurrence of key species or trophic groups, which are simultaneously capable of nearly

complete harvest of prey organisms but which are also unusually susceptible to rapid and efficient capture by their own predators, fundamentally influences food webs (Mills *et al.* 1993; Menge *et al.* 1994). In fresh water, the life history of *Daphnia* includes a reproductive strategy designed for rapid colonization and export to new environments, and also a motility pattern fatal in the presence of visual predators (Jurgens 1994). In marine waters, gelatinous zooplankton may play a similar role, although changes in their population abundance may reflect rapid starvation as well as predation (Mountford 1980; Ishii & Bamstedt 1998). However, it is intriguing that the predators often common in marine cascades (gelatinous zooplankton) are essentially absent from fresh water, where cascades have been more commonly described, while the cladocerans typically linked to freshwater cascades are unimportant in marine waters (Greene 1985; Lehman 1988). Verity and Smetacek (1996) discuss other examples of key species or trophic engineers (*sensu* Lawton & Jones 1995), the morphologies and life histories of which result in their contributing the bulk of biogenic fluxes or fish production in specific ecosystems.

#### Pelagic morphology: food acquisition or predator avoidance?

Consideration of zooplankton and fish morphology also supports the notion that predation significantly influences the structure of marine pelagic ecosystems. For example, oceanic zooplankton are extremely widespread and have an extraordinary long history of evolutionary continuity, but the dominant species of copepods, euphausiids, pteropods and chaetognaths that contribute the bulk of the biomass, include only a few morphotypes (Boltovskoy 1999). The variety of morphotypes within dominant benthic groups, such as amphipods, decapods, gastropods, polychaetes, bivalves and corals, and also exhibited by meroplanktonic larvae, contrasts so strikingly with the paucity of shapes among holoplankton that happenstance can no longer be invoked. Rather, it seems that dominant status in the ocean's pelagial can only be attained within a restricted range of morphotypes. A similar hypothesis was proposed for phytoplankton because surface area:volume ratios of dominant taxa fluctuate considerably less than is geometrically feasible (Lewis 1976).

Among fish, the sleek, streamlined form of the dominant epipelagic fish is, like zooplankton, maintained over the size spectrum from anchovies to tuna. The bodies of these fish consist largely of flight muscle, with a correspondingly lesser investment in tissue dedicated to normal swimming (Bone 1978; Driedzic & Hochachka 1978). As in the case of copepods, fish morphology becomes more diverse wherever the environment offers protection from visual predators, from the myriad shapes of deepsea fish to the effective camouflage of surface-living *Sargassum* fish. Thus, escape from predators and not resource acquisition appears to be the major factor constraining morphotype of epipelagic fishes. This may also explain why gelatinous zooplankton are not a staple food of the commercially important fish; feeding on them inevitably

requires large gut volume that critically reduces escape speed. Freed from the need to escape from attacking predators, gelatinous zooplankton exhibit a much wider range of shapes than their muscular counterparts (Verity & Smetacek 1996). Koehl (1996) provides other examples of how the performance characteristics of pelagic organisms are linked via morphology to their fitness and ecological roles.

### Evolution within the marine pelagic ecosystem

From this perspective, an essential goal of pelagic life cycles is to reduce mortality of the genome. If organisms successfully divert 10% of their resources from growth to defence, population accumulation rates will be identical, but net productivity, energy transfer and nutrient regeneration will be reduced (Jurgens & Gude 1994).

Iron-limited diatoms make thicker frustules with as much as three times more silicate than cells which are not iron-limited (Queguiner *et al.* 1997), apparently because internal silicate deposition is metabolically inexpensive (Raven 1983) and is not inhibited by iron availability (Hutchins & Bruland 1998; Takeda 1998). While compelling arguments can be made that diatom frustules may function to impede parasitoids and viruses (Smetacek 1999), whether thicker frustules reduce grazing by metazoans is unknown. However, the biogeochemical impact is clearly evident: the Antarctic Circumpolar Current, where thick-shelled diatoms predominate (Smetacek 1999), is currently the major burial site of silicate in the global ocean (Treguer *et al.* 1995). The thickest frustules coincide with the lowest ambient Si:N ratios, because the last dissolved silicate goes into making thicker frustules. The elevated sedimentary accumulation can only occur if diatoms are not eaten in the same proportion of their production as occurs elsewhere in the ocean. These considerations suggest that trying to understand marine pelagic ecosystems, succession, or ocean biogeochemistry from a perspective limited to competition for resources is futile. Competitors that are less vulnerable to predation, through morphological, chemical, behavioural, or life history defences, should be highly favoured by natural selection, and therefore common in nature (Grover 1989).

