

The deep-sea floor ecosystem: current status and prospects of anthropogenic change by the year 2025

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SUMMARY

The goal of this paper is to review current impacts of human activities on the deep-sea floor ecosystem, and to predict anthropogenic changes to this ecosystem by the year 2025. The deep-sea floor ecosystem is one of the largest on the planet, covering roughly 60% of the Earth's solid surface. Despite this vast size, our knowledge of the deep sea is poor relative to other marine ecosystems, and future human threats are difficult to predict. Low productivity, low physical energy, low biological rates, and the vastness of the soft-sediment deep sea create an unusual suite of conservation challenges relative to shallow water. The numerous, but widely spaced, island habitats of the deep ocean (for example seamounts, hydrothermal vents and submarine canyons) differ from typical deep-sea soft sediments in substrate type (hard) and levels of productivity (often high); these habitats will respond differently to anthropogenic impacts and climate change. The principal human threats to the deep sea are the disposal of wastes (structures, radioactive wastes, munitions and carbon dioxide), deep-sea fishing, oil and gas extraction, marine mineral extraction, and climate change. Current international regulations prohibit deep-sea dumping of structures, radioactive waste and munitions. Future disposal activities that could be significant by 2025 include deep-sea carbon-dioxide sequestration, sewage-sludge emplacement and dredge-spoil disposal. As fish stocks dwindle in the upper ocean, deep-sea fisheries are increasingly targeted. Most (perhaps all) of these deep-sea fisheries are not sustainable in the long term given current management practices; deep-sea fish are long-lived, slow growing and very slow to recruit in the face of sustained fishing pressure. Oil and gas exploitation has begun, and will continue, in deep water, creating significant localized impacts resulting mainly from accumulation of contaminated drill cuttings. Marine mineral extraction, in particular manganese nodule mining, represents one of the most

significant conservation challenges in the deep sea. The vast spatial scales planned for nodule mining dwarf other potential direct human impacts. Nodule-mining disturbance will likely affect tens to hundreds of thousands of square kilometres with ecosystem recovery requiring many decades to millions of years (for nodule regrowth). Limited knowledge of the taxonomy, species structure, biogeography and basic natural history of deep-sea animals prevents accurate assessment of the risk of species extinctions from large-scale mining. While there are close linkages between benthic, pelagic and climatic processes, it is difficult to predict the impact of climate change on deep-sea benthic ecosystems; it is certain, however, that changes in primary production in surface waters will alter the standing stocks in the food-limited, deep-sea benthic. Long time-series studies from the abyssal North Pacific and North Atlantic suggest that even seemingly stable deep-sea ecosystems may exhibit change in key ecological parameters on decadal time scales. The causes of these decadal changes remain enigmatic. Compared to the rest of the planet, the bulk of the deep sea will probably remain relatively unimpacted by human activities and climate change in the year 2025. However, increased pressure on terrestrial resources will certainly lead to an expansion of direct human activities in the deep sea, and to direct and indirect environmental impacts. Because so little is known about this remote environment, the deep-sea ecosystem may well be substantially modified before its natural state is fully understood.

Keywords: deep-sea ecosystem, sea floor, anthropogenic change, environmental impacts, waste disposal, deep-sea fisheries, oil and gas drilling, drill cuttings, manganese nodules, deep-sea mining, climate change, long-term trends, future status

INTRODUCTION

We define the 'deep-sea floor' as that portion of the ocean bottom overlain by at least 1000 m of water column. The deep-sea floor is a vast region covering roughly 300×10^6

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km², or approximately 60% of the Earth's solid surface. It has a number of distinct habitats. These include sediment filled basins, continental slopes and abyssal plains, deep ocean trenches and the exposed pillow basalts of young mid-ocean ridges, seamounts rising >1000 m above the general seafloor, and submarine canyons cutting through the continental slopes. The 'mud' (or more correctly, 'silt and clay') clad plains of the slope and abyss are by far the most extensive habitats, constituting >90% of the deep-sea floor. They often extend for thousands of kilometres without any substantial physical or biological barriers. Deep ocean trenches, where old ocean crust is subducted beneath the margins of continental plates, constitute 1–2% of the deep-sea floor. While significant in total area, the rocky substrates of mid-ocean ridges (forming ribbons of habitat ~10 km wide and, in total, ~60 000 km long), seamounts (perhaps 50 000–100 000 in number; Epp & Smoot 1989; Rogers 1994; Smith & Jordan 1998) and submarine canyons are rare habitats in the enormous expanses of the deep sea, occupying <4% of the sea floor.

Most deep-sea floor habitats have several characteristics that distinguish them from other of Earth's ecosystems and that influence their susceptibility to environmental change and human impacts. Perhaps the most important characteristic is low productivity. Except for hydrothermal vents and some cold seeps, the energy for the deep-sea biota is ultimately derived from an attenuated 'rain' of detritus from remote surface waters (typically 1–10 g C_{org} m⁻² yr⁻¹). Detrital food particles range from the fresh remains of phytoplankton (or 'phytodetritus') to the carcasses of whales. The purely detrital base of deep-sea food webs contrasts sharply with those of most epipelagic, shallow-water and terrestrial ecosystems, which are sustained largely by locally produced organic matter (Polunin *et al.* 2001). Because of the low flux of organic energy, the biomass of deep benthic communities is typically only 0.001–1% of that in shallow-water benthic or terrestrial communities (Smith & Demopoulos 2003). Low food flux, in concert with low temperatures (~1–4°C), yield relatively low rates of growth, respiration, reproduction, recruitment and bioturbation in the deep sea (Gage & Tyler 1991; Smith & Demopoulos 2003).

In general, the deep-sea floor is also characterized by very low physical energy, including sluggish currents (<0.25 knots), very slow sediment accumulation rates (0.1–10 cm per thousand years), and an absence of sunlight (Gage & Tyler 1991; Smith & Demopoulos 2003). To the initial surprise of ecologists, deep-sea soft-sediment communities often exhibit very high local species diversity, with 0.25 m² of deep-sea mud containing 21–250 macrofaunal species (Snelgrove & Smith 2002).

Not all deep-sea habitats are low in energy and productivity. Exceptions include hydrothermal vents, and to lesser degree, cold seeps, where bacterial chemoautotrophic production fuelled by reduced chemicals such as hydrogen sulphide support communities high in biomass and

productivity but relatively low in diversity (Van Dover 2000). Seamounts, canyons and whale falls also violate the low-energy deep-sea 'rule' by focusing flow and organic-matter flux; this enhancement of physical and/or biological energy can yield high biomass communities, at least by deep-sea standards (Koslow 1997; Vetter & Dayton 1998; Smith & Baco 2003; Smith & Demopoulos 2003).

The sheer size and inaccessibility of the deep sea has undoubtedly limited the intensity of direct human impacts and kept the percentage of sea floor area influenced by humans very low compared to most other ecosystems. In fact, we might expect the deep sea to be one of the most pristine ecosystems on the planet, with the best prognosis for remaining so. Nonetheless, human impacts are occurring, and because of the sensitivity of the deep-sea ecosystem to changes in organic carbon flux, it may be unusually susceptible to global climate change and its cascading effects on oceanic productivity (Hannides & Smith 2003). Although the remoteness of the deep sea would appear to attenuate anthropogenic impacts, it has also severely hampered evaluation of human influences and long-term change. It has also limited understanding of the basic ecology of deep-sea ecosystems. In particular, for those few deep-sea habitats in which long-term trends have been documented (discussed below), the underlying causes remain enigmatic.

Like the Amazon basin, the deep-sea ecosystem has been considered to be both an unexplored wilderness, and a resource frontier. The potential resources of the deep sea are tremendous, while scientific understanding of natural processes in this ecosystem is very poor. This is a dangerous combination. The goal of this review is to highlight what scientific knowledge we do have, and to use the resultant insight to predict future threats.

Deep-sea biology remains a young science; basic observational studies and serendipitous discoveries continue to reveal new secrets (e.g. Corliss *et al.* 1979; Smith *et al.* 1989). Recent process-based studies have elucidated long-term trends in the surface ocean (Karl 2002), but long time-series data are lacking for most of the deep sea. The inaccessibility and costs associated with deep-sea work limit the scope for time-series sampling. Recent technological improvements promise exciting new discoveries over the next decades, but predicting the status of the deep sea in 2025, a goal of this paper, is a difficult task.

Our perception of the deep sea has changed remarkably during the course of the 20th century. Early expeditions, such as that of the British *HMS Challenger* (Murray 1895) and the Danish *Galathea*, conclusively demonstrated the presence of abundant life in all areas of the deep ocean, and dispelled myths of an archaic fauna. Most recovered animals were easily classified into higher-level taxa known from shallow water. Although Murray (1895) reported that deep-sea samples often contained many species, the true species richness of the deep ocean was not appreciated until the 1960s, when studies from the north-west Atlantic reported

more than 360 macrofaunal species from a single epibenthic sled haul (Hessler & Sanders 1967).

One of the early paradigms of marine ecology was the 'slow, steady pace of life' at the deep-sea floor (Smith 1994). The deep was viewed as 'an environment remote and deliberate', where nutrient flux from surface waters was attenuated and buffered by the vast water column above. Slow current speeds, and a gentle rain of organic material, were thought to drive biological processes at slow, relatively constant, rates. This hypothesis was supported by studies in the 1970s and early 1980s documenting low metabolic rates, long generation times, and low bioturbation rates. This evidence agreed with the prevailing view that high species diversity in deep-sea sediments was generated by extreme resource partitioning under stable conditions persisting for very long time scales (Sanders 1968).

This view of invariance in biological processes began to change in the 1980s. Data from deep sediment traps in the Sargasso Sea and from time-lapse photography in the North Atlantic showed dramatic temporal variability in particulate organic flux, and in the accumulation of fresh phytodetritus, at the abyssal seafloor (Deuser & Ross 1980; Tyler *et al.* 1982; Billet *et al.* 1983; Tyler 1988; Thiel *et al.* 1989). Other lines of evidence also countered the notion of a 'slow and stable' deep sea. Physical disturbance, in the form of high energy benthic storms, was observed over large areas on the Scotia Rise (Hollister & McCave 1984). Strong evidence for pulsed biogenic disturbance and successional processes was found in experimental studies in the Santa Catalina Basin (Smith *et al.* 1986; Kukert & Smith 1992).

The current view is of an ecosystem relatively homogeneous in space and time, punctuated by biogenic pulses of disturbance and organic enrichment at scales ranging from centimetres to thousands of kilometres (Smith 1994). Physical heterogeneity also occurs at scales ranging from nodules on the seafloor to seamounts and mid-ocean ridges. A crucial question is the degree to which these natural perturbations are analogous to potential human impacts (Tyler 2003). The traditional view of a vast and deliberate deep-sea ecosystem suggested a system with high assimilative capacity and substantial inertia in the face of external forcing factors. But scientists are just beginning to understand natural temporal variability in the deep sea,

and predicting the impact of potential anthropogenic impacts is extremely difficult without accurate time-series data.

As mentioned above, productivity, biomass and physical energy are all relatively low in the deep sea, increasing the potential sensitivity to human impacts (Table 1). Species diversity, in terms of the number of species per sample, is relatively high in the deep sea, again likely making the habitat more sensitive to human impacts (there are more species to be extinguished). Yet the size of the ecosystem is far greater, and for abyssal soft-sediments, habitats are nearly continuous across ocean basins. The large habitats of the deep-sea may make the fauna more resistant to extinctions caused by local processes, with a greater potential for recolonization from widespread source populations (Table 1). However, the size of source populations depends to a large extent on the biogeographical distribution of deep-sea species, which are very poorly known (Glover *et al.* 2002). Large, continuous habitats may also allow stressors, such as disease agents or radioactive contaminants, to be transported over vast distances. Contaminants such as radioactive wastes could potentially move through the deep-sea food web, via wide-ranging pelagic species, and impact very large areas. Clearly, the unusual characteristics of deep-sea ecosystems present a different set of conservation challenges from shallow-water ecosystems (Table 1).

We consider below a number of potential natural and anthropogenic 'agents of change' and, using available long-term datasets, make a best guess at the likely state of the deep-sea ecosystem in 2025. Potential human impacts in the deep sea include those from past activities (for example waste disposal), current undertakings (for example deep-sea fisheries, oil and gas exploration), and future potential influences (for example climate change, CO₂ sequestration, polymetallic nodule mining and methane hydrate extraction) (Fig. 1, Table 2). In order to understand long-term trends, we first describe significant impacts on the deep sea, highlighting for each case the past, present and future effects. This is followed by a review of documented long-term (decadal) trends in the deep sea from time-series data in the Pacific and Atlantic. Finally, we outline potential ecosystem states in 2025, and indicate principal gaps in knowledge of the deep-sea ecosystem.

Table 1 A relative comparison of broad ecological characteristics in the deep sea and shallow water, and their relevance to deep-sea conservation.

Characteristic	Deep sea	Shallow water	Relevance to deep-sea conservation
Productivity	Low	High	Deep-sea more sensitive
Biomass	Low	High	Deep-sea more sensitive
Physical energy	Low	High	Deep-sea more sensitive
Size of habitat	Large, contiguous	Small, non contiguous	Deep-sea more robust
Species diversity	High	Moderate, variable	Deep-sea more sensitive
Species distributions	(poor evidence)	Narrow, variable	(no evidence)

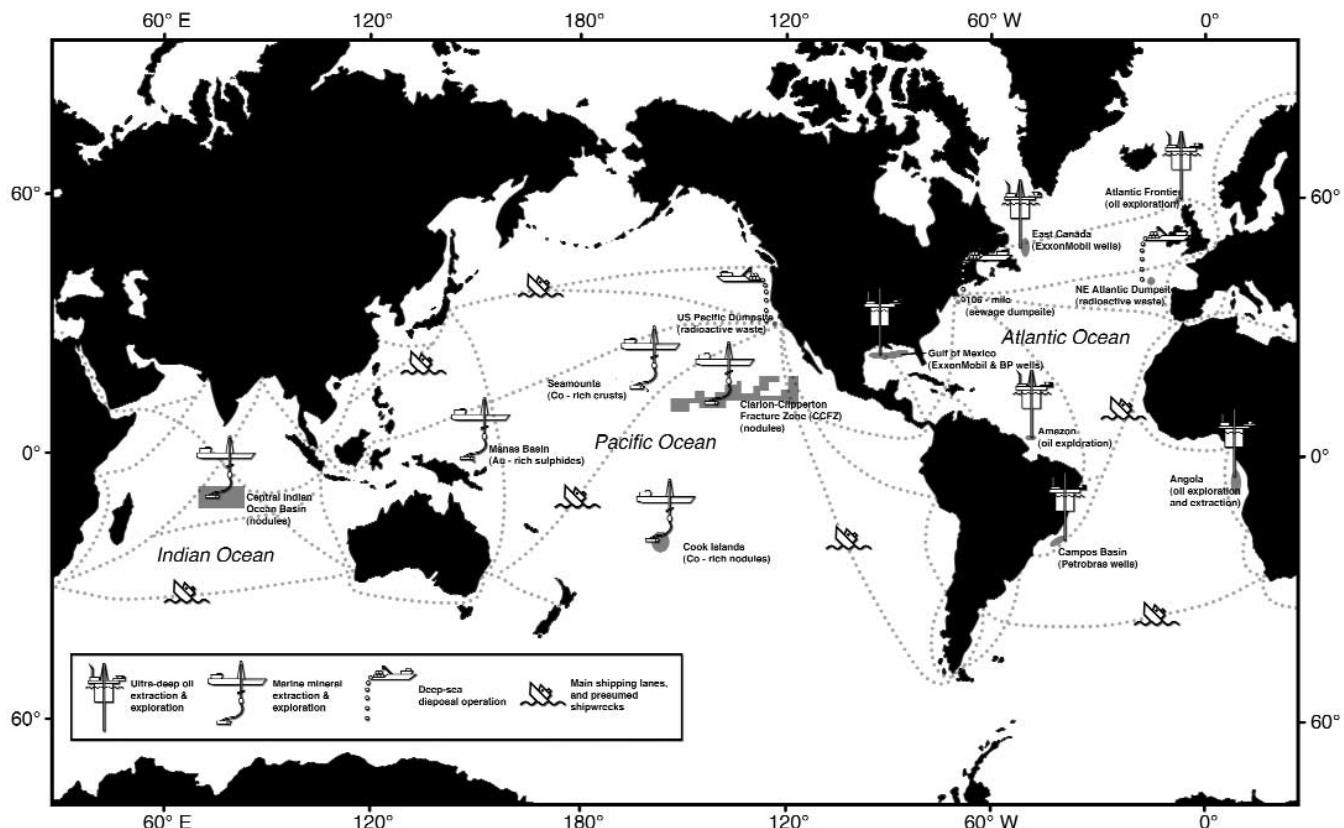


Figure 1 Map showing the distribution of current and future direct human impacts on the deep-sea ecosystem. Shaded zones depict approximate areas of potential impact.

