CHAPTER ONE

TEMPORAL CHANGE IN DEEP-SEA BENTHIC ECOSYSTEMS: A REVIEW OF THE EVIDENCE FROM RECENT TIME-SERIES STUDIES

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Abstract

Societal concerns over the potential impacts of recent global change have prompted renewed interest in the long-term ecological monitoring of large ecosystems. The deep sea is the largest ecosystem on the planet, the least accessible, and perhaps the least understood. Nevertheless, deep-sea data collected over the last few decades are now being synthesised with a view to both measuring global change and predicting the future impacts of further rises in atmospheric carbon dioxide concentrations. For many years, it was assumed by many that the deep sea is a stable habitat, buffered from short-term changes in the atmosphere or upper ocean. However, recent studies suggest that deep-seafloor ecosystems may respond relatively quickly to seasonal, inter-annual and decadal-scale shifts in upper-ocean variables. In this review, we assess the evidence for these long-term (i.e. inter-annual to decadal-scale) changes both in biologically driven, sedimented, deep-sea ecosystems (e.g. abyssal plains) and in chemosynthetic ecosystems that are partially geologically driven, such as hydrothermal vents and cold seeps. We have identified 11 deep-sea sedimented ecosystems for which published analyses of long-term biological data exist. At three of these, we have found evidence for a progressive trend that could be potentially linked to recent climate change, although the evidence is not conclusive. At the other sites, we have concluded that the changes were either not significant, or were stochastically variable without being clearly linked to climate change or climate variability indices. For chemosynthetic ecosystems, we have identified 14 sites for which there are some published long-term data. Data for temporal changes at chemosynthetic ecosystems are scarce, with few sites being subjected to repeated visits. However, the limited evidence from hydrothermal vents suggests that at fast-spreading centres such as the East Pacific Rise, vent communities are impacted on decadal scales by stochastic events such as volcanic eruptions, with associated fauna showing complex patterns of community succession. For the slow-spreading centres such as the Mid-Atlantic Ridge, vent sites appear to be stable over the time periods measured, with no discernable long-term trend. At cold seeps, inferences based on spatial studies in the Gulf of Mexico, and data on organism longevity, suggest that these sites are stable over many hundreds of years. However, at the Haakon Mosby mud volcano, a large, well-studied seep in the Barents Sea, periodic mud slides associated with gas and fluid venting may disrupt benthic communities, leading to successional sequences over time. For chemosynthetic ecosystems of biogenic origin (e.g. whale-falls), it is likely that the longevity of the habitat depends mainly on the size of the carcass and the ecological setting, with large remains persisting as a distinct seafloor habitat for up to 100 years. Studies of shallow-water analogs of deep-sea ecosystems such as marine caves may also yield insights into temporal processes. Although it is obvious from the geological record that past climate change has impacted deep-sea faunas, the evidence that recent climate change or climate variability has altered deep-sea benthic communities is extremely limited. This mainly reflects the lack of remote sensing of this vast seafloor habitat. Current and future advances in deep-ocean benthic science involve new remote observing technologies that combine a high temporal resolution (e.g. cabled observatories) with spatial capabilities (e.g. autonomous vehicles undertaking image surveys of the seabed).

1. INTRODUCTION

The recent rise of 'global change science', fuelled by concerns over the Earth's changing climate, has demanded a more integrated and holistic outlook from ecologists. Within the working lifetimes of scientists, large-scale climatic changes are occurring as a result of radiative forcing caused mainly by the rapid rise in atmospheric concentrations of carbon dioxide, methane, and nitrous oxide (IPCC, 2007). Although computer-based modelling approaches have been the mainstay of climate science itself, the enormously complex nature of the biosphere and its interacting ecosystems, communities, and populations has made modelling the actual impacts of climate change notoriously difficult. Furthermore, ecologists have struggled to either maintain or activate the long-term ecological monitoring stations that are required to validate any predictive models. Nowhere is this more of an issue than in the deep ocean, an environment that covers approximately 60% of the Earth's surface.

Deep-sea biology is a relatively young science. Prior to the nineteenth century, almost nothing was known about environments deeper than the shallow sub-tidal. The industrial revolution, the rise of evolutionary theory, and the laying of deep telegraphic cables led to the first deep-sea biology expeditions of the nineteenth century, and the discovery of abundant, diverse life at all depths of the ocean. The twentieth century saw the detection of high biodiversity in deep-sea sediments (Hessler and Sanders, 1967; Grassle, 1991) and the paradigm-shifting discovery of life at deep hydrothermal vents (Lonsdale, 1977) and cold hydrocarbon seeps (Paull *et al.*, 1984). Yet, we enter the twenty-first century—perhaps, the climate-change century—knowing little about temporal processes in deep ecosystems, and even lacking basic knowledge of their biological composition. Without doubt, there is a pressing need for both data-mining of existing collections, and the initiation of new, science and technology-driven monitoring programmes in the deep ocean. This review of long-term change in deep-sea benthic ecosystems is intended to highlight these gaps, and to draw together data from a diverse range of ongoing temporal studies in the deep sea.

Historically, the deep ocean was considered a relatively stable environment, buffered from the climatic and geological drivers that dominate terrestrial and littoral marine ecosystems. This view led nineteenth and early twentieth century deep-sea explorers to believe that relic faunas known only from the fossil record might still exist in isolated deep-sea basins (reviewed in Koslow, 2007). More recent studies have failed to find much support for this; deep-sea faunas are often remarkably similar in higher-level taxonomic composition to those in shallow sub-tidal and even inter-tidal systems. Even at deep-sea hydrothermal vents, the hard-substrate community often shows both evolutionary and ecological links to analogous communities in shelf habitats. Process-based ecological studies are now starting to show that far from being a stable, buffered system, the deep ocean is 'punctuated' in time and space by a range of powerful drivers