Such relationships between predator and prey do not develop overnight: marine pelagic life cycles, behaviours and morphologies have evolved to be independent of proximate factors. Evolution shapes organisms through predator-prey arms races. In eutrophic aquatic systems, organisms that are competitive can overwhelm their predators with biomass (Ryther 1954). But since the ability to assimilate and sequester resources in the marine pelagial is restricted, evolution among the plankton has led to enhanced defence systems. Likewise the great proliferation of feeding types within the omni- and herbivorous protists reflects their evolution in response to prey defences (Geider *et al.* 2001). This evolution can be quite rapid, as in *Daphnia* evolving genotypes resistant to toxic cyanobacteria in merely one decade (Hairston *et al.* 1999). Elegant arguments have been

marshalled that top-down effects are not only important in the modern pelagial, but were also critical throughout the history of evolution of plankton and are responsible for patterns of paleobiogeochemistry (Vermeij 1990; Morris 1993; Signor & Vermeij 1994; Logan *et al.* 1995; Rigby & Milsom 1996; Butterfield 1997).

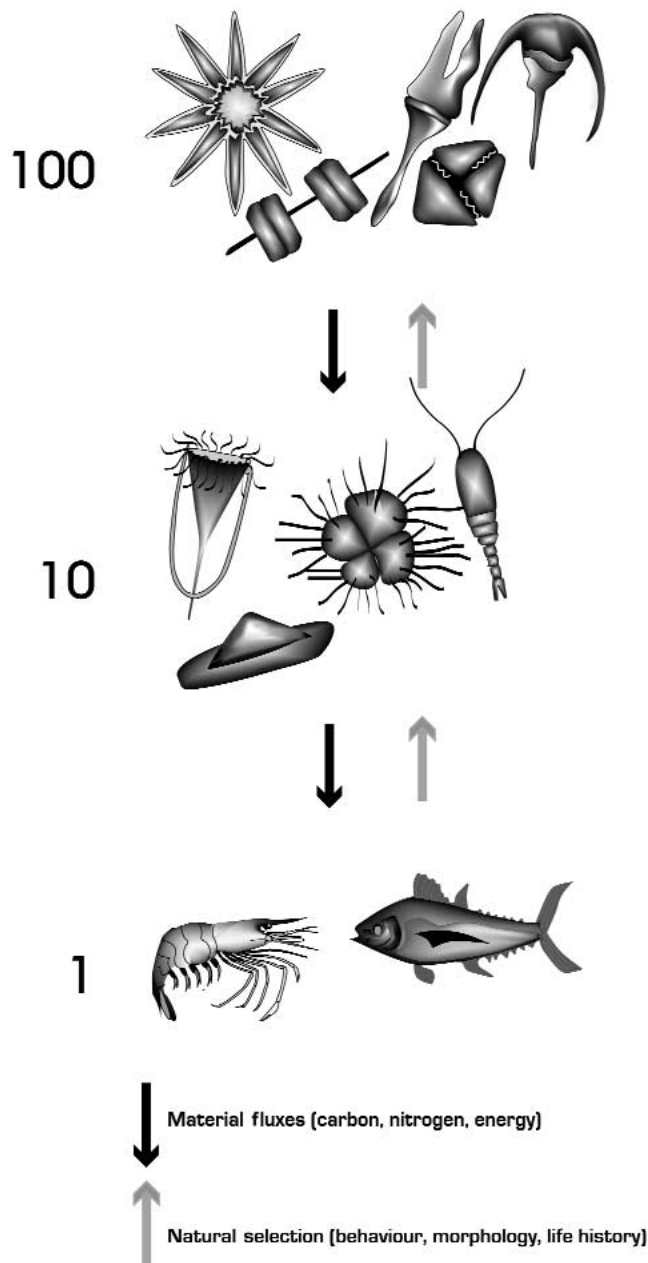
Flagellates evolved long before diatoms and larger plankton, at a time when protozoans and medusae were abundant herbivores and carnivores (Parsons 1979), thus establishing an evolutionary link between flagellates and the gelatinous predators associated with marine pelagic trophic cascades. Only much later, when diatoms evolved in apparent response to silicate infusions derived from Triassic volcanic activity (Maldonado *et al.* 1999), did crustacean zooplankton such as copepods and euphausiids, and eventually large fish and mammalian planktivores, proliferate (Parsons 1979; Rigby & Milsom 2000); this is the food chain traditionally linked to bottom-up control and the great fisheries. Evolutionarily-old food chains of flagellates and gelatinous zooplankton tend to dominate in systems driven by regenerated nutrients, while more evolutionarily-recent food chains of diatoms and fisheries are more important in systems with significant inputs of new nutrients.