Table 2 Summary of anthropogenic environmental forcing factors at the deep-sea floor, ranked in order of importance, within each category. Spatial scale of impact is indicated at the level of local (linear scale of 0–100 km), regional (100–1000 km) and basin (1000–10 000 km). * In the deep sea, due to low biological and chemical rates, the time scale of deep-sea impact typically extends far beyond the time scales of activity. For example, the impacts of a large shipwreck, or of deep seabed mining are expected to last >100 years.

Human forcing factor	Temporal scale of activity*	Knowledge of impact/severity/ spatial scale	Estimated importance in 2025
<i>Past impacts</i>			
Dumping of oil/gas structures	isolated incidents (now banned)	good/low/regional	low
Radioactive waste disposal	1950s–1990s	good/low/local	low
Lost nuclear reactors	1960s onwards	good/low/local	low
Dumping of munitions	1945–1976 (now banned)	poor/low/local	low
<i>Present impacts</i>			
Deep-sea fisheries	1950s onwards	good/high/regional	high (unsustainable)
Collateral damage by trawling	1950s onwards	good/high/regional	high
Deep-sea oil and gas drilling	1990s onwards	poor/moderate/basin	moderate
Dumping of bycatch causing food falls	1900s onwards	poor/moderate/basin	moderate
Research and bioprospecting at vents	1960s onward	good/low/local	very low
Underwater noise	1960s onward	poor/low?/local	probably low for benthos
<i>Future impacts</i>			
Polymetallic nodule mining	10–20 yr timescale	poor/very high/regional-basin	high
CO ₂ sequestration	10–30 yr timescale	poor/very high/local-regional	high
Dumping of sewage sludge	5–10 yr timescale	good/moderate/local-regional	moderate
Dumping of dredge spoil	5–10 yr timescale	poor/low/local	moderate
Climate change	50–100 yr timescale	poor/very high/basin-global	low
Manganese crust mining	unknown	poor/high/local	low
Polymetallic sulphide mining	unknown	poor/high/local	low
Methane hydrate extraction	unknown	poor/moderate/regional	low

ENVIRONMENTAL FORCING FACTORS

Disposal of wastes

Structures

In April 1912, the *RMS Titanic* sank in 3800 m of water with the loss of 1503 lives. Seventy-three years later, the wreck was discovered on the seafloor in two pieces within a large debris field. Sessile marine fauna had colonized the wreck, which also attracted deep-sea fish. Accidental sinkings, such as that of the *Titanic*, have occurred since ships first put to sea, and many wrecks must lie in water deeper than 1000 m. During World War I, 7 million tonnes of Allied merchant shipping (equivalent to roughly 1700 ships) were sunk. Similarly, during World War II, over 21 million tonnes of Allied merchant shipping (or about 5000 ships) were lost (Thiel 2003). During the period 1971–1990 a total of 3701 ships, or nearly 13 million tonnes were lost at sea (Thiel 2003).

Few studies exist on the impact of shipwrecks. Depending on the cargo, they may generate localized reducing habitats (Dando *et al.* 1992), release petroleum hydrocarbons, and/or provide a habitat for hard substrate biota (Hall 2001). In general, shipwrecks are considered to have no more than local impact. More recently, the proposed deliberate scuttling of oil and gas storage structures has received considerable attention (Rice & Owen 1998). Working groups have since recommended studies of the impact of existing shipwrecks to predict the effects of ocean disposal of such structures (NERC [Natural Environment Research Council] 1996). Rational decisions concerning the relative merits of onshore versus offshore disposal require substantially more quantitative investigation of the potential environmental impacts of large structures (like shipwrecks) at the deep-sea floor (Tyler 2003).

Large structures may sometimes have a beneficial effect as artificial reefs. On the Gulf of Mexico (GOM) continental shelf, a programme to convert disused oil platforms into artificial reefs has proved successful. Since operations began, some 5800 oil platforms have been installed in the GOM region, and approximately 4000 remain in place today. Many of these older structures are retired, and a programme has been implemented to convert the supporting structures into reefs. Studies indicate that oil platform structures in the GOM may attract 20–50 times the fish density of the surrounding waters (Dauterive 2000). In the GOM, the removal of thousands of disused oil and gas platforms could conceivably have a detrimental effect on the region's fish stocks.

Table 3 Number of radioactive waste containers dumped in the deep sea from 1946–1982 by various countries (Thiel 2003). Dumping was banned in 1983.

Location	Years	Countries	Amount of material (drums)
North-east Atlantic	1949–1982	UK, Germany, Italy, Netherlands, France, Switzerland, Belgium, Sweden	about 220 000
West Atlantic	1949–1967	USA	34 282
North-east Pacific	1946–1970	USA	56 261
West Pacific	1954–1976	Japan, South Korea, New Zealand	3185

Approximately 150 of these platforms have so far been sunk in the continental shelf region as part of the 'rigs-to-reefs' programme, with oil companies donating 50% of the money saved from decommissioning costs to state environmental programmes. The expansion of the oil and gas industry into deeper water (see below) will be likely to result in these kinds of programmes being suggested for deep-sea structures; clearly the impact will depend on the size and nature of the structure, and the presence of any potential contaminants.

Munitions and radioactive waste

Over the last century the deep sea has been used as a dumpsite for dangerous wastes. From the end of World War II until 1976, several million tonnes of conventional and chemical weapons were dumped into the waters surrounding the UK and other European countries (Thiel *et al.* 1998). This practice is now banned by the London Dumping Convention (LDC) of 1972 (Thiel *et al.* 1998). However, the large quantities of munitions dumped in boxes or in scuttled ships remain a hazard to both humans and marine life. Most chemical agents, such as nerve gas, hydrolyse rapidly in seawater and are broken down into non-toxic chemicals. However, explosives, and more insoluble chemicals such as mustard gas, remain a significant hazard to fisherfolk. Field surveys of major munitions dumpsites have not shown any significant contamination of marine life, and the majority of loose munitions and boxes have been colonized by sessile organisms (Thiel *et al.* 1998). Existing munitions dumpsites are unlikely to have significant, widespread impacts on deep-sea ecosystems, but do pose a danger to human users of the deep sea.

Low and intermediate-level radioactive wastes have also been dumped into the deep sea (Table 3) (Smith *et al.* 1988; Thiel *et al.* 1998). Between 1949 and 1982 about 220 000 drums of low level waste were disposed in the north-east Atlantic by European countries. Between 1946 and 1970, over 75 000 drums of low-level waste were dumped by the USA at three sites in the north Atlantic and Pacific. In 1983, parties to the LDC agreed a moratorium on the dumping of radioactive waste, and a dumping ban followed in 1993. Few data are available on the amount of radioactive waste dumped at sea by the former USSR. The dumping of high-level nuclear waste has not progressed beyond feasibility studies.

The north-Atlantic radioactive waste dumpsites have been monitored periodically (Smith *et al.* 1988). Very little change

in radionuclide levels has been recorded, although a single anemone species, *Chitoanthus abyssorum*, was found to have increased levels of ^{90}Sr and ^{137}Cs , either caused by drum leakage or normal biogeochemical processes (Feldt *et al.* 1985). At the USA dumpsites, measurable levels of radionuclide contamination have been recorded in sessile suspension feeders (anemones), deposit feeders (holothurians and asteroids) and mobile predators (rattails, bathypterooids and decapods) associated with sediments close to waste materials (Smith *et al.* 1988). Significant transfer mechanisms for radionuclides include bioturbation into sediments, bioaccumulation in deposit and suspension feeders, and uptake by mobile benthopelagic fish species, which may ultimately provide a pathway to humans. Remarkably, the largest amounts of radioactive waste were dumped in the deep sea in years coinciding with the sudden rise in deep-sea fisheries (see below).

With the existing bans on ocean disposal of both low-level and intermediate-level radioactive wastes, it seems unlikely that high-level waste will ever be dumped in the deep ocean. However, options to dispose of high-level waste below the sea floor in penetrating canisters have been considered by various committees (Hollister & Nadis 1998). Further research is required to evaluate the potential impacts of this kind of disposal, although, in the absence of radiation leakage from the sediment, any ecosystem impacts are likely to be very localized.

Sewage sludge

As the human population increases by 1.5–2 billion over the next 20 years (UN [United Nations] 1998), it is likely that increasing pressures will be placed upon the ocean for human waste disposal. The disposal of sewage sludge at sea is already permitted under the London Dumping Convention. Most developed countries currently use a combination of recycling, land-fill, ocean out-falls and shallow-water dumping to deal with standard domestic waste streams. Offshore dumping is now under serious consideration by a number of countries (Thiel *et al.* 1998).

Sewage sludge is highly variable in both oxygen demand and the degree of contamination with hydrocarbons and heavy metals. The main potential impacts of sewage sludge disposal are animal burial, clogging of feeding apparatus, increases in turbidity, toxicity from sludge components, reductions in bottom-water oxygen concentrations, and changes in community structure due to organic enrichment (Thiel *et al.* 1998). All of these impacts have been studied at the '106-mile' dumpsite, off the coast of New York. This is the only study thus far of the impacts of sewage sludge on the deep sea benthos (Van Dover *et al.* 1992; Takizawa *et al.* 1993; Bothner *et al.* 1994).

The deep-water dumpsite (DWD 106) is located in about 2500 m of water approximately 106 miles offshore of New York and New Jersey. Between March 1986 and July 1992 approximately 36 million tonnes of wet sewage sludge were dumped in surface waters at this site, and the impact was

monitored throughout this time period. After dumping, the distribution of sewage sludge was determined from silver concentrations, linear alkylbenzenes (wetting agents in detergents) and spores of *Clostridium perfringens*, which originate from mammalian faecal material (Bothner *et al.* 1994; Thiel 2003). At the dump site, significant increase in the abundance of macrofauna was recorded (Grassle 1991) although changes in total community structure were not dramatic. Stable isotope ratios indicated that sea urchins and other large megafauna were assimilating sewage-sludge material at the dumpsite (Van Dover *et al.* 1992). In addition, the level of silver in sediments at DWD 106 was 20 times higher than in background reference areas, and contaminants appeared to penetrate at least 5 cm into the sediment (Bothner *et al.* 1994). Environmental concerns halted the dumping at DWD 106 in 1992; ongoing studies are investigating the dispersal of contaminants from the site.

Dredge spoil

Sediments dredged from coastal waterways and harbours frequently contain high levels of contaminants such as hydrocarbons, heavy metals and synthetic organic substances (Thiel 2003). The disposal of dredge spoils in the deep sea poses a similar threat to that from sewage sludge disposal, although the spoils contain less organic matter. To date, no significant deep-sea dumping operation has occurred, although dredge-spoil dumping is being considered. The simplest method of disposal would be to take the spoil out over deep water, open the hatches and let it sink. However, this is thought to pose a number of problems (Tyler 2003). Fine particles sink more slowly, and could become very widely distributed in the water column. Very fine particles may remain indefinitely in suspension, or become trapped at the pycnocline. By the time material reached the seafloor, it would be spread over a wide area, forming a thin veneer. The alternative method, lowering the spoil directly to the seabed using a pipe, is likely to result in more intense, but much more localized impacts. Local oxygen demand at the dumpsite could be high, and contaminants might still be dispersed through the action of deep-water currents and food-web processes.

CO₂ sequestration in the deep ocean

Current computer models, assuming the burning of fossil fuels at a 'business as usual' rate, predict a doubling of atmospheric CO₂ concentration by the middle of the next century, with a very significant impact on the ecology of the planet (IPCC [Intergovernmental Panel on Climate Change] 1996). Governments and industry initially approached this problem by sponsoring research and development into energy efficiency and alternative fuel sources. More recently, studies have begun to investigate options for directly managing the carbon budget by sequestering carbon in terrestrial and oceanic sinks, rather than releasing CO₂ into the atmosphere. For example, one Norwegian energy firm at the Sleipner oil and gas field already practises the direct injection of CO₂ into

sub-sea rock strata. Another carbon sequestration scheme under examination is the direct injection of industry-generated CO₂ into the deep ocean.

At ocean depths greater than 500 m, temperature is nearly always below 11°C, and CO₂ may be injected in liquid form. At lower temperatures and higher pressures, CO₂ can form a crystal structure known as a gas hydrate, essentially a lattice of water molecules trapping the 'guest' CO₂ molecules. At depths greater than 3700 m, liquid CO₂ becomes denser than water, and if released at that depth it may form lakes in depressions on the seafloor. The various methods of deep ocean CO₂ injection are well reviewed elsewhere (Handa & Ohshumi 1995). All of the systems are designed to encourage dissolution of the CO₂ into deep oceanic waters, where, due to the slow circulation, it may be trapped for several hundred years. The principal impact general to benthic ecosystems is likely to be reduced pH, and for those organisms directly in the path of the CO₂ plume, physiological stress caused by an elevated partial pressure of CO₂.

At least two field studies have already been carried out to assess effects of elevated CO₂ on deep-sea animals (Brewer *et al.* 1999; Tamburri *et al.* 2000). In one experimental situation, food odour was released from a vessel containing liquid CO₂; fish and invertebrates were observed to migrate towards the food odour, and contrary to expectations, were relatively unharmed even within several centimetres of the liquid CO₂. One hagfish (*Eptatretus stouti*) entered the beaker containing the liquid CO₂, lost consciousness within 5 s and drifted out to regain consciousness within 20 s. This hagfish repeated the behaviour three times in all, recovering after each event. The interpretation was that the animal was more affected by respiratory stress associated with the high partial pressure of CO₂ than by the lowered pH (Tamburri *et al.* 2000).