It seems that whatever characteristics or events determine key species, morphologies, or life histories also dictate the extent to which pelagic ecosystem structure is regulated from above or below. The evidence is increasing that plants and animals in the sea dedicate considerable resources to prevent being eaten: there is much to learn from their defences and the consequences of those evolutionary manifestations. While it is clear that energy and materials flow up from the base of the food web and that quantitative knowledge of this process is essential, natural selection operates on organisms from both directions (Fig. 4). The structure of the marine pelagic ecosystem, and hence its function and response to perturbations, must therefore be interpreted from a conceptual model which incorporates both perspectives.

### TOWARDS UNDERSTANDING AND PREDICTION

A revised approach to interpreting marine pelagic ecosystems is clearly needed because a century of applying the current terrestrially-derived conceptual model has not led to a significant level of understanding or predictability of ecosystem structure or function. Without revision, limited progress is to be expected in the next 100 years. While a few examples of revision can be found which indicate a top-down concept of food webs (e.g. Christiansen & Pauly 1993), the problem is that changing the paradigm about marine pelagic ecosystems will take time to implement. In the meantime, it seems quite likely that the ecosystem will continue along its anthropogenically-induced trajectory, and several potential impacts may occur by 2025.

In an economic sense and perhaps in due recognition of our higher moral ground as the potential keeper or reaper of the diversity of life on this planet, man is clearly the top



**Figure 4** Simplified conceptual model incorporating the proposed dual components of evolutionary selective pressures that structure marine pelagic ecosystems. Left-hand side: competition for resources or bottom-up regulation, which determines the raw magnitude of material fluxes through food webs. A hypothetical food web with three trophic levels might have 100 units of phytoplankton production, which supports 10 units of zooplankton production, which supports 1 unit of fish yield. Right-hand side: predation pressure or top-down regulation determines the species composition, size structure, morphology, behaviour, and life history attributes of organisms at each trophic level. This structure feeds back to determine the actual magnitude of the material fluxes. The feedback is not in steady-state, as the risks to find food and the need to avoid being eaten oscillate according to environmental controls.

predator in the ocean. Will the propensity for overharvesting of fish stocks cause additional changes at related or lower trophic levels that might be unwanted or unintended, i.e. accidental biomanipulation? *Homo sapiens* has apparently done this on land in the past (Diamond 1989; Wilson 1992; Steadman 1995). In North America, megafaunal removal may have indirectly altered the landscape from grasslands to forests, which in turn impacted local climate patterns. The relative roles of changing climate and human activities as the major source for historic extinctions are debated (Martin & Klein 1984; Stuart 1991), but humans continue to change the earth's biota directly (Phillips & Gentry 1994; Vitousek *et al.* 1997; Polis 1999), and the ultimate change, extinction, is occurring today in probably all habitats, including the marine pelagic ecosystem (Wilson 1992).

The global stock sizes of blue whales (*Balaenoptera musculus*) and especially right whales may now be too low to maintain genetic variability and sustain viable reproducing species (Schaeff *et al.* 1997; MPB [Marine Pollution Bulletin News] 1999). The same may be true of the Saharan population of Mediterranean monk seals (Forcada *et al.* 1999), subpopulations of which appear to be non-viable in the long term or to have a high risk of extinction (Durant & Harwood 1992; Harwood *et al.* 1998). The Caribbean monk seal is currently considered to be extinct, following a century of decline accompanied by high population fragmentation (Boyd & Stanfield 1998). The Hawaiian monk seal has witnessed dramatic declines in recent decades and its short-term recovery is doubtful (Gilmartin & Eberhardt 1995). While the outlook for monk seals is not optimistic, other seals have shown superior resilience. After hundreds of years of sealing, Antarctic fur seals (*Arctocephalus gazella*) recovered from populations of only dozens in the 1930s to hundreds of thousands 40 years later (Payne 1979). Northern elephant seals (*Mirounga angustirostris*) on Guadeloupe Island were similarly decimated by the end of the 19th century, but 100 years later their population was estimated at 127 000 animals (Stewart *et al.* 1994).

### Exploitation

Continued regional overharvesting can be expected as long as science, legislation, culture and technology cannot be moulded into effective and fair policy (Longhurst 1999). Some resource stocks appear to recover quickly under favourable conditions when given a reprieve from harvest pressure, such as Barents Sea cod, while other stocks take surprisingly long, for example Georges Bank cod stocks (Myers *et al.* 1996). The ability to establish the population of origin for individual fish may prove invaluable in maximizing sustainable exploitation (Nielsen *et al.* 2001), however there is little evidence for rapid recovery from large population reductions (Hutchings 2000, 2001). This suggests that, from fisheries management or conservation perspectives, assignment of extinction risk for marine fish should be no different from that of other animals. In the future, it may become

necessary to consider general solutions, for example resources determining human exploitation instead of the converse (Ludwig *et al.* 1993), as well as specific solutions, such as widespread protected areas (Goñi *et al.* 2000). Again, a problem is that there is no synthetic understanding of processes influencing the natural operation of the marine pelagic ecosystem.

The effects of overfishing are diverse and complex; indirect effects can be particularly devastating, for example, drastic reductions in porpoises by tuna and salmon drift/gill-net fisheries, and incidental catch of hatchling, juvenile and adult turtles (Dayton *et al.* 1995). The impact of by-catch is particularly vexing, as it affects fisheries management, conservation, and economics and sociology of fishing (Hall *et al.* 2000; Musick *et al.* 2000). Projections of world fish demand are increasing (FAO 1997) but fisheries yield is expected to remain constant (IPCC 1996). In the 1980s, harvesting of Southern Ocean krill, the annual production of which is estimated to easily exceed the global catch of all fisheries (Nicol & de la Mare 1993), was proposed to solve global protein needs, but processing the catch in such a remote environment has proved challenging. There is need for aquaculture to take pressure off fisheries, but if fisheries yield remains constant (an optimistic perspective) then aquaculture production must double by 2010, which actually may be feasible since global production of farmed fish, shellfish and its contribution to world fish supplies, doubled from 1987 to 1997 (FAO 1997; Naylor *et al.* 2000). However, mass culture of marine taxa which feed high up in the food web may not be a viable, long-term solution (Naylor *et al.* 2000).

### Harmful algal blooms and habitat invasions

The incidence, frequency, duration, and geographic coverage of HABs can be expected to increase worldwide (Smayda 1990; Hallegraeff 1993). Similarly, increased frequency and ultimately adverse impacts of species invasions can be expected in the pelagic ecosystems of coastal waters and isolated seas (Carlton 1999) because international commerce using ocean trade routes continues to increase yearly. Ship-mediated transport of non-indigenous species from Europe to the USA is thought to have started 400 years ago (Fofonoff *et al.* 1999). Some of these introductions may have little if any impact on the regional pelagic ecosystem. Others may cause temporary or long-term changes in ecosystem function, as has the invasion of the Black Sea by the ctenophore *Mnemiopsis leidyi* (Zaitsev 1992), which was probably introduced with ballast water (Shiganova 1997; Niermann & Greve 1997) and is implicated in the sudden decline in zooplankton abundance and collapse of the anchovy fishery (Zaitsev 1992; Möller 1984; Kideys *et al.* 2000), although these are linked to eutrophication. A similar eutrophication sequence in the upper Gulf of Mexico now coincides with massive blooms of a large jellyfish transported from Australia (Graham *et al.* 2001).

The most adverse impacts will occur if the invading

species is toxic or supplants a naturally established keystone species and thereby rearranges ecosystem structure and function. Alien species may cause ecosystem changes disproportionate to their biomass, and invaders are most likely to be successful if the new ecosystem does not have the control processes in place which kept the invader in check in its original environment (Power *et al.* 1996). Ironically, much of the knowledge about keystone species, trophic cascades, and top-down effects is derived from anthropogenically-induced natural experiments, such as the overexploitation of walleye pollock (Springer 1992), sea otters (Estes *et al.* 1978), and baleen whales (May *et al.* 1979). Unfortunately, current ignorance of keystone species, including an inability to objectively define them and to quantify the complexity of their ecological interactions (Mills *et al.* 1993), mitigates against use of the concept of either keystone species or indicator species (Landres *et al.* 1988) from the perspective of environmental conservation (Power *et al.* 1996). This is because keystone organisms derive that status from their individual properties but also the physical and chemical environment and the other species in the ecosystem.