If industrial-scale disposal of CO₂ were to occur in the deep sea, it is unlikely that organisms in the direct path of the concentrated plume would survive. Additionally, the food odour from dead organisms may attract mobile scavengers to the area, which in turn die and attract still more scavengers, resulting in a 'mortality sink'. Such a sink effect could cause death of scavengers from a much larger area than the plume itself. Thus, both sessile and motile benthic organisms are likely to be impacted by a very large scale plume (Tyler 2003). Substantially more research is required to fully evaluate potential local and regional impacts of CO₂ injection into the deep sea.

CO₂ sequestration may have both the 'near-field' impacts described above, and 'far-field', longer-term impacts that may be felt globally. The impact of deep-ocean CO₂ sequestration has been modelled recently on a global scale (Caldeira & Wickett 2002). Two scenarios were modelled using an ocean general-circulation model, one where CO₂ is released into the atmosphere at fixed rate of 7 Gt C yr⁻¹, and a second scenario where the same assumed emissions were released at seven points at 3000 m depth in the ocean. In both scenarios, ocean pH dropped substantially over timescales of 100–500 years. In the atmosphere-emission scenario, surface-ocean

pH was reduced, while in the deep-sequestration scenario, deep-water pH was reduced while surface-ocean pH remained relatively unchanged (Caldeira & Wickett 2002). In the atmosphere-emission scenario, the reduction in ocean pH occurred much more evenly (in spatial terms), whereas in the deep-sequestration scenario, pH changes were concentrated near the hypothetical point sources (Caldeira & Wickett 2002). The advantages of deep-ocean sequestration in this model are the almost complete mitigation of atmospheric CO₂ increases and associated reductions in surface-ocean pH. The disadvantages are of course, substantial reductions in deep-ocean pH.

The model results are not discussed in terms of impacts on the atmosphere and land systems, including global warming; these issues would clearly be exacerbated in the atmosphere-emission scenario. Additionally, the global CO₂ emission scenario (7 Gt C yr⁻¹) used is extremely optimistic given that current anthropogenic CO₂ emissions are roughly 6 Gt C yr⁻¹ and rising (Gerard Nihous, personal communication 2003). It is also highly unlikely, due to financial and engineering constraints, that 100% of emissions could be sequestered at 3000 m depth (Caldeira & Wickett 2002). However, as an evaluation of the pH impacts of deep-ocean sequestration, the model is conservative. Thus, the end result is likely to be less than the model-predicted pH impact at depth, and greater impact on the surface water and atmosphere. From a societal standpoint, the modelling results tend to favour the ocean sequestration option for mitigating effects on the full biosphere, causing the modellers to conclude that 'ocean CO₂ sequestration probably makes [the] most sense within the context of the evolution towards a carbon-emission free economy' (Caldeira & Wickett 2002). Such conclusions highlight the need for more comprehensive studies of the impacts of CO₂ on the deep-sea biota.

Future trends in deep-sea waste disposal

Due to the vastness of the deep ocean, limited ocean disposal to date has left the deep-sea floor relatively unscathed compared to many terrestrial and coastal habitats. Given current population trends, this could change. Economic globalization will continue to fuel increases in shipping, and the number of ships lost at sea will presumably increase, although with very limited environmental impact. Increased offshore oil and gas drilling will lead to renewed pressure to dispose of retired structures in the deep ocean. The quantities of sewage sludge and dredge spoil produced annually will increase, and by 2025 it is conceivable that a significant proportion of this might be disposed offshore. Munitions and radioactive wastes will continue to pose a problem with regard to disposal. However, it is unlikely that deep-ocean dumping of these hazards will be politically or publicly acceptable for the foreseeable future.

A potentially much more significant impact in size and intensity could result from deep-ocean CO₂ sequestration. By 2025, the US Department of Energy seeks to sequester 1 Gt C yr⁻¹ (US DOE 1999). By 2050, that figure is projected to

be 4 Gt Cyr⁻¹. Other countries such as Japan are also seriously considering substantial deep-sea CO₂ sequestration. With ‘business as usual’ emissions predicted to be approximately 11 Gt Cyr⁻¹ by 2025, sequestration of CO₂ could conceivably exceed gigatonnes of carbon per year.

Deep-sea fisheries

The earliest deep-sea fishing was probably practised by South Pacific islanders, using handlines and specialized hard-wood hooks for such species as the oil fish, *Ruvettus pretiosus*, at depths of 150–750 m (Merrett & Haedrich 1997). Large-scale deep-sea fishing was not practiced until new fisheries technology in the 1950s, especially the invention of the factory trawler, allowed efficient exploitation of the deep benthos. Few modern deep-sea vessels are currently fishing below 1000 m, but this is likely to change in the future. Hence we include here case studies of fisheries centred at depths of less than 1000 m to provide a clue to future deep-sea threats. Additionally, many of the current target species range well below 1000 m depths so indirect fisheries impacts may also be felt in what we define as the deep sea.

Key characteristics

The deep sea, traditionally perceived as a cold, low energy system, has only recently begun to be exploited for fish resources. Presently, these fisheries centre on the upper continental slope at depths ranging from 600–1000 m. Species currently targeted include the orange roughy (*Hoplostethus atlanticus*), oreos (*Allocyttus niger*, *Pseudocyttus maculatus*), roundnose grenadier (*Coryphaenoides rupestris*), roughhead grenadier (*Macrourus berglax*), blue ling (*Molva dypterygia*), black scabbardfish (*Aphanopus carbo*), redfish (for example *Sebastes mentella*, *S. marinus*), Greenland halibut (*Reinhardtius hippoglossoides*), sable fish (*Anoplopoma fimbria*), and dogfish (for example *Centroscymnus coelolepis*) (Clark 2001). Deep-sea species already fished to commercial extinction include the pelagic armorhead, *Pseudopentaceros wheeleri* (Koslows *et al.* 2000).

The natural histories typical of deep-sea fish would seem to make them particularly vulnerable to overfishing. The majority of deep-sea fish have low metabolic rates, low growth rates, low fecundity and late reproduction (Clark 2001; Roberts 2002). For example, radiometric ageing of the rockfish *Sebastes* spp. reveal that longevity increases exponentially with depth of occurrence, and that some species may live to 200 yr (Caillet *et al.* 2001). The Atlantic roundnose grenadier, *Coryphaenoides rupestris* lives to over 70 yr, and matures at 14–16 yr (Bergstad 1990). The orange roughy, *Hoplostethus atlanticus*, can reach 150 yr in age, and matures at 20–30 yr (Horn *et al.* 1998). Some deep-sea fish are also known to aggregate for spawning or feeding, making them very easy to fish but allowing concentrated fishing activities to reduce populations drawn from much larger areas (Clark 2001). The standard scenario for shallow-water fisheries has been sequential stock depletion, and the setting

of lower and lower quotas in retroactive policy decisions. With this in mind, the characteristics of deep-sea fish would seem to make them even more vulnerable to overexploitation, and it is unfortunate that most of the studies of these fish only commenced after fishing had begun in earnest. Below we outline a series of case studies and highlight future trends in the deep-sea fishing industry.

Pelagic armorhead fishery

While most deep-sea fisheries are relatively recent and still highly active, some stocks have already been driven to commercial extinction. One such example is the pelagic armorhead, *Pseudopentaceros wheeleri*. This is a benthopelagic ray-finned fish native to seamounts of the North Pacific from Japan to the Hawaiian Islands (Hardy 1983). Abundant stocks of this species were discovered by the Soviet Union in 1967. Between 1969 and 1977, between 50 000 and 200 000 tonnes of this fish were landed annually by Soviet and Japanese factory trawlers (Koslows *et al.* 2000). These fishing efforts on the relatively sparse seamounts of the Emperor-Northern Hawaiian Ridge system were extremely intense, with the Soviets fishing 18 000 trawler days. The fishery collapsed in 1977 and no major landings of this fish have been reported since.

Macrourid fisheries

The macrourid (or rattail) fisheries, begun in the early 1970s, are a classic example of an exploited deep-sea fish resource (Merrett & Haedrich 1997). Macrouridae are relatives of cod, and are widespread on the upper continental slope. The most common genera on the upper slope are *Nezumia*, *Macrourus* and *Coryphaenoides*. There are three species of *Coryphaenoides* considered large and abundant enough to fish commercially, namely *C. acrolepis* (pacific grenadier), *C. rupestris* (roundnose grenadier) and *C. armatus*. *Coryphaenoides armatus* is confined to waters deeper than 2000 m and not yet exploited commercially. Other fished macrourids include *Macrourus berglax*, the onion-eye grenadier, which is common in the far North Atlantic (Merrett & Haedrich 1997).

Macrourid fisheries, such as that for the roundnose grenadier, were managed initially through a simple quota system based on a crude assessment of stock size and the setting of a total allowable catch (TAC) (Atkinson 1995; Merrett & Haedrich 1997). In the early days, no formal TAC was set, but a crude catch limit of 30 000 tonnes, based largely on guesswork, was suggested for *C. rupestris*. In the following years, the TAC was continually adjusted downwards in a ‘reactive’ rather than ‘proactive’ manner, and the actual catch never equalled the TAC. This was not a promising beginning for the fishery. By the late 1970s, catches had declined to less than 10 000 tonnes and have never recovered. Remarkably little was actually known about the basic biology of this fishery prior to commercial exploitation. A study in 1997 was one of the first to document the age and growth of *C. rupestris*, confirming it to be a long-lived, slowly maturing

fish and vulnerable to overexploitation (Kelly *et al.* 1997). Unfortunately, this was nearly 30 years after commercial fishing had begun. With a population turnover time estimated to be 20–50 yr, the only conceivable outcome for the roundnose grenadier fishery appears to be commercial extinction.

Orange roughy fishery

The orange roughy, *Hoplostethus atlanticus*, is a member of the family Trachichthyidae (Merrett & Haedrich 1997). The species occurs in most oceans, but is especially abundant around the islands of New Zealand, where it aggregates close to deep banks and seamounts. At certain times of the year, the species forms large spawning aggregations that are especially susceptible to deep-sea otter trawling. At spawning times, trawl nets take a nearly 100% pure catch, making the fishery highly efficient. One of the first studies to investigate the growth rate of orange roughy indicated exceptionally slow growth, with the fish only reaching maturity at 20 years, and many living for over 50 years (Mace *et al.* 1990). This study was the basis of the New Zealand stock assessments, and the setting of a prudent TAC. This ‘tailor-made’ quota system for the orange roughy was designed to prevent overshoot of the TAC and received considerable press attention (Merrett & Haedrich 1997). Unfortunately, the early 1990s saw a decline in *H. atlanticus* stocks, with landings dwindling from a high of 50 000 tonnes in 1989 to just 15 000 tonnes in 1997 (Fig. 2). Ominously, this declining catch has occurred without any observable reduction in the mean body size of the population, indicating a lack of recruitment (Clark 2001).

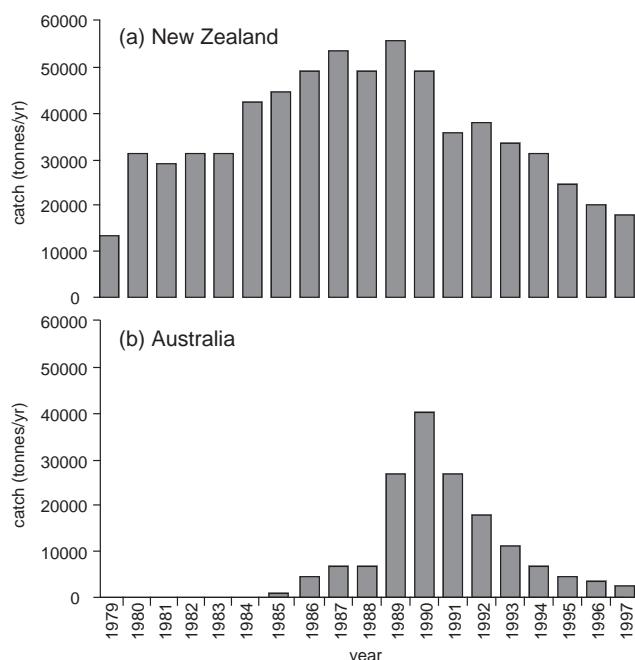


Figure 2 Catch history (tonnes) of orange roughy (*Hoplostethus atlanticus*) fisheries in (a) New Zealand and (b) Australian waters. Modified from Clark (2001).

With a steadily declining catch, and no observed recruitment response, the fishery looks unsustainable in the long-term under current management practices.

Collateral damage caused by trawling

Deep-sea fisheries are thought to cause considerable ‘collateral damage’ to the benthic ecosystem (Roberts 2002). Deep-sea fish themselves are probably highly susceptible to damage by trawls, having weak skin, large scales and watery tissues. This results in a high level of mortality for fish that pass through the net, and there is 100% mortality for deep-sea fish and invertebrates discarded at the surface as ‘by catch’. Most deep-sea fisheries focus around seamounts, where there are high levels of biodiversity and endemism within the macro- and megafauna (de Forges *et al.* 2000; Koslow *et al.* 2001). Studies of trawling impacts suggest up to 95% loss of large sessile fauna in fished seamounts compared to unfished seamounts south of Tasmania (Koslow *et al.* 2001). Trawling impact studies have been instrumental in creating the first deep-sea marine protected areas, 12 seamounts south of Tasmania at minimum depths of 1100 m, and 19 seamounts in the New Zealand exclusive economic zone (EEZ) (A. Koslow, personal communication 2003).

In the northern North Sea, colonies of the deep-water cold coral *Lophelia pertusa* are at risk from deep-sea trawling activities (Rogers 1999; Roberts 2002). These colonies may reach up to 200 m in height and 4 km in length along the Norwegian slope, and harbour a highly diverse associated fauna (Rogers, 1999). Significant portions of the *L. pertusa* beds have already been impacted by trawling activities (Rogers 1999; Roberts 2002). Better knowledge of the distribution and species structure of these deep-water reefs is needed to help assess and control future damage from fisheries.

Future trends in deep-sea fisheries

It has been argued that there may be no such thing as an economically sustainable deep-sea fishery (Merrett & Haedrich 1997; Roberts 2002). Deep-sea fish are increasingly being viewed by the fishing industry as a non-renewable resource, to be effectively ‘mined’ until no longer economically viable (Clark 2001). We can say with near certainty that all current deep-sea fisheries are not sustainable, given current management practices, over time scales of 10–20 yr. What must be decided is whether it is environmentally, economically and politically acceptable to continue exploiting these fisheries, and whether the fishing industry should be encouraged to explore and exploit new fisheries at ever greater depths.