A major developing ecological issue is how the disrupted, indigenous communities accommodate such species invasions. Does the species fill an open niche, or does it successfully outcompete an indigenous species and assume its niche? How are community dynamics and trophic processes modified? Must a new equilibrium be established? Does the altered community structure come into a new equilibrium of predator-prey relationships favourable to energy transfer among the plankton, benthic and nekton components making up the food web, or does the disrupted community and food web structure lack resiliency to offset such disruptive perturbations? These are fundamental issues that will become increasingly problematic in the decades ahead, and will compromise efforts towards quantitative modelling and prediction of biological oceanographic processes and, where desired, mitigation of less desirable effects and change. The great difficulty expected to increasingly compromise future plankton and trophodynamic investigations is the growing, globally-experienced confluences of bioinvasions, eutrophication of coastal waters, overfishing, and climate change effects which are collectively impinging upon, modifying and regulating plankton processes, blooms and food web behaviour (Fig. 2). The intense anthropogenic modification of the oceanic habitat and trophic structure clearly has evolutionary consequences, and is blurring the 'normal', evolutionarily acquired 'natural processes'. These disruptions may be masking actual baseline conditions. Given the increasing need for quantitative, planetary-based ecological theory and management, the great dilemma of future investigators will be to sort out the effects of these sometimes synergistic, sometimes antagonistic anthropogenic disruptions. A pessimistic view is that this challenge will be further compromised by a major and intrinsic difficulty faced by biological oceanographers, namely their ability to carry out meaningful ecological experiments using natural assemblages, with suit-

able controls. Unless this is achieved, the anticipated, future pressures to apply engineering solutions (whether genetically or via habitat modification) to contravene undesirable anthropogenic assaults and biotic shifts will suffer a high level of uncertainty, both with regard to the causes of the undesirable disruptions and degradations, and desired corrected behaviour.

### Transgenic organisms

A category of habitat invasion that has received considerable recent attention is the potential impact of genetically-altered organisms either accidentally or intentionally released to the wild. Transgenic technology is being used to grow larger fish in shorter times and, because growth hormone genes are now well known, their sequences have been implanted in several popular freshwater fish and at least one marine fish, the Atlantic salmon (Rokkones *et al.* 1989; Kapuscinski & Hallerman 1990). A decade ago, at least 22 laboratories were pursuing research on transgenic fish (Hallerman & Kapuscinski 1990), and that number has almost certainly increased considerably, as transgenic strains were being developed for some 35 species of fish in 1999 (Reichhardt 2000). Agencies with jurisdiction over aquaculture, mariculture, and specific natural ecosystems will undoubtedly receive an increasing number of requests to release transgenic fish to the marine environment, especially given the rapidly-growing fish farming industry, including salmon breeding programmes (Gjoen & Bentsen 1997) and commercial netpens in Norway and elsewhere (McGinnity *et al.* 1997; Aarset 1998 and references therein).

In general, the ecological risks associated with transgenic organisms are not unlike those of invading or introduced species, but because larger body size often confers enhanced fitness in competitive interactions and in fecundity (Valiela 1995), transgenic fish have the potential to outcompete their wild conspecifics in nature via the same mechanisms of domination of native fish by introduced species, through predation, interference, reproductive inhibition, and hybridization (Moyle *et al.* 1986). Behavioural changes might include migrations, habitat selection, territoriality, and mate selection (Kapuscinski & Hallerman 1990). Other potential changes might include susceptibility to diseases and pathogens, reduced survival as larvae or juveniles, novel host-parasite relationships and vectors, exacerbations or introduction of pests, negative impacts on species with similar niches, and widespread food web alterations (Tiedje *et al.* 1989; Kent 2000; Fig. 2). However, while these individual potential effects can be studied in controlled environments, the complexity of their interactions, the likely indirect effects, and the expected time lags all conspire to make prediction of the ecosystem effects of transgenic fish very difficult. Accordingly, public policies and regulations governing distribution and use of transgenic marine organisms should be ecologically conservative and carefully framed within a quantitative analysis of the environmental risks

based upon fundamental principles of pelagic ecology (Hallerman & Kapuscinski 1990; Thompson *et al.* 1995). Otherwise, the release of transgenic fish, especially piscivorous species like salmon, could destabilize and eventually reorganize pelagic ecosystems. For example, natural spawning by feral Atlantic salmon (*Salmo salar*) in British Columbia suggests increasing competition with native Pacific salmon (*Oncorhynchus* spp.) (Volpe *et al.* 2000), which have been extirpated from 40% of their habitat and are threatened with significant loss of genetic diversity (Levin & Schiewe 2001). Escaped juvenile salmon in north-west Ireland have been reported to mature and successfully interbreed with native fish (Clifford *et al.* 1998), and the resulting genetic changes are still observed (Crozier 2000) indicating that the farmed fish have the potential to alter the genetic composition of wild populations thereby affecting fitness and other characteristics (McGinnity *et al.* 1997).

### Nutrient enrichment

Regional changes in the marine pelagic ecosystem will be likely to accompany major alterations in either resource supply at the base of the food web or in removal of important herbivores or carnivores (Fig. 1). Excluding the Antarctic, Greenland and upwelling regions, coastal waters and inland seas globally are becoming nutrient-enriched and chemically altered through riverine and atmospheric delivery of nutrients (Walsh 1987; Nixon 1995; Boesch *et al.* 2001). The sources of nutrients include watersheds as a result of intervention including deforestation, erosion control, wastewater effluent, agriculture (particularly its increasing use of fertilizers), and atmospheric deposition of industrial stack effluent. If the phytoplankton cells that are produced by nutrient enrichment are unpalatable for some reason to grazers, or exceed their grazing capacity, or if the bloom population can no longer be nourished by available nutrient, these nutrient-deficient and ungrazable cells sink and decompose. During their remineralization by bacteria, oxygen consumption may exceed supply and can result in hypoxia or anoxia causing die-offs of the flora and fauna (Granéli *et al.* 1989; Boesch *et al.* 2001). Thus, a continuum of possible effects may occur, ranging from growth stimulation to anoxic die-offs to chronic overenrichment with sustained high nutrient levels. Nutrient-enrichment affects water quality, productivity and food web dynamics, with the specific impacts on a given recipient coastal system varying within this spectrum of potential effects. The evidence clearly points to the increasing threat to coastal ecosystems accompanying anthropogenic disruption of nutrient biogeochemical cycles and marine discharge of nutrient by-products of human activities.

Similarly, changes in nutrient ratios are important because they influence the community composition of phytoplankton. Excluding a few organisms of minor abundance, diatoms are dependent upon silicate while non-diatoms are not (Schelske & Stoermer 1971, 1972; Officer & Ryther 1980; Ryther &

Officer 1981). Diatom food webs are associated with extensive fisheries and therefore desirable, while flagellate food webs are undesirable because they coincide with higher trophic levels that are not economically useful (gelatinous zooplankton), or are associated with hypoxia (Boesch *et al.* 2001). While such changes are most likely to occur in coastal waters, *c.* 75% of global fish resources depend upon near shore or estuarine habitats during portions of their life cycle (IPCC 1996). Stress is also thought to favour smaller organisms (Rapport *et al.* 1985), and it may be that ecosystems under stress respond by switching their trophic structure to dominance by gelatinous forms (e.g. Mee 1992; Boesch *et al.* 2001).

### Predator removal

Top-down effects may accompany massive fish removal at regional or global scales (Steneck 1997), including declines in average trophic level of commercially important fish and changes in stock sizes of their prey (Pauly *et al.* 1998; WWF [World Wildlife Fund for Nature] 2000). Biomanipulation concepts are being expanded from fresh water (Benndorf *et al.* 1987) to include biological pest control in marine systems (Lafferty & Kuris 1996). The extent to which changes such as excessive primary production are predictable and controllable in marine pelagic ecosystems remains to be seen (Christensen *et al.* 1996), nonetheless, there is little doubt that global removal of predatory and forage fishes by humans is significant and may already be impacting marine pelagic food webs (Aronson 1990; Parsons 1992; Fig. 1). Fishing down apex predators theoretically should contribute to increases in forage fish, but this can also be obscured by bottom-up effects (Caddy 2000). There is clear evidence of carnivore impacts on herbivores in marine pelagic ecosystems, and therefore pelagic fisheries are expected to influence other ecosystem components (Micheli 1999) and processes such as carbon fixation, sequestration, and exchanges with the atmosphere (Schindler *et al.* 1997).