Oil and gas drilling rigs

Key characteristics

The oil industry usually classifies oil fields below 500 m of water as ‘deep’ and those below 1000 m as ‘ultra-deep’. In the 1990s, the offshore oil industry commenced exploratory

drilling and production in deep and ultra-deep waters. The Brazilian oil company Petrobras has begun production at the ultra-deep Roncador field in the Campos Basin in 1853 m of water. BP, Shell, and ExxonMobil dominate exploratory activities at up to 3000 m in the Gulf of Mexico, where deep reserves are thought to attain 12 billion boe (barrels of oil equivalent; Douglas-Westwood 2002). Very large oil reserves have been discovered in ultra-deep water off West Africa and are currently being drilled by TotalFinaElf and ExxonMobil. Approximately 60% of world oil production comes from non-OPEC nations, and the majority of this is from declining terrestrial and shallow-water reserves. Hence, in the next 20 years, non-OPEC oil production may shift substantially to deep and ultra-deep fields.

Several oil companies with deep-sea interests are conducting baseline studies and environmental impact assessments (Bett 2001). The general impacts of deep-sea drilling activities will be similar to those already studied from shallow water, and we review those here in the context of what is known about deep-sea ecology (Table 1).

Impact of drilling in shallow-water

The principal benthic impacts of the offshore oil and gas industry, aside from the presence of the metal structures themselves, is the release of drilling muds and drill cuttings. Drilling muds, an essential tool in the safe recovery of oil from high-pressure subterranean sources, are composed of a mixture of water, ground rock and clays. More recently, drilling muds with synthetic components have also been used. The mud lubricates and cools the drill bit and allows the pressure to be controlled to prevent blow-outs. Drilling mud also carries the drill cuttings up out of the well. Refined oils are usually added to the drilling mud as a lubricant. The drill cuttings and drilling mud are separated back on the platform, the drilling muds recycled, and the cuttings discharged back into the sea, where they accumulate on the seabed. The piles of cuttings are usually contaminated with drilling muds, and are thought to pose a significant risk to marine life (Daan & Mulder 1996; Raimondi *et al.* 1997; Mauri *et al.* 1998; Grant & Briggs 2002).

Offshore operators usually have economic as well as regulatory incentives to reduce the quantities of drilling muds and cuttings released onto the seabed. Nonetheless, large quantities of drill cuttings have accumulated around platforms; for example, 30 years of North Sea drilling have left between 1 and 1.5 million tonnes of drill cuttings on the seafloor (UKOOA [UK Offshore Operators Association] 2002). The principal impacts of drill cuttings on the seabed are well documented. Physical smothering, organic enrichment and chemical contamination (by hydrocarbons, heavy metals, special chemicals and sulphides) are known to occur close to the pollutant source (Daan & Mulder 1996; Mauri *et al.* 1998; Grant & Briggs 2002). Experimental studies have indicated that the presence of drilling muds can inhibit larval settlement of certain marine invertebrates (Raimondi *et al.* 1997).

In addition to the problem of chronic pollution from drill cuttings, deep-sea drilling also includes risks resulting from catastrophic failures in offshore operations. For example, in March 2001, the US\$ 350 million 'P-36' giant deep-water drilling rig exploded and sank in 2000 m of water at the Brazilian Petrobras Roncador oil field, with unknown environmental consequences. In reality, the impacts of this event may be localized. The environmental impact of such disasters depends on the frequency of their occurrence, which is usually low, but future expansion of offshore activities may increase the threat.

Increased sensitivity of deep-sea habitats to drill cuttings and muds

When drill cuttings are deposited in areas of high current-speeds, such as the southern North Sea fields, the fine rock chips are usually dispersed quickly, allowing biodegradation of drilling-mud contaminants to take place. In the northern North Sea, where water is deeper and current speeds are lower, drill cuttings have accumulated, causing significant localized environmental impacts (UKOOA 2002). This is important if we are to consider the potential impacts of drill cuttings on deep-sea ecosystems. Although no major studies have been carried out, it seems probable that drill cuttings will pose a greater local environmental hazard in the deep sea than in shallow water due to low community resistance and slow recovery in the deep sea. Low current speeds and sediment accumulation rates are normal in deeper waters, and the low background levels of productivity and biomass will make the impact of organic enrichment more significant. Furthermore, the removal and onshore processing of drill cuttings (currently in feasibility studies in the UK) will be much more costly, and hence less likely to occur in deep operations conducted far offshore.

Quantifying the environmental impact of shallow-water and potential deep-water drill cuttings is problematic given the uncertainties with regard to future oil discoveries. Studies from the North Sea indicate that there are approximately 1.3 million m³ of drill cuttings on the seabed surrounding the 121 installations for which data are available (UKOOA 2002). Hence, for each installation, a volume of approximately 10 000 m³ exists, which is equivalent to a sediment mound 10 m in diameter and 1 m thick for each installation. Currently, the most active region of deep-water drilling in the world is the Gulf of Mexico, with approximately 50 deep-water and ultra-deep water drilling rigs in operation. Hence if each rig has an 'impact zone' of 2 km², this amounts to a total of 100 km² of deep-sea impact. The areal impact of deep-sea oil drilling is clearly very small in comparison with, for example, the total area of the deep Gulf of Mexico (1.2 million km²).

Future trends in oil and gas extraction

For the past 20 years, oil demand has increased steadily with human population growth, and oil production has ramped up to support it. Forecasts now predict that by

2025, the demand for oil will be in excess of 120 million bpd (barrels per day) (Douglas-Westwood 2002). With production from OPEC countries in decline, the extra oil required will likely come from non-OPEC sources, including deep water.

Regulations are currently in place to ensure that oil companies make appropriate environmental impact assessments in exploratory regions. For example, a consortium of oil companies has recently funded an extensive survey of the deep benthic ecosystem west of Scotland (Bett 2001). These surveys will undoubtedly have some influence on the choice of drilling sites. Thus, it is unlikely that drilling in the well-publicized deep-water coral beds off the Norwegian and Scottish coasts would be publicly acceptable. The same cannot be said for soft-sediment benthic habitats, which also harbour high levels of biodiversity (Gage 2001; Snelgrove & Smith 2002), yet are not so picturesque.

Extraction of mineral and alternative fuel resources

Key characteristics

Although dwarfed by the US\$100 billion yr⁻¹ offshore oil industry, the marine minerals industry has recently seen unprecedented expansion. The discovery of high quality diamonds in the offshore deposits of Namibia, coupled with developments in marine sand and gravel extraction, has created industries valued at US\$2 billion yr⁻¹ (Wiltshire 2001). In waters deeper than 1000 m potential mineral resources include manganese nodules and crusts, polymetallic sulphides, phosphorites and methane hydrates.

Mineral extraction at great depth involves technological, economic, environmental and legal hurdles, which have together hindered mineral exploitation to date. Thus far, no commercially profitable extraction of deep-sea minerals has occurred. The majority of marine minerals lie outside national jurisdictions (i.e. beyond Exclusive Economic Zones). The UN created the International Seabed Authority (ISA) in 1994 to oversee mining claims in international waters, and to ensure adequate environmental impact assessments. It was realized early on that deep-seabed mining would be highly environmentally destructive, akin to strip mining in terrestrial environments (Jumars 1981). Technological challenges, and a changing economic outlook for deep-sea mineral resources (such as cobalt, copper and nickel), have slowed the development of deep-water mining. Legal development of international mining codes, and the increasing realization that the most valuable ores lie in sea floor regions with very high local biodiversity, have added further complications. Ultimately, the most significant mining resource from the deep-sea could be methane hydrate. Methane gas, frozen at ocean depths between roughly 500 and 1200 m, is conservatively estimated to hold over twice the total combustible carbon known from all other fossil fuels on the planet (USGS [United States

Geological Survey] 2002). Japanese and USA scientific programmes are currently evaluating the feasibility of mining this resource.

Manganese nodule mining

In 1873, the first manganese nodules were dredged from the seafloor by the early oceanographic vessel, *HMS Challenger*. The nodules were found to be rich in manganese, iron and a number of other metals. These potato-sized accretions were long considered no more than a scientific curiosity, but in the mid 1960s a potential commercial value was recognized (Mero 1965). Nodules are formed by the precipitation of dissolved metals onto a hard substrate; typically a nucleus of foreign material such as a shark's tooth, and then the nodule surface itself. Two types of growth are identified: hydrogeometric accretion of hydrated metal oxides present in sea water, and diagenetic accretion of metals and metal compounds from the interstitial waters of the sediment (Halbach *et al.* 1988). Nodules in the abyssal Pacific accrete very slowly, typically increasing in diameter at rates of 1–2 mm per million years (Ghosh & Mukhopadhyay 2000; McMurtry 2001). Thus, a nodule 4 cm in diameter may be 10–20 million years old.

The abundance of nodules on the seabed and the grade of the ore are the critical terms in determining the commercial value of nodule deposits. In the Clarion-Clipperton Fracture Zone, north-east Pacific, nodules may reach abundances of 10–15 kg m⁻², potentially enough to sustain the estimated 6000 metric tonnes per day minimum mining requirement (Thiel *et al.* 1998; Oebius *et al.* 2001). The principal metals of commercial interest contained in manganese nodules are copper, nickel and, most importantly, cobalt. Cobalt is a 'strategic' metal, vital for the manufacture of super-alloys in jet engines and other high-performance applications; recent discoveries of cobalt-rich nodules around the Cook Islands of the south Pacific have aroused particular mining interest (Clark *et al.* 1995).

The proposed methods for the mining of manganese nodules are important when environmental impacts are to be considered (Fig. 3). Some of the advanced technologies developed for the oil and gas industry, the offshore diamond industry, and the laying of deep-sea cables may be of use in marine mineral mining (Wiltshire 2001). For example, remotely operated vehicles (ROVs) capable of heavy work at 3000 m depth are now available. For the laying of deep-sea cables, tracked cutting vehicles have also been developed. Specially designed nodule-mining vehicles are now being developed; the most promising systems combine a tracked collector vehicle with a hydraulic lift to carry the nodules to a mother-ship (Oebius *et al.* 2001; Thiel 2003). Simpler early mining concepts such as the 'continuous-line-bucket' or the basic dredge are now outdated. The reality is that the technology required to mine nodules is substantially developed; other factors, mainly the global market demand for cobalt, and environmental issues, will most likely dictate when mining operations commence in earnest.

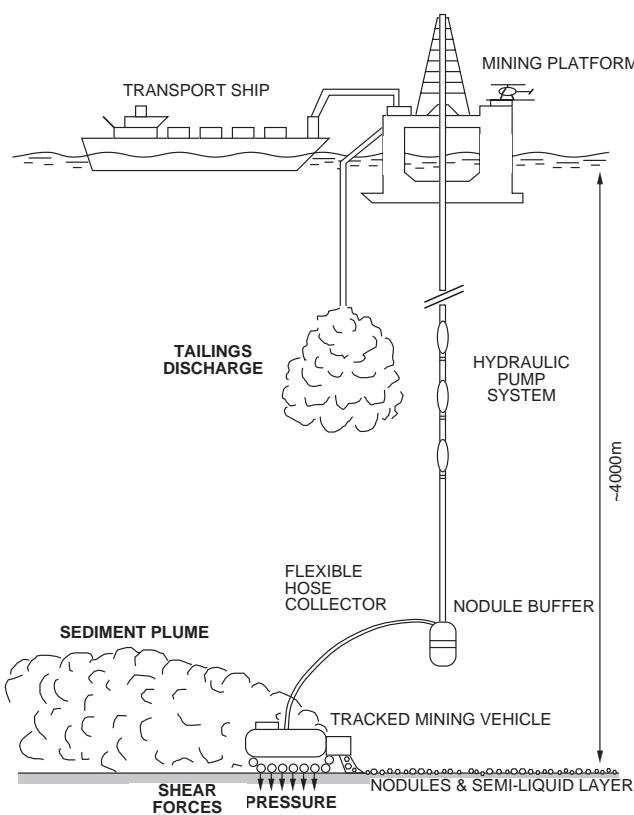


Figure 3 The manganese nodule mining concept, involving a tracked collector vehicle, hydraulic riser, mining platform and transport ship. The principal anticipated environmental impacts are highlighted in bold. Modified from Oebius *et al.* (2001)

Manganese nodule mining may ultimately be the largest-scale human activity to directly impact the deep-sea floor. Twelve pioneer investor countries and consortia have conducted hundreds of prospecting cruises to investigate locations of high manganese nodule coverage, especially in the area between the Clipperton and the Clarion fracture zones (Glasby 2000). This region extends over 6 million km² (out of a total of 46 million nodule-rich km² worldwide) and may contain 7.5 billion tonnes of manganese, 78 million tonnes of cobalt, 340 million tonnes of nickel and 265 million tonnes of copper (Ghosh & Mukhopadhyay 2000; Morgan 2000). Currently, seven contractors are licensed by the International Seabed Authority to explore nodule resources and to test mining techniques in seven claim areas, each covering 75 000 km² (i.e., an area roughly half the size of the state of Florida).

When mining begins (probably not for >10–20 yr), each mining operation is projected to directly disrupt, through nodule ‘harvesting’, 300–800 km² yr⁻¹ of seafloor (Oebius *et al.* 2001; ISA, personal communication 2002), and to disturb the seafloor biota over a poorly constrained area perhaps 2–5 fold larger due to redeposition of suspended sediments (Smith 1999; Thiel *et al.* 2001). Thus, in any given year, nodule mining by two to three contractors might severely

damage abyssal sea floor communities over areas of 1200–12 000 km², and 15 years of such mining could impact as much as 180 000 km² of sea floor (a total area of disturbance half the size of Germany). A clear direct impact of nodule mining will be removal of the nodules themselves, which will require millions of years to re-accrete (Ghosh & Mukhopadhyay 2000; McMurtry 2001). The mining will thus remove the only hard substrate present over much of the abyssal seafloor, yielding habitat loss and at least local extinction of the nodule fauna, which differs markedly from the fauna of surrounding sediments (Mullineaux 1987; Bussau *et al.* 1995).

Nodule-harvesting activities will also remove much of the top 5 cm of sediment, distributing a substantial fraction of this material into the water column (Oebius *et al.* 2001; Thiel *et al.* 2001). In the direct path of the nodule collector, many sediment-dwelling animals will be killed immediately, and compacted, organic-poor subsurface sediments will be at least temporarily exposed (Jumars 1981; Smith 1999; Oebius *et al.* 2001; Thiel *et al.* 2001). Resuspended sediments will rain out onto the seafloor, burying benthos to varying depths, and covering the sediment-water interface with layers of subsurface sediments (Jumars 1981; Smith 1999; Sharma *et al.* 2001). Because abyssal nodule habitats normally are very stable (possibly the most physically stable habitats on Earth) and are dominated by very small and/or fragile animals, the direct effects of commercial-scale nodule collection are predicted to be devastating to the benthos (Jumars 1981). The indirect impacts of even modest sediment redeposition may also be deleterious because much of the abyssal macrofauna and megafauna appears to be surface-deposit feeders that consume the meagre flux of particulate organic matter arriving from the water column. Redeposition of subsurface, food-poor sediment from the mining plume will dilute food resources, potentially yielding nutritional stress to the benthos. Nutritional stress will be enhanced if redeposition is chronic, in other words recurs over extended time periods (months) due to concentration of mining activities in a single area.

A number of impact experiments have been conducted to evaluate the sensitivity and recovery times of abyssal benthic communities subjected to nodule-mining disturbance. The impact experiments have used disturbances of the following two types. (1) In ploughing disturbance, an 8-m wide frame with multiple plough heads was dragged over the ocean floor in the south equatorial abyss, directly impacting ~20% of the seafloor within a circular area of 11 km² (the DISCOL experiment; Thiel *et al.* 2001). (2) In sediment removal and redeposition disturbance, a sediment-pumping system was towed up to 49 times through a seafloor zone 200–400 m wide and 2–3 km long, sucking up ~20% of the sediments from a track 5–10 cm deep and ~1 m wide and then disgorging them in a plume at an altitude of ~5 m (Thiel *et al.* 2001).

Although these experiments produced disturbances much lower in intensity and many orders of magnitude smaller in spatial scale than would result from commercial mining, they

provide some insights into the sensitivity and minimum recovery times of abyssal nodule communities subjected to mining disturbance. Direct ploughing disturbance (DISCOL) dramatically reduced the abundances of macrofaunal polychaetes (51.4%), tanaids (72%), isopods (81.5%) and bivalves (90.7%) (Borowski & Thiel 1998). The megafauna (for example holothurians and ophiuroids) was also heavily impacted immediately after the disturbance, decreasing sharply in abundance within plough tracks (Bluhm *et al.* 1995). In areas of resettling sediment, the disturbances of macrofaunal and megafaunal abundance varied from quite low to negligible (Bluhm *et al.* 1995; Borowski & Thiel 1998). Three years after the disturbance event, the abundance of dominant macrofaunal taxa, especially polychaetes, had reached pre-disturbance levels, but macrofaunal diversity remained depressed even after seven years (Borowski & Thiel 1998; Borowski 2001). The abundance and diversity of megafauna also remained below pre-disturbance levels seven years after disturbance (Bluhm 2001). Based on small sample sizes, nematode densities and biomass were not detectably affected by the disturbance event, while benthic copepods showed some decrease in diversity at the species level seven years later (Ahnert & Schriever 2001; Vopel & Thiel 2001).

Results from sediment removal/redeposition (or BIE) experiments demonstrate similar high sensitivity of abyssal seafloor communities to physical disturbance. Immediately following apparent redeposition of <1 cm of sediment (Yamazaki *et al.* 1997), reductions have been observed in the abundance of many components of the biological community, including megafauna (21–48%), macrofauna (up to 63%), meiofauna (23%) and microbiota (one to three orders of magnitude), possibly due to burial by settling sediment, and interference with respiratory and feeding functions (Ingole *et al.* 2001; Raghukumar *et al.* 2001; Rodrigues *et al.* 2001). Two years after redeposition, the abundance of surface-deposit-feeding and mobile megafauna may remain low, suggesting lingering impacts on their food resources (Fukushima *et al.* 2000).

We must be extremely cautious in extrapolating these experimental results to the impacts of commercial mining, which would be much more intense, and would devastate much larger areas of seafloor (i.e., 10 000–100 000 km² versus 1–11 km²). However, abyssal benthic communities will be substantially disturbed by even modest amounts (about 1 cm) of sediment redeposition resulting from mining activities, and full sediment-community recovery from major mining disturbance will take much longer than seven years. We cannot predict the likelihood of species extinctions from nodule mining because we do not know the typical geographic ranges of species living within the nodule regions (are ranges large or small relative to the potential spatial scales of mining disturbance?). Preliminary data based on morphological analyses suggest that common polychaete species may range well beyond the scales of impact of individual mining operations (Glover *et al.* 2002), but these

results must be verified with molecular techniques due to the frequency of cryptic species in marine invertebrates (Knowlton 2000). However, we can predict that the recovery of the nodule fauna within a mined area will take millions of years due to the extremely slow regeneration rate of their required substrate, manganese nodules. It is clear that to predict fully commercial mining impacts, substantially more information is required concerning species ranges, sensitivity to sediment burial, and the spatial-scale dependence of recolonization in abyssal benthic communities.

This review deals with deep-sea benthos, so we have not discussed the potential impacts of sediment plumes on the biota of the deep water-column. Sediment plumes from mining have the potential to substantially alter the concentrations of suspended particles for 10 s to 100 s of kilometres downstream from the release point (Rolinski *et al.* 2001). An increase in the concentration of non-nutritive sediment grains in the usually very particle-poor deep water column could interfere with the feeding activities of particle grazers and suspension feeders over large areas.

Manganese crust mining

Manganese crusts are pavement-like, concretionary masses formed on submarine rock outcroppings, which are found near the summits and flanks of seamounts, ridges, undersea volcanoes and other areas where sediment does not accumulate. They are usually formed through the same hydrogeologic processes that create manganese nodules. Although initially ignored as a mineral resource in favour of manganese nodules, there has been renewed interest in crusts because they are very rich in cobalt (Halbach & Manheim 1984). The presence of crusts at shallower depths, and within EEZs, makes them a potentially more favourable short-term mining option than manganese nodules.

Mining technologies for the extraction of cobalt-rich crusts are much less developed than those for nodules. Most concepts envisage a tracked cutting/collector vehicle and hydraulic riser system (Thiel *et al.* 1998). Although no experimental studies have been conducted, the environmental consequences of crust mining are likely to be more localized than those from nodule mining. The principal impacts will be the destruction of sessile fauna on the crusts themselves, and the potential impacts of discharges from the processing ship. While the areas to be mined are much smaller, the potential for species extinctions may be larger due to the high diversity and endemic nature of seamount biota (Koslow *et al.* 2001), and because the hard substrate lying under the crust may not be equally suitable for sessile faunal colonization. More realistic assessments of the environmental consequences will only be possible once the mining technology becomes closer to reality, and the potential spatial scale of mining activities is better known.

Polymetallic sulphide mining

Polymetallic sulphides occur in two forms, namely metalliferous muds and massive consolidated sulphides. Metals in

the earth's crust are leached into circulating subterranean waters; these warm, metal-rich waters are expelled back into the sea, whereupon metals are precipitated. If precipitation occurs in sediments, the metals become associated with muds, as has occurred in the central graben of the Red Sea (Degens & Ross 1969) and the Gulf of California. Eventually, these muds may be deeply buried and, under pressure, form consolidated massive sulphides. Hard consolidated sulphides may also be precipitated directly, for example at hydrothermal vents (Scott 1992).

Polymetallic sulphides are common at spreading centres along mid-ocean ridges, but only limited research has been conducted on their ore-resource potential. At the Atlantis II Deep in the central Red Sea, a hot brine pool covers the seafloor, trapping sediments in an ore-rich fluid mud (Karbe 1987). A mining operation taking 100 000 metric tonnes of mud per day would yield commercially viable quantities of copper, cobalt, gold and silver for 16 years (Mustafa *et al.* 1997; Thiel 2003).

The only massive consolidated sulphides of current commercial interest are the deposits in the Manus Basin, north of New Guinea, and in the Havre Basin within New Zealand's EEZ. These are inactive hydrothermal vent sites, and mining leases have already been issued by the Papua New Guinea and New Zealand governments (Wiltshire 2001). Exploration cruises and some preliminary tests have been conducted in the Manus Basin, the primary economic goals being gold and silver, with secondary targets being zinc, lead and copper.

As is the case with manganese crusts, it is difficult to predict the environmental impacts of polymetallic sulphide mining. So far, mining targets include inactive hydrothermal vents, a habitat supporting the low-biomass communities typical for deep-sea hard substrates, rather than the chemoautotrophy-based assemblages characteristic of active hydrothermal vents (Van Dover 2000). Potential mining activities are likely to result in localized destruction of this fauna, and there may be some indirect seafloor impacts caused by on-ship processing. If mining activities were to switch to active hydrothermal vents, the local community impacts would be much more dramatic because active vents have the highest biomass levels recorded in the deep sea (Van Dover 2000). However, the general nature of vent habitats, which tend to be physically dynamic, temporally varying, and geographically fragmented, appears to have selected for a biota with high dispersal abilities and rapid population growth rates (Van Dover 2000). These characteristics may well allow vent communities to recover rapidly from localized mining disturbance. Nonetheless, environmental impact studies are needed in the specific vent fields of commercial interest to predict and effectively manage the deleterious effects of the deep-sea mining of massive sulphides.

Methane hydrate extraction

Methane-hydrate deposits in the deep sea and Arctic permafrost are thought to represent the largest single source

of combustible organic carbon on the planet. A hydrate is formed when, under high pressure and low temperatures, methane molecules become trapped in a solid 'cage' of water molecules. The widespread nature of these hydrates in slope sediments has led to research into both their role in regulating the earth's climate, and their potential use as an energy resource (DeLong 2000; Adam 2002).

Several countries have commenced feasibility studies for the extraction of methane hydrate, but only two drilling operations have so far been carried out, in Japan's Nankai Trough, and in a permafrost region in northern Canada. Little is known about the potential environmental impacts of hydrate extraction. As most hydrate deposits are buried in relatively shallow sediments, it seems probable that there will be significant impacts on the sediment-dwelling fauna. Potentially more catastrophic impacts may occur if drilling activities promote rapid dissociation of methane hydrate deposits, causing massive seafloor slumping (Adam 2002). Further research into methane hydrate extraction will undoubtedly take place, and with the projected decline in oil and gas production from 2030 onwards, large-scale methane hydrate extraction may begin by the middle of the 21st century.

Future trends in mineral and fuel extraction

Future trends in the marine minerals industry will depend to a large extent on economics, notably the cost of extraction and the market value of the minerals. For example, recent declines in the price of cobalt, related to an economic downturn in the high-technology sector, coupled with the development of new terrestrial cobalt-mining operations in Australia and Canada, will probably delay commercial mining ventures in the deep sea (Roskill-Consulting 2002). However, the long-term demand for cobalt is likely to remain strong (it is used in batteries, a rapid-growth sector), so its price may rise again and marine mineral extraction may become economic. Furthermore, cobalt is a 'strategic' mineral, necessary for a number of high-performance military applications; governments are thus continuing to explore cobalt reserves even if current extraction costs are not profitable on the global market.

Although most of the research into deep-sea mineral extraction has concentrated on manganese nodules, the first minerals to be commercially extracted from below 1000 m will probably be gold and silver from polymetallic sulphide deposits in the Manus Basin, Papua New Guinea (Wiltshire 2001). There are few legal complications (as the deposits lie within an EEZ) and the depth is not as great as that for nodules. Successful mining at this site may create a technological expertise that reduces the cost of mining elsewhere in the deep ocean. Developing countries, particularly South Pacific nations lacking major industries, may well be prepared to take greater risks in the development of such mining operations, and it is likely there will be a gradual emergence of deep-sea marine mineral industries from small start-up ventures in a 10–20 yr time frame.

Climate change

Key characteristics

The Earth has warmed by approximately 0.6°C during the past 100 years, and from 1976 to 2002 the rate of warming has been greater than at any time during the last 1000 years (IPCC 2001; Walther *et al.* 2002). In the marine ecosystem, recent studies indicate a general warming trend over large parts of the world ocean during the past 50 years (Levitus *et al.* 2000), although there are regional differences. The IPCC suggests that by 2020 the climate will be a further 0.3–0.6°C warmer, and that sea level will rise between 2.6 cm and 15.3 cm (IPCC 1996).

Individuals, populations and communities in the deep sea are unlikely to respond to overall global averages; rather, they will respond to local and regional changes in primary production, organic-carbon flux, and current regimes driven by climate change. Such changes may be spatially and temporally heterogeneous over a broad range of scales. Some studies have suggested that under future greenhouse conditions, El Niño events, and consequent temporal variations in primary production and particulate organic-carbon flux to the seafloor in the equatorial Pacific (Dymond & Collier 1988; Smith *et al.* 1996), will be more frequent (Timmermann *et al.* 1999). However, sea-surface temperatures in the eastern equatorial Pacific in fact declined over the course of the 20th century, and this has been attributed to atmospheric warming causing a strengthening of the Pacific trade winds (Cane *et al.* 1997).

Given the great uncertainty with regard to climatic influences on the surface ocean, predicting specific impacts in the deep sea is very difficult indeed. For example, researchers are just beginning to understand the potential impacts of climate change on global thermohaline circulation (Schmittner & Stocker 1999), which could have catastrophic consequences on deep-sea life. Evidence from the fossil record shows major extinctions of deep-sea benthic taxa at the end of the Palaeocene epoch, 65–55 million years ago (mya) associated with a rise in bottom temperature (Rogers 2000), one possible cause being a change or cessation of global thermohaline circulation causing widespread anoxia in deep-ocean bottom waters (Kennett & Stott 1991).

Less drastic changes in surface water processes created by global warming, particularly changes in primary production and phytoplankton community structure, will make themselves felt in the deep-sea ecosystem through benthopelagic coupling.

Benthopelagic coupling

While the deep sea is often considered stable compared to shelf or coastal environments, this is only a relative comparison. In reality, deep-sea benthic processes are often tightly linked, or coupled, to particulate-organic flux from the pelagic realm. Coupling occurs because the deep sea is highly dependent on sinking food material, the quality and quantity of which varies spatially and temporally across the

ocean surface on seasonal, interannual and decadal time scales.

Food supplies at the sea floor can arrive directly from the simple sinking of phytoplankton material and marine snow, or in the form of larger organic parcels such as fish, whale carcasses and macrophytic debris (such as kelp and *Sargassum* weed). Studies that measure the downward flux of food material in the water column have reported both seasonal, interannual and decadal scale variability (Smith & Kaufmann 1999; Gooday 2002). The impact on benthic animals of temporal variability is of direct relevance to climate change, which may cause major changes in ocean productivity regimes. Current evidence indicates that smaller, more rapidly reproducing biota, such as microbes and foraminifera, show a rapid population response to episodic food input at the deep-sea floor, whereas larger, more long-lived taxa generally integrate seasonal changes and may only respond to interannual and decadal changes (Gooday 2002). Some megafaunal animals may also respond to the arrival of food by synchronizing their reproductive activity (Tyler 1988).

Predicting the full response of deep-sea ecosystems to climate change, via benthopelagic processes, is difficult, although we can hazard some educated guesses. A number of studies have shown that benthic biomass and abundance, bioturbation rates, the depth of the bioturbated layer, and organic-carbon burial in sediments co-vary with particular organic-carbon flux to the deep-sea floor (Emerson 1985; Smith *et al.* 1997; Smith & Rabouille 2002; Smith & Demopoulos 2003). Similar correlations have been documented between these benthic parameters and primary production in overlying waters (Rowe 1971; Smith 1992; Glover *et al.* 2001, 2002). However, the relationship between particulate-organic-carbon flux (or food availability) and species diversity is not so obvious (Levin *et al.* 2001; Glover *et al.* 2002). In fact, the communities of the least productive regions of the abyssal plain, such as those underlying oligotrophic gyre waters, are highly diverse. In very general terms, climatic changes resulting in increased near-surface productivity and consequently, deep organic-carbon flux, will almost certainly lead to increases in benthic standing crop, bioturbation rates and depths, and carbon sequestration in deep-sea sediments. Beyond this general prediction, the precise nature of ecosystem change (for example in biodiversity levels) will depend on many factors, such as the temporal scale over which changes occur, the quality of particles reaching the sea floor (such as fresh diatom aggregates versus heavily reworked marine snow) and the original composition of the benthic fauna. Different types of deep-sea communities (for example in the oligotrophic abyss and within oxygen minimum zones) will respond in markedly different ways.