### Climate change

Climate variability, both natural and anthropogenically-induced, may also stimulate changes in the marine pelagic ecosystem. Interannual effects have already been described (e.g. Aebischer *et al.* 1990). Global warming at decadal scales may also alter pelagic communities for example by causing collapse of some fisheries and expansion of others (IPCC 1996). With temperature increase plankton show increased extinction risk according to trophic status but independent of biodiversity (Petchey *et al.* 1999) and become dominated by autotrophs and bacteria at the expense of top predators and herbivores, while the outcome of competition between benign and harmful plankton species may be altered (French & Smayda 1995). Climate-induced changes may interact with overfishing by shifting production areas or by altering community dominance, and may even exceed overfishing in

altering global fish stocks in 50–100 years (IPCC 1996). Positive aspects of global warming, for example increased per caput growth rates and growing seasons, and reduced winter mortality may be negated or even overwhelmed by food web (prey availability) alterations, range contractions, and altered migration routes. Independent of long-term climatic trends, climatic variability can alter water column temperature and salinity characteristics and thermohaline circulation patterns, and thereby disrupt ecosystem function at local and regional scales (Aebischer *et al.* 1990; Heyen *et al.* 1998; Ottersen *et al.* 2001).

### Diseases and pollutant stresses

A global increase in marine-related diseases is occurring, characterized by a rise in emergent new diseases and spreading of old diseases across a wide range of marine life (Epstein *et al.* 1998; Harvell *et al.* 1999). A combination of ecosystem stress and anthropogenic activity are plausible contributors to the resurgence in marine diseases (Epstein *et al.* 1998). Eutrophication, increased UV-B radiation, global warming and the influx of hormone-disrupting pollutants are suspected factors, many of these interfering with hormone, endocrine, or immune functions, including those in fish and mammals (Dean *et al.* 1990; Colborn *et al.* 1993). Upon exposure to endocrine disruptors, reproductive and developmental abnormalities occur in marine fish, invertebrates, and mammals (Campbell & Hutchinson 1998). Endocrine disruptors can also alter sex determination in fishes, thus potentially affecting the aquaculture industry which uses knowledge of the sex determination process to develop mono-sex strains of, for example, salmon, for production or genetic security reasons (Campbell & Hutchinson 1998). Because reproductive success is key to organism viability but also influences natural selection, further knowledge of the importance of pollutants as agents of individual, population, community and ecosystem effects is required (Colborn & Clement 1992).

While the linkages between environmental degradation and increased disease remain to be quantified, it appears that they, too, are provocative indicators of a decline in marine epipelagic ecosystem health. Marine mammals, especially, represent some of the most contaminated organisms in the entire world, and certainly in the marine pelagic food web (Ross 2000). Humans who feed extensively at similar trophic levels also are highly contaminated with synthetic fat-soluble contaminants (De Wit *et al.* 1992; Dewailly *et al.* 1993; Pellettieri *et al.* 1996; Ayotte *et al.* 1997; Ross 2000).

### Biodiversity

Decreases in biodiversity have been observed during the past 30 years and can be expected to continue. The Marine Ecosystem Index (MEI), a composite parameter representing trends in the abundances of 102 species (44 marine fishes, 25 mammals, 24 seabirds, 5 turtles, 4 invertebrates) has decreased *c.* 35% since 1970 and is predicted to decline from

55% in 2000 to *c.* 20% in 2025 if current trends continue (WWF 2000). While species extinctions have been relatively rare, population extinctions are relatively common (Ehrlich & Daily 1993; Hilton-Taylor 2000), and many marine species must now have moved closer to global extinction (Roberts & Hawkins 1999). Biological diversity is central to ecosystem productivity and sustainability, especially when faced with extreme fluctuations engendered by anthropogenic activities. Loss of biodiversity coupled with ecosystem disturbances, for example overharvesting of resources, enhances the likelihood of unstable trajectories in ecosystem structure and function (Zaitsev 1992; Christensen *et al.* 1996). For many reasons, there is an increasingly urgent need to protect marine biodiversity especially among fish (Ryman *et al.* 1994) or biotic evolution may essentially be over (Woodruff 1989).