Future trends

Although some impacts of climate change are evident (Walther *et al.* 2002), the main threats lie in the future. Many more long-term datasets are required to establish baseline

data to allow evaluation of the direction and magnitude of changes to deep-sea ecosystems resulting from climate change. However, it seems unlikely that drastic changes in deep-sea ecosystems will occur as a result of climate change by 2025.

Natural versus anthropogenic influences

An important question is the degree to which natural forcing factors, such as biogenic disturbance, may be a useful analogue for potential human impacts (Strömberg 1997; Tyler 2003). With a few exceptions, these natural factors do not make useful analogues of anthropogenic disturbance due to dramatic differences in the nature, intensity and spatial scales of impacts (Table 4).

For example, variations in the natural vertical flux of particulate-organic carbon may bear certain superficial similarities to the dumping of sewage sludge. However, the principal impacts of sewage sludge, outlined above, include both organic enrichment as well as introduction of unnatural toxicants. Similarly, although benthic storms may yield rapid sediment resuspension and deposition over large areas of the sea floor (Hollister & McCave 1984), community resistance to these natural events will differ fundamentally from that in response to nodule-mining redeposition. Deposition from

natural benthic storms impacts species exposed (and adapted) to such disturbances over ecological and evolutionary time-scales. The response of communities routinely exposed to such natural perturbations is likely to differ substantially (in intensity of population reductions and rates of community recovery) from the response of communities living in the very physically stable, extremely food-poor nodule provinces, where burial events are not part of the local ecological and evolutionary history.

The use of natural analogues to predict future human impacts in the deep sea is problematic. Future research to elucidate human impacts should concentrate on clever experimental studies (both small and large scale) in combination with acquiring better knowledge of natural processes in deep-sea ecosystems.

IDENTIFIED LONG-TERM TRENDS

To predict the status of the ecosystem in 25 years time, it is valuable to examine existing long-term studies of ecological changes in the deep sea, however, these studies are few in number. In the 1980s, long-term ecological studies were initiated to explore temporal variability in the abyssal north-east Atlantic and north-east Pacific. At the same time, the first palaeoceanographic studies of long-term changes in the

Table 4 Summary of major natural environmental forcing factors in the deep sea.

<i>Natural forcing factor</i>	<i>Major impact on benthos</i>	<i>Human analogue?</i>	<i>Temporal scale</i>	<i>Spatial scale</i>	<i>Reference</i>
<i>Food input</i>					
Organic carbon flux (phytodetrital impact)	abundance and diversity	disposal of organic waste	seasonal, interannual	regional	Tyler (1988)
Whale-falls	abundance and diversity	disposal of organic waste	1–100 years	local (0–30 m)	Smith & Baco (2003)
Changes in surface water productivity (e.g. ENSO)	abundance and diversity	climate change	interannual, decadal	regional	Karl <i>et al.</i> (1996); Smith <i>et al.</i> (1997)
<i>Biogenic disturbance</i>					
Small-scale faecal mound formation	abundance and diversity		days–months	local (0–1 m)	Smith (1994)
Whale-falls	abundance and diversity	disposal of organic waste	1–100 years	local (0–30 m)	Smith & Baco (2003)
Wood and kelp falls	abundance and diversity		1–5 years	local (0–5 m)	Smith & Baco (2003)
<i>Hydrodynamics</i>					
Benthic storms	smothering, reduced diversity	sediment plumes from mining, dredge spoil disposal	days	100–1000 km	Hollister & McCave (1984)
Turbidity currents	smothering, reduced diversity, inhibit settlement		1000–100 000 year	basin	Nardin <i>et al.</i> (1979); Glover <i>et al.</i> (2001)
<i>Chemical emissions</i>					
CO ₂ release	lowering of pH, toxicity	CO ₂ sequestration	decades	0–10 km (plume)	Sakai <i>et al.</i> (1990)
Methane hydrate release	unknown		not studied	localized emissions	Kvenvolden (1988)
Hydrogen sulphide and trace metals from vents	toxicity, and energy source for microbes	trace metal contamination	decades	localized emissions	Van Dover (2000)

deep-sea sedimentary record began. On the time-scale of millions of years, Mesozoic oxygen minima events, generated by apparent shut-downs in global thermohaline circulation, are thought to have caused widespread extinctions in the deep-sea benthic fauna (Kennett & Stott 1991; Rogers 2000). During the Pliocene (5.4–1.6 mya), deep-sea benthic ostracod diversity was possibly altered by glacial/interglacial climate shifts over timescales of 40 000 years (Cronin & Raymo 1997). Similarly, late Quaternary climatic events appear to have influenced deep-sea benthic diversity on millennial time scales (Cronin *et al.* 1999).

Changes over ecological timescales are much more relevant to the 2025 time horizon than longer-term geological patterns. We thus focus on the only two major long-term ecological studies of the abyssal deep-sea (covering decadal-scale changes), and discuss their significance to predicting the status of deep-sea ecosystems in 2025.

Long-term trends in the north-east Pacific abyss

At the ‘Station M’ site in the north-east Pacific, a detailed long time-series investigation of food supply and demand at the benthos was carried out between 1989 and 1996 (Smith & Kaufmann 1999). The site is located 220 km west of the Californian coast, in 4100 m of water and is characterized by silty-clay sediments with low topographic relief. Surface waters over this site have well developed spring-summer blooms, with considerable interannual variability in primary production. Researchers at this site have measured the particulate organic carbon (POC) flux into deep sediment traps (a measure of food flux to the sea floor), sediment community oxygen consumption (SCOC, a measure of total metabolic activity within the sediments) and have taken time-lapse photographic images over a period of seven years, allowing investigation of both seasonal and interannual changes in a number of ecosystem parameters.

On a seasonal scale, peaks of POC flux at sediment traps moored 600 m above the bottom (above the influence of resuspension) were recorded, coinciding with summer phytoplankton blooms in the surface waters (Baldwin *et al.* 1998). These seasonal events also resulted in the deposition of phytodetrital aggregates on the sea floor (Beaulieu & Smith 1998). On an interannual time scale, significantly higher flux was recorded in 1991, 1993 and 1994, coinciding with peaks in observed SCOC (Smith & Kaufmann 1999). Finally, and potentially most significantly, the POC:SCOC ratio (a ratio indicating surplus or deficit of food settling as small particles) progressively decreased over the period 1989–1996 from about 0.99 to about 0.30 (Smith & Kaufmann 1999). This suggests that the proportion of food arriving as small particulate flux from surface waters fell by two-thirds, while the metabolic demands of the sediment community remained roughly the same.

One explanation for the decline in POC flux over the 1989–1996 period could be increasing sea-surface temperatures in the eastern North Pacific (Roemmich 1992; Smith &

Kaufmann 1999). Surface warming is thought to lead to a reduction in the depth of the mixed layer, reducing the supply of nutrients to the euphotic zone and hence reducing the export of primary production to the sea floor (McGowan *et al.* 1998). Increased sea-surface temperatures are also correlated with a number of biological impacts in north-east Pacific coastal ecosystems, such as the reduction in the abundance and size of kelp populations, and changes in the faunal composition of rocky shores (Barry *et al.* 1995; Smith & Kaufmann 1999).

Smith and Kaufmann (1999) suggest three possible explanations for the discrepancy between food supply and demand over the seven-year period at Station M. The first is a methodological problem with the sediment traps, in particular the clogging of sediment traps during periods of high particle flux. The second is that additional food material, which bypasses the sediment traps (such as large organic parcels or material laterally transported down the continental slope), has become increasingly important at Station M. The final possibility is that the response of the benthic community to this reduction in food input has yet to be observed, either because of the slow response of the abyssal benthos, or the presence of a persistent ‘food bank’ in the sediments (Smith *et al.* 2002). The evidence for the first two scenarios seems weak; if POC flux decreased over the sampling period, problems of sediment trap clogging would also decrease. Additionally, camera-sled tows across the seafloor at Station M showed no evidence of large food parcels, and lateral input was thought to be low in view of data from sediment traps moored at two heights above the bottom (Smith & Kaufmann 1999).

These data seem to suggest that climatic influences on sea surface temperature in the North Pacific may be translated through the water column into the deep sea. If the decline in POC flux is real, it should produce long-term changes in faunal community structure, with concomitant impacts on biogeochemical cycling and other deep-sea processes (Smith *et al.* 1997; Hannides & Smith 2003). In particular, we would expect reductions in both the abundance and biomass of the abyssal fauna, as well as in the rates and depths of bioturbation (Smith & Rabouille 2002). Long time-series measurements are clearly needed to resolve ecological changes in the abyss resulting from productivity changes driven by global climate change.

Long-term trends in the north-east Atlantic abyss

The Porcupine Abyssal Plain (PAP) in the north-east Atlantic has been intensively studied since the mid 1980s; a number of research programmes investigated the downward flux and fate of organic material at the deep-sea floor (Billet & Rice 2001). A 10-year dataset of trawl samples has recently revealed a long-term change in the abundance and faunal composition of the invertebrate megafauna on the PAP (Billet *et al.* 2001).

Two major trends are apparent. Firstly, a general increase in the abundance of megafaunal animals (such as actinarians,

annelids, pycnogonids, tunicates, ophiuroids and holothurians) over the 1989–1999 sampling period has occurred, and secondly, there has been a major shift in megafaunal community composition (Billet *et al.* 2001). Before 1995, the deep-sea holothurian *Amperima rosea* was relatively rare, with a density of 2–6 individuals ha⁻¹. By September 1996, its abundance had increased to 75 individuals ha⁻¹ and, by March 1997, 20-fold to approximately 230 individuals ha⁻¹, at which time it represented 70% of total megafaunal abundance. Time-lapse photography documented even higher local abundances of *A. rosea*, with a maximum value of 6000 individuals ha⁻¹ (Bett *et al.* 2001). The high abundance of *A. rosea* persisted to the end of the sampling programme in 1999. This dramatic change in the fauna of the PAP was dubbed the ‘*Amperima* event’.

Concomitant with increases in *A. rosea* abundance were smaller increases in the abundance of the holothurian *Ellipinopin molle* and the ophiuroid *Ophiocten hastatum*. Stable-isotope and sterol chemistry analyses suggest that all three of these species are primary consumers of freshly settled phytoplankton detritus (Ginger *et al.* 2001; Iken *et al.* 2001). This common nutritional link among the species increasing in abundance suggests a response to a change in the quantity or quality of organic-matter flux to the sea floor. However, no clear temporal change in organic-carbon supply is evident from time-series sediment trap data for the PAP, although there is considerable interannual variability (Lampitt *et al.* 2001).

It is not yet apparent whether the observed long-term changes at the PAP are episodic, cyclic or related to an ecosystem regime-shift (Billet *et al.* 2001). However, the data both from the north-east Atlantic and from the north-east Pacific indicate that major ecological changes can and do occur in the abyssal deep sea over timescales of roughly 10 years.

POTENTIAL STATE OF THE DEEP SEA IN 2025

Knowledge of deep-sea ecosystems is too sparse to make rigorous predictions of the status of the deep sea in 2025. Although there is evidence of temporal change at the abyssal seafloor in both the Atlantic and Pacific over 10-year timescales, the causes of these changes are too poorly known to generalize. However, with our current understanding of potential climate change, it seems probable that significant changes in faunal abundance, community composition and biogeochemical processes will be observed at the abyssal benthos by the 2025 time horizon as a consequence of changing production regimes in the upper ocean.

Twenty-five years ago, drilling for oil at 3000 m, sequestration of carbon dioxide in the deep sea, or the mining of hydrothermal chimneys (hydrothermal vents had not even been discovered in 1977) would have seemed very far-fetched. Today all those things are possible, and in fact are only awaiting a suitable economic and political climate. Knowledge of atmosphere–ocean linkages has been completely trans-

formed, and it is only recently that the importance of the deep ocean in global climatic cycles has been recognized. With this in mind, we highlight below what we believe will, or will not, be changed significantly in deep-sea ecosystems in 2025.

Deep-sea waste disposal in 2025

- Ships will continue to sink, but will not pose any greater environmental hazard than today.
- Sewage sludge and dredge spoil disposal will have begun in the deep sea, with significant localized impacts.
- Large quantities of CO₂ (up to 1 Gt Cyr⁻¹) will be sequestered in the deep ocean; major environmental effects will initially be localized to within 10–100 km of injection points, but traceable far-field effects will begin to be observed.

Deep-sea fisheries in 2025

- All existing deep-sea fisheries will be commercially extinct.
- New fisheries will have been discovered and ‘mined’, but each fishery will have 20–30 year lifespans or less.
- Significant environmental impacts will have occurred on seamounts and deep-water coral beds; extinctions may have been prevented through the setting up of marine protected areas.

Deep-sea oil and gas drilling in 2025

- Deep (>500 m) drilling will be commonplace, and may dominate the offshore market by 2025. Ultra-deep (>1000 m) drilling rigs will be coming on line at depths up to 4000 m.
- Significant, but localized, impacts will be occurring at the deep-sea floor surrounding deep oil drilling structures, but oil companies will be mandated to minimize the impacts and acquire baseline survey data before commencing drilling operations.
- Large-scale accidents will be an occasional hazard to marine life, but are unlikely to cause more than temporary ecological incidents.

Deep-sea mineral and methane fuel extraction in 2025

- The first deep-sea marine mineral extraction of gold-rich hydrothermal sulphide deposits will have proved commercially successful.
- Developing countries will begin to encourage high-risk mining ventures on offshore deposits.
- Developed countries will continue to rely on land-based mineral extraction, but will maintain strategic interests in offshore deposits.
- Offshore oil industries, faced with declining oil and gas reserves, will start to extract methane hydrate at commercially viable quantities.

- The vast bulk of the bathyal and abyssal deep sea will remain untouched by mineral and methane extraction and there will be no convincing evidence of species extinctions (in part due to the difficulty in detecting extinctions in this poorly studied ecosystem).

Climate change impacts on the deep sea in 2025

- Generally speaking, it will be too early for major effects of climate change (such as changes in thermohaline circulation) to be felt in the deep ocean, although subtle shifts in benthic standing crop and biogeochemical recycling in sea floor sediments may be detectable.

CONCLUSIONS

In spite of the changes predicted above, deep-sea ecosystems will remain relatively unimpacted by human activities in 2025, compared to most of the planet. Nonetheless, unprecedented pressure on terrestrial natural resources will have led to significant expansion of human activities in the deep sea. Because our knowledge of the deep sea is so poor, many changes in this enormous ecosystem are likely to go undetected. Humans are in danger of modifying one of the largest, most intriguing, ecosystems long before its natural state is fully understood.

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References

- Adam, D. (2002) Methane hydrates: fire from ice. *Nature* **418**: 913–914.
- Ahnert, A. & Schriever, G. (2001) Response of abyssal Copepoda Harpacticoida (Crustacea) and other meiobenthos to an artificial disturbance and its bearing on future mining for polymetallic nodules. *Deep-Sea Research II* **48**: 3779–3794.
- Atkinson, D.B. (1995) The biology and fishery of roundnose grenadier (*Coryphaenoides rupestris* Gunnerus, 1976) in the northwest Atlantic. In: *Deep-Water Fisheries of the North Atlantic Oceanic Slope*, ed. A.G. Hopper, pp. 51–112. Dordrecht, the Netherlands: Kluwer Academic Publishers.
- Baldwin, R.J., Glatts, R.C. & Smith, K.L. (1998) Particulate matter fluxes into the benthic boundary layer at a long time-series station in the abyssal NE Pacific: composition and fluxes. *Deep-Sea Research II* **45**: 643–665.
- Barry, J.P., Baxter, C.H., Sagarin, R.D. & Gilman, S.E. (1995) Climate-related, long-term faunal changes in a California rocky intertidal community. *Science* **267**: 672–675.
- Beaulieu, S.E. & Smith, K.L. (1998) Phytodetritus entering the benthic boundary layer and aggregated on the sea floor in the abyssal NE Pacific: macro- and microscopic composition. *Deep-Sea Research II* **45**: 781–815.
- Bergstad, O.A. (1990) Distribution, population structure, growth and reproduction of the roundnose grenadier (*Coryphaenoides rupestris*) (Pisces: Macrouridae) in the deep waters of the Skagerrak. *Marine Biology* **107**: 25–39.
- Bett, B.J. (2001) UK Atlantic Margin Environmental Survey: introduction and overview of bathyal benthic ecology. *Continental Shelf Research* **21**: 917–956.
- Bett, B.J., Malzone, M.G., Narayanaswamy, B.E. & Wigham, B.D. (2001) Temporal variability in phytodetritus and megabenthic activity at the seabed in the deep northeast Atlantic. *Progress in Oceanography* **50**: 349–368.
- Billet, D.S.M. & Rice, A.L. (2001) The BENGAL programme: introduction and overview. *Progress in Oceanography* **50**: 13–25.
- Billet, D.S.M., Bett, B.J., Rice, A.L., Thurston, M.T., Galéron, J., Sibuet, M. & Wolff, G.A. (2001) Long-term change in the megabenthos of the Porcupine Abyssal Plain (NE Atlantic). *Progress in Oceanography* **50**: 325–348.
- Billet, D.S.M., Lampitt, R.S., Rice, A.L. & Mantoura, R.F.C. (1983) Seasonal sedimentation of phytoplankton to the deep-sea benthos. *Nature* **302**: 520–522.
- Bluhm, H. (2001) Re-establishment of an abyssal megabenthic community after experimental physical disturbance of the seafloor. *Deep-Sea Research II* **48**: 3841–3868.
- Bluhm, H., Schriever, G. & Thiel, H. (1995) Megabenthic recolonization in an experimentally disturbed abyssal manganese nodule area. *Marine Georesources and Geotechnology* **13**: 393–416.
- Borowski, C. (2001) Physically disturbed deep-sea macrofauna in the Peru Basin, southeast Pacific, revisited 7 years after the experimental impact. *Deep-Sea Research II* **48**: 3809–3839.
- Borowski, C. & Thiel, H. (1998) Deep-sea macrofaunal impacts of a large-scale physical disturbance experiment in the south-east Pacific. *Deep-Sea Research II* **55**: 55–81.
- Bothner, M.H., Takada, H., Knight, I.T., Hill, R.T., Butman, B., Farrington, J.W., Colwell, R.R. & Grassle, J.F. (1994) Sewage contamination in sediments beneath a deep-ocean dump site off New York. *Marine Environmental Research* **38**: 43–59.
- Brewer, P.G., Friedrich, G., Peltzer, E.T. & Orr, F.M. (1999) Direct experiments on the ocean disposal of fossil fuel CO₂. *Science* **284**: 943–945.
- Bussau, C., Schriever, G. & Thiel, H. (1995) Evaluation of abyssal metazoan meiofauna from a manganese nodule area of the eastern South Pacific. *Vie Milieu* **45**: 39–48.
- Caillet, G.M., Andrews, A.H., Burton, E.J., Watters, D.L., Kline, D.E. & Ferry-Graham, L.A. (2001) Age determination and

- validation studies of marine fishes: do deep-dwellers live longer? *Experimental Gerontology* **36**: 739–764.
- Caldeira, K. & Wickett, M.E. (2002) Comparing pH impacts of oceanic CO₂ injection and atmospheric CO₂ release. *EOS Transactions of the American Geophysical Union* **83**: Ocean Sciences Meeting Supplement, Abstract OS51F-01.
- Cane, M.A., Clement, A.C., Kaplan, A., Kushir, Y., Pozdayakov, R., Seager, S. & Zebiak, E. (1997) Twentieth century sea surface temperature trends. *Science* **275**: 957–960.
- Clark, A.L., Lum, J.A., Li, C., Icay, W., Morgan, C. & Igarashi, Y. (1995) *Economic and Developmental Potential of Manganese Nodules within the Cook Islands Exclusive Economic Zone (EEZ)*. Honolulu, Hawaii, USA: East-West Center, University of Hawaii.
- Clark, M. (2001) Are deepwater fisheries sustainable? – the example of the orange roughy (*Hoplostethus atlanticus*) in New Zealand. *Fisheries Research* **51**: 123–135.
- Corliss, J.B., Dymond, J., Gordo, L.I., Edmond, J.M., von Herzen, R., Ballard, R.D., Green, K., Williams, D., Bainbridge, A., Crane, K. & van Andel, T.H. (1979) Submarine thermal springs on the Galapagos Rift. *Science* **203**: 1073–1083.
- Cronin, T.M. & Raymo, M.E. (1997) Orbital forcing of deep-sea benthic species diversity. *Nature* **385**: 624–626.
- Cronin, T.M., DeMartino, D.M., Dwyer, G.S. & Rodriguez-Lazaro, J. (1999) Deep-sea ostracod species diversity: response to late Quaternary climate change. *Marine Micropaleontology* **37**: 231–249.
- Daan, R. & Mulder, M. (1996) On the short-term and long-term impact of drilling activities in the Dutch sector of the North Sea. *ICES Journal of Marine Science* **53**: 1036–1044.
- Dando, P.R., Southward, A.J., Southward, E.C., Dixon, D.R., Crawford, A. & Crawford, M. (1992) Shipwrecked tube worms. *Nature* **356**: 667.
- Dauterive, L. (2000) Rigs-to-reefs policy, progress, and perspective. New Orleans, USA: US Department of the Interior, Minerals Management Service, Gulf of Mexico OCS Region Report.
- de Forges, R., Koslow, J.A. & Poore, G.C.B. (2000) Diversity and endemism of the benthic seamount fauna in the southwest Pacific. *Nature* **405**: 944–947.
- Degens, E.T. & Ross, D.A., eds. (1969) *Hot Brines and Recent Heavy Metal Deposits in the Red Sea (A Geochemical and Geophysical Account)*. New York, NY, USA: Springer Verlag.
- DeLong, E.F. (2000) Microbiology: resolving a methane mystery. *Nature* **407**: 577–579.
- Deuser, W.G. & Ross, E.H. (1980) Seasonal change in the flux of organic carbon to the deep Sargasso Sea. *Nature* **283**: 364–365.
- Douglas-Westwood (2002) Into the deep [www document]. URL <http://www.dw-1.com>
- Dymond, J. & Collier, R. (1988) Biogenic particle fluxes in the equatorial Pacific: evidence for both high and low productivity during the 1982–1983 El Niño. *Global Biogeochemical Cycles* **2**: 129–137.
- Emerson, S. (1985) Organic carbon preservation in marine sediments. In: *The Carbon Cycle and Atmospheric CO₂: Natural Variations Archean to Present*, ed. E.T. Sundquist & W. Broecker, pp. 78–86. Washington, DC, USA: AGU Geophysical Monograph 32.
- Epp, D. & Smoot, N.C. (1989) Distribution of seamounts in the North-Atlantic. *Nature* **337**: 254–257.
- Feldt, W.G., Kanisch, G., Kanisch, M. & Vobach, M. (1985) Radioecological studies of sites in the northeast Atlantic used for dumping low-level radioactive wastes – results of the research cruises of FRV ‘Walter Herwig’. *Archiv für Fischereiwissenschaft* **35**: 91–195.
- Fukushima, T., Shirayama, Y. & Kuboki, E. (2000) The characteristics of deep-sea epifaunal megabenthos community two years after an artificial rapid deposition event. *Publications of the Seto Marine Laboratory* **39**: 17–27.
- Gage, J.D. (2001) Deep-sea benthic community and environmental impact assessment at the Atlantic Frontier. *Continental Shelf Research* **21**: 957–986.
- Gage, J.D. & Tyler, P.A. (1991) *Deep-sea Biology: A Natural History of Organisms at the Deep-Sea Floor*. Cambridge, UK: Cambridge University Press.
- Ghosh, A.K. & Mukhopadhyay, R. (2000) *Mineral Wealth of the Ocean*. Rotterdam, Netherlands: A.A. Balkema.
- Ginger, M.L., Billet, D.S.M., Mackenzie, K.L., Kiriakoulakis, K., Neto, R., Boardman, D.K., Santos, V.L.C.S., Horsfall, I.M. & Wolff, G.A. (2001) Organic matter assimilation and selective feeding by holothurians in the deep sea: some observations and comments. *Progress in Oceanography* **50**: 407–421.
- Glasby, G.P. (2000) Lessons learned from deep-sea mining. *Science* **289**: 551–553.
- Glover, A.G., Paterson, G., Bett, B., Gage, J., Sibuet, M., Shearer, M. & Hawkins, L. (2001) Patterns in polychaete abundance and diversity from the Madeira Abyssal Plain, northeast Atlantic. *Deep-Sea Research I* **48**: 217–236.
- Glover, A.G., Smith, C.R., Paterson, G.L.J., Wilson, G.D.F., Hawkins, L. & Shearer, M. (2002) Polychaete species diversity in the central Pacific abyss: local and regional patterns, and relationships with productivity. *Marine Ecology Progress Series* **240**: 157–170.
- Gooday, A.J. (2002) Biological responses to seasonally varying fluxes of organic matter to the ocean floor: a review. *Journal of Oceanography* **58**: 305–332.
- Grant, A. & Briggs, A.D. (2002) Toxicity of sediments from around a North Sea oil platform: are metals or hydrocarbons responsible for ecological impacts? *Marine Environmental Research* **53**: 95–116.
- Grassle, J.F. (1991) Effects of sewage sludge on deep-sea communities (abstract). *EOS* **72**: 84.
- Halbach, P., Friedrich, G. & von Stackelberg, U. (1988) *The Manganese Nodule Belt of the Pacific Ocean: Geological Environment, Nodule Formation, and Mining Aspects*. Stuttgart, Germany: F. Enke Verlag.
- Halbach, P. & Manheim, F.T. (1984) Potential of cobalt and other metals in ferromanganese crusts on seamounts of the Central Pacific Basin. *Marine Mining* **4**: 319–335.
- Hall, S.J. (2001) Is offshore exploration good for benthic conservation? *Trends in Ecology and Evolution* **16**: 58.
- Handa, N. & Ohshumi, T. (1995) *Direct Ocean Disposal of Carbon Dioxide*. Tokyo, Japan: Terra Scientific Publishing Company (TERRAPUB).

- Hannides, A.K. & Smith, C.R. (2003) Chapter 10: The northeastern Pacific abyssal plain. In: *Biogeochemistry of Marine Systems*, ed. K.D. Black & G.B. Shimmield (in press). Oxford, UK: Blackwell Science.
- Hardy, G.S. (1983) A revision of the fishes of the family Pentacerotidae (Perciformes). *New Zealand Journal of Zoology* 10: 177–220.
- Hessler, R.R. & Sanders, H.L. (1967) Faunal diversity in the deep-sea. *Deep-Sea Research* 14: 65–78.
- Hollister, C.D. & McCave, I.N. (1984) Sedimentation under deep-sea storms. *Nature* 309: 220–225.
- Hollister, C.D. & Nadis, S. (1998) Burial of radioactive waste under the seabed. *Scientific American* January 1998: 40–45.
- Horn, P.L., Tracey, D.M. & Clark, M.R. (1998) Between-area differences in age and length at first maturity of the orange roughy *Hoplostethus atlanticus*. *Marine Biology* 132: 187–194.
- Iken, K., Brey, T., Wand, U., Voigt, I. & Junghans, P. (2001) Food web structure of the benthic community at Porcupine Abyssal Plain (N. Atlantic): a stable isotope analysis. *Progress in Oceanography* 50: 383–405.
- Ingole, B., Ansari, Z.A., Rathod, V. & Rodrigues, N. (2001) Response of deep-sea macrobenthos to a small-scale environmental disturbance. *Deep-Sea Research II* 48: 3401–3410.
- IPCC (1996) *Climate Change 1995: The Science of Climate Change*. Cambridge, UK: Cambridge University Press.
- IPCC (2001) *IPCC Third Assessment Report – Climate Change 2001*. Cambridge, UK: Cambridge University Press.
- Jumars, P.A. (1981) Limits in predicting and detecting benthic community responses to manganese nodule mining. *Marine Mining* 3: 213–229.
- Karbe, L. (1987) Hot brines and the deep sea environment. In: *Red Sea (Key Environment Series)*, ed. A.J. Edwards & S.M. Head, pp. 70–89. Oxford, UK: Pergamon Press.
- Karl, D. (2002) Nutrient dynamics in the deep blue sea. *Trends in Microbiology* 10: 410–418.
- Karl, D.M., Christian, J.R., Dore, J.E., Hebel, D.V., Letelier, R.M., Tupas, L.M. & Winn, C.D. (1996) Seasonal and interannual variability in primary production and particle flux at Station ALOHA. *Deep-Sea Research II* 43: 539–568.
- Kelly, C.J., Connolly, P.L. & Bracken, J. (1997) Age estimation, growth, maturity and distribution of the roundnosed grenadier from the Rockall Trough. *Journal of Fish Biology* 50: 1–17.
- Kennett, J.P. & Stott, L.D. (1991) Abrupt deep-sea warming, palaeoceanographic changes and benthic extinctions at the end of the Palaeocene. *Nature* 353: 225–229.
- Knowlton, N. (2000) Molecular genetic analyses of species boundaries in the sea. *Hydrobiologia* 420: 73–90.
- Koslow, J.A. (1997) Seamounts and the ecology of deep-sea fisheries. *American Scientist* 85: 168–176.
- Koslow, J.A., Boehlert, G.W., Gordon, D.M., Haedrich, R.L., Lorance, P. & Parin, N. (2000) Continental slope and deep-sea fisheries: implications for a fragile ecosystem. *ICES Journal of Marine Science* 57: 548–557.
- Koslow, J.A., Gowlett-Holmes, K., Lowry, J.K., O'Hara, T., Poore, G.C.B. & Williams, A. (2001) Seamount benthic macrofauna off southern Tasmania: community structure and impacts of trawling. *Marine Ecology Progress Series* 213: 111–125.
- Kukert, H. & Smith, C.R. (1992) Disturbance, colonization and succession in a deep-sea sediment community: artificial-mound experiments. *Deep-Sea Research I* 39: 1349–1371.
- Kvenvolden, K.A. (1988) Methane hydrate – a major reservoir of carbon in the shallow geosphere. *Marine Geology* 71: 41–51.
- Lampitt, R.S., Bett, B.J., Kiriakoulakis, K., Popova, E.E., Raguenau, O., Vangriesheim, A. & Wolff, G.A. (2001) Material supply to the abyssal seafloor in the northeast Atlantic. *Progress in Oceanography* 50: 27–64.
- Levin, L.A., Etter, R.J., Rex, M.A., Gooday, A.J., Smith, C.R., Pineda, J., Stuart, C.T., Hessler, R.R. & Pawson, D. (2001) Environmental influences on regional deep-sea species diversity. *Annual Review of Ecology and Systematics* 32: 51–93.
- Levitus, S., Antonov, J.I., Boyer, T.P. & Stephens, C. (2000) Warming of the world ocean. *Science* 287: 2225–2229.
- Mace, P.M., Fenaughty, J.M., Coburn, R.P. & Doonan, I.J. (1990) Growth and productivity of orange roughy (*Hoplostethus atlanticus*) on the North Chatham Rise. *New Zealand Journal of Marine and Freshwater Research* 24: 105–119.
- Mauri, M., Polimeni, R., Modica, A. & Ferraro, M. (1998) Heavy metal bioaccumulation associated with drilling and production activities in middle Adriatic Sea. *Fresenius Environmental Bulletin* 7: 60–70.
- McGowan, J.A., Cayan, D.R. & Dorman, L.M. (1998) Climate-ocean variability and ecosystem response in the northeast Pacific. *Science* 281: 210–217.
- McMurtry, G. (2001) Authigenic deposits. In: *Encyclopedia of Ocean Sciences*, ed. S.A. Thorpe & K.K. Turekian, pp. 201–220. London, UK: Academic Press.
- Mero, J.L. (1965) *The Mineral Resources of the Sea*. New York, USA: Elsevier.
- Merrett, N.R. & Haedrich, R.L. (1997) *Deep-Sea Demersal Fish and Fisheries*. London, UK: Chapman & Hall.
- Morgan, C.L. (2000) Resource estimates of the Clarion–Clipperton manganese nodule deposits. In: *Handbook of Marine Mineral Deposits*, ed. D.S. Cronan, pp. 145–170. Boca Raton, USA: CRC Press.
- Mullineaux, L.S. (1987) Organisms living on manganese nodules and crusts: distribution and abundance at three North Pacific sites. *Deep-Sea Research* 34: 165–184.
- Murray, J. (1895) A summary of the scientific results obtained at the sounding, dredging and trawling stations of HMS Challenger. *Challenger Report Summary of Research* 2: 797–1608.
- Mustafa, Z., Nawab, Z., Horn, R. & Le Lann, F. (1997) Economic interest of hydrothermal deposits – the Atlantis II project. *Proceedings of the International Symposium on Environmental Studies of Deep-Sea Mining*, pp. 3–9. Tokyo, Japan: Metal Mining Agency of Japan.
- Nardin, T.R., Hein, F.J., Gorsline, D.S. & Edwards, B.D. (1979) A review of mass movement processes, sediment and acoustic characteristics, and contrasts in slope and base-of-slope systems versus canyon-fan-basin floor systems. *Special Publications of the Society of Economic Paleontologists and Mineralogists* 27: 61–73.
- NERC (1996) Scientific Group on Decommissioning Offshore

- Structures: first report. Report by the Natural Environment Research Council for the Department of Trade and Industry, UK.
- Oebius, H.U., Becker, H.J., Rolinski, S. & Jankowski, J. (2001) Parametrization and evaluation of marine environmental impacts produced by deep-sea manganese nodule mining. *Deep-Sea Research II* **48**: 3453–3467.
- Polunin, N., Morales-Nin, B., Pawsey, W., Cartes, J., Pinnegar, J. & Moranta, J. (2001) Feeding relationships in Mediterranean bathyal assemblages elucidated by stable nitrogen and carbon isotope data. *Marine Ecology Progress Series* **220**: 13–23.
- Raghukumar, C., Loka Bharathi, P.A., Ansari, Z.A., Nair, S., Ingole, B., Sheelu, G., Mohandass, C., Nagender Nath, B. & Rodrigues, N. (2001) Bacterial standing stock, meiofauna and sediment-nutrient characteristics: indicators of benthic disturbance in the Central Indian Basin. *Deep-Sea Research II* **48**: 3381–3399.
- Raimondi, P.T., Barnett, A.M. & Krause, P.R. (1997) The effects of drilling muds on marine invertebrate larvae and adults. *Environmental Toxicology and Chemistry* **16**: 1218–1228.
- Rice, A.L. & Owen, P. (1998) *Decommissioning the Brent Spar*. London, UK: E. and F. N. Spon.
- Roberts, D. (2002) Deep impact: the rising toll of fishing in the deep sea. *Trends in Ecology and Evolution* **17**: 242–245.
- Rodrigues, N., Sharma, R. & Nagender Nath, B. (2001) Impact of benthic disturbance on megafauna in Central Indian Basin. *Deep-Sea Research II* **48**: 3411–3426.
- Roemmich, D. (1992) Ocean warming and sea level rise along the southwest US coast. *Science* **257**: 373–375.
- Rogers, A.D. (1994) The biology of seamounts. *Advances in Marine Biology* **30**: 306–350.
- Rogers, A.D. (1999) The biology of *Lophelia pertusa* (Linnaeus 1758) and other deep-water reef-forming corals and impacts from human activities. *International Review of Hydrobiology* **84**: 315–406.
- Rogers, A.D. (2000) The role of oceanic oxygen minima in generating biodiversity in the deep sea. *Deep-Sea Research II* **47**: 119–148.
- Rolinski, S., Segschneider, J. & Sündermann, J. (2001) Long-term propagation of tailings from deep-sea mining under variable conditions by means of numerical simulations. *Deep-Sea Research II* **48**: 3469–3485.
- Roskill-Consulting (2002) Cobalt [www document]. URL <http://www.roskill.co.uk/cobalt.html>
- Rowe, G.T. (1971) Benthic biomass and surface productivity. In: *Fertility of the Sea*, ed. J.D. Costlow, pp. 97–122. New York, USA: Gordon & Beach.
- Sakai, H., Gamo, T., Kim, E.S., Tsutsumi, M., Tanaka, T., Ishibashi, J., Wakita, H., Yamano, M. & Oomori, T. (1990) Venting of carbon-dioxide rich fluid and hydrate formation in Mid-Okinawa Trough Back-arc basin. *Science* **248**: 1093–1096.
- Sanders, H.L. (1968) Marine benthic diversity: a comparative study. *American Naturalist* **102**: 243–282.
- Schmittner, A. & Stocker, T.F. (1999) The stability of the thermo-haline circulation in global warming experiments. *Journal of Climate* **12**: 1117–1133.
- Scott, S.D. (1992) Polymetallic sulfide riches from the deep: fact or fallacy? In: *Use and Misuse of the Seafloor*, ed. K.J. Hsu & J. Thiede, pp. 87–115. Chichester, UK: John Wiley & Sons, Ltd.
- Sharma, R., Nagender Nath, B., Parthiban, S. & Jai Sankar, S. (2001) Sediment redistribution during simulated benthic disturbance and its implications on deep seabed mining. *Deep-Sea Research II* **48**: 3363–3380.
- Smith, C.R. (1992) Factors controlling bioturbation in deep-sea sediments and their relation to models of carbon diagenesis. In: *Deep-Sea Food Chains and the Global Carbon Cycle*, ed. G.T. Rowe & V. Pariente, pp. 375–393. Dordrecht, the Netherlands: Kluwer Academic Publishers.
- Smith, C.R. (1994) Tempo and mode in deep-sea benthic ecology: punctuated equilibrium revisited. *Palaios* **9**: 3–13.
- Smith, C.R. (1999) The biological environment in the nodule provinces of the deep sea. In: *Deep-Seabed Polymetallic Nodule Exploration: Development of Environmental Guidelines*, ed. N. Odunton, pp. 41–68. Kingston, Jamaica: International Seabed Authority.
- Smith, C.R. & Baco, A.R. (2003) Ecology of whale falls at the deep-sea floor. *Oceanography and Marine Biology: an Annual Review* (in press).
- Smith, C.R. & Demopoulos, A. (2003) Ecology of the deep Pacific Ocean floor. In: *Ecosystems of the World, Volume 28: Ecosystems of the Deep Ocean*, ed. P.A. Tyler (in press). Amsterdam, the Netherlands: Elsevier.
- Smith, C.R., Berelson, W., Demaster, D.J., Dobbs, F.C., Hammond, D., Hoover, D.J., Pope, R.H. & Stephens, M. (1997) Latitudinal variations in benthic processes in the abyssal equatorial Pacific: control by biogenic particle flux. *Deep-Sea Research II* **44**: 2295–2317.
- Smith, C.R., Hoover, D.J., Doan, S.E., Pope, R.H., Demaster, D.J., Dobbs, F.C. & Altabet, M.A. (1996) Phytodetritus at the abyssal seafloor across 10° of latitude in the central equatorial Pacific. *Deep-Sea Research II* **43**: 1309–1338.
- Smith, C.R., Jumars, P.A. & DeMaster, D.J. (1986) *In situ* studies of megafaunal mounds indicate rapid sediment turnover and community response at the deep-sea floor. *Nature* **323**: 251–252.
- Smith, C.R., Kukert, H., Wheatcroft, R.A., Jumars, P.A. & Deming, J.W. (1989) Vent fauna on whale remains. *Nature* **341**: 27–28.
- Smith, C.R., Mincks, S.L., Glover, A.G., DeMaster, D.J. & Sumida, P.Y.G. (2002) FOODBANCS on the Antarctic Peninsula shelf: the benthic food bank hypothesis and the seasonal deposition pulse. *EOS Transactions of the American Geophysical Union* **83**: OS223–OS224.
- Smith, C.R., Present, T.M.C. & Jumars, P.A. (1988) Development of benthic biological monitoring criteria for disposal of low-level radioactive waste in the abyssal deep sea. Final report for EPA Contract No. 68-02-4303, Washington, DC, USA.
- Smith, C.R. & Rabouille, C. (2002) What controls the mixed-layer depth in deep-sea sediments? The importance of POC flux. *Limnology and Oceanography* **47**: 418–426.
- Smith, D.K. & Jordan, T.H. (1988) Seamount statistics in the Pacific Ocean. *Journal of Geophysical Research* **93**: 2899–2919.

- Smith, K.L. & Kaufmann, R.S. (1999) Long-term discrepancy between food supply and demand in the deep eastern north Pacific. *Science* **284**: 1174–1177.
- Snelgrove, P.V.R. & Smith, C.R. (2002) A riot of species in an environmental calm: the paradox of the species-rich deep sea. *Oceanography and Marine Biology Annual Review* **40**: 311–342.
- Strömberg, J.-O. (1997) Human influence or natural perturbation in oceanic and coastal waters – can we distinguish between them? *Hydrobiologia* **352**: 181–193.
- Takizawa, M., Straube, R.T. & Colwell, R.R. (1993) Near-bottom pelagic bacteria at a deep-water sewage sludge disposal site. *Applied and Environmental Microbiology* **59**: 3406–3410.
- Tamburri, M.N., Peltzer, E.T., Friedrich, G.E., Aya, I., Yamane, K. & Brewer, P.G. (2000) A field study of the effects of CO₂ ocean disposal on mobile deep-sea animals. *Marine Chemistry* **72**: 95–101.
- Thiel, H. (2003) Anthropogenic impacts on the deep sea. In: *Ecosystems of the World: The Deep Sea*, ed. P.A. Tyler (in press). Amsterdam, the Netherlands: Elsevier.
- Thiel, H., Angel, M.V., Foell, E.J., Rice, A.L. & Schriever, G. (1998) Environmental risks from large-scale ecological research in the deep sea. Report for the Commission of the European Communities Directorate-General for Science, Research and Development, Bremerhaven, Germany.
- Thiel, H., Pfannkuche, O., Schriever, G., Lochte, K., Gooday, A.J., Hemleben, C., Mantoura, R.F.C., Turley, C.M., Patching, J. & Riemann, F. (1989) Phytodetritus on the deep-sea floor in a central oceanic region of the north-east Atlantic. *Biological Oceanography* **6**: 203–239.
- Thiel, H., Schriever, G., Ahnert, A., Bluhm, H., Borowski, C. & Vopel, K. (2001) The large-scale environmental impact experiment DISCOL – reflection and foresight. *Deep-Sea Research II* **48**: 3869–3882.
- Timmermann, A., Oberhuber, J., Bacher, A., Esch, M., Latif, M. & Roeckner, E. (1999) Increased El Niño frequency in a climate model forced by future greenhouse warming. *Nature* **398**: 694–696.
- Tyler, P.A. (1988) Seasonality in the deep sea. *Oceanography and Marine Biology: An Annual Review* **26**: 227–258.
- Tyler, P.A. (2003) Disposal in the deep sea: analogue of nature or *faux ami*? *Environmental Conservation* **30**(1): (in press).
- Tyler, P.A., Grant, A., Pain, S.L. & Gage, J.D. (1982) Is annual reproduction in deep-sea echinoderms a response to variability in their environment? *Nature* **300**: 747–750.
- UKOOA (2002) UKOOA drill cuttings initiative final report, United Kingdom Offshore Operators Association [www document]. URL <http://www.oilandgas.org.uk>
- UN (1998) *World Population Prospects: The 1998 Revision*. New York, USA: United Nations Secretariat, Department of Economic and Social Affairs, Population Division.
- US DOE (1999) Carbon sequestration research and development. Office of Science, Office of Fossil Energy, US Department of Energy Report, USA.
- USGS (2002) United States Geological Survey fact sheet [www document]. URL <http://marine.usgs.gov/fact-sheets/gas-hydrates/title.html>
- Van Dover, C.L. (2000) *The Ecology of Deep-Sea Hydrothermal Vents*. Princeton, NJ, USA: Princeton University Press.
- Van Dover, C.L., Grassle, J.F., Fry, B., Garritt, R.H. & Staczek, V.R. (1992) Stable isotopic evidence for entry of sewage-derived organic material into a deep-sea food web. *Nature* **360**: 153–156.
- Vetter, E.W. & Dayton, P.K. (1998) Macrofaunal communities within and adjacent to a detritus-rich submarine canyon system. *Deep-Sea Research II* **45**: 25–54.
- Vopel, K. & Thiel, H. (2001) Abyssal nematode assemblages in physically disturbed and adjacent sites of the eastern equatorial Pacific. *Deep-Sea Research II* **48**: 3795–3808.
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Guldberg, O. & Bairlein, F. (2002) Ecological responses to recent climate change. *Nature* **416**: 391–395.
- Wiltshire, J. (2001) Future prospects for the marine minerals industry. *Underwater* **13**: 40–44.
- Yamazaki, T., Barnett, B. & Suzuki, T. (1997) Optical determination of the JET deep sea sediment disturbance. *Proceedings of the International Symposium on Environmental Studies of Deep-Sea Mining*, pp. 153–168. Tokyo, Japan: Metal Mining Agency of Japan.