## CONCLUSIONS

Which of these will come to pass by 2025, or which will be the most salient changes in the marine pelagic ecosystem? All seem possible at some level because of public and government perception that pelagic resources are limitless or can absorb sustained punishment without significant changes. In that sense, contemporary science and society are not far removed from 50–100 years ago; in both times, use of the resources for the benefit of humanity was the prime objective. Then, little concern existed about where resources came from, what factors influenced them, and whether human activities made any difference; now, if the answer is economically painful, it is hoped the problem will go away by itself (Woodard 2000). Some generic examples come to mind. Certain nations will not join the near-global moratorium on whaling, despite clear scientific evidence and international pressure to do so. Many fishers feel it is their right to make a living at fishing, no matter what such an attitude costs to the ecosystem. Despite international advice and financial assistance, population growth in developing countries that depend upon pelagic resources continues to accelerate, forcing environmental conservation to be relatively ignored. Biotechnologists, who may ultimately be the saviours of marine pelagic resource use, say ecologists are crying wolf when they ask for caution in the application of genomic alterations of organisms grown in or adjacent to their natural environment. In general, nations, sectors, groups and societies have not coped well with environmental change, whatever the cause. This lethargy reflects myriad causes and excuses, including incomplete or inaccurate knowledge, unwillingness to act, insufficient resources, and lack of authority (IPCC 1996).

It is becoming increasingly apparent that anthropogenic activities have significantly impacted the marine pelagic ecosystem, through diverse and disturbing vectors. For example, eight different types of environmental disturbances have been recognized globally (HEED 1998), and they have been categorized as anoxic-hypoxic, bio-toxin-exposure, disease, keystone-chronic, mass-lethal, new-novel-invasive,

physically forced and trophic-magnification disturbances. All of these appear to have increased in marine pelagic ecosystems during the past century, with the result that chronic illnesses, disease epidemics, morbidity and mass mortality events are being observed across an array of taxonomic groups (Costanza 1992; Epstein 1996). A variety of pathogens, invasions of alien and often toxic species, and human illnesses appear to be increasing in frequency and spatial extent (Harvell *et al.* 1999). The structure and function of marine ecosystems, including coastal and open ocean pelagic systems, are being altered, as is their ability to recover from natural and anthropogenic perturbations (Sherman 2000). Climate change may exacerbate these deteriorations in ecosystem health (IPCC 1996; Harvell *et al.* 1999).

The general hypothesis that the marine pelagic ecosystem is not showing significant signs of anthropogenic impact, and that this conclusion is based on adequate data and understanding of the ecosystem, is increasingly untenable. In part this may reflect that 'the ecosystem concept is very much like the concept of the hereafter: everyone understands what is meant by it but no one can define exactly what it is' (Daan *et al.* 1996). The objectives in this review are to explore the evidence and potential solutions for the alternative hypothesis that significant components of the ecosystem are under anthropogenic stress. This review posits that there is a 'flock' of miner's canaries signalling change, degradation and cryptic reorganization of marine communities, leading to a new equilibrium driven by the need to adapt to the multiple marine ecological disturbances. There is reason to believe that this new equilibrium will not be anthropogenic. It is proposed that reconsideration of existing dogma may prove useful in understanding such a complex ecosystem, not by discarding the old paradigms, but by suggesting their expansion. In addition to these modifications of the fundamental conceptual basis of marine pelagic science, there are several other pathways for motivated scientists to help improve this situation, for example through advocacy (Rohlf 1991; Knauss 1994; Shaw *et al.* 2000). Valuable keys are education of the public in the value of pelagic resources and the limitations to (over)use, an appreciation of the need for scientific data which will enhance understanding and predictability, and involvement in the processes of management and conservation (e.g. Campbell 1998). It is becoming more apparent that linking research and education is fundamental to achieving success in any endeavour where public policy, environmental conservation, and stewardship of natural resources are all equal players.

## ACKNOWLEDGEMENTS

We wish to thank the Foundation for Environmental Conservation for inviting this review and N.V.C. Polunin for his help with it. The ideas presented here have benefited from insight of several colleagues, particularly T. Anderson, M. Angel, K.G. Banse, J. Dolan, N.G. Hairston Jr, P. Kremer, J.C. Roff and J.H. Steele. Support has been

provided by the National Science Foundation (grants OCE-99-82133 and OPP-00-83381) and the Department of Energy (grant DE-FG02-98ER62531) [to PGV], and NSF grant OCE-95-30200 [to TJS]. We gratefully acknowledge the help of E. Cooksey and J. Lopez, for thorough internet searches and D. Peterson for patiently and efficiently typing. Core ideas in this review would not have been possible without the outstanding computer and internet services provided aboard R/V *Polarstern*.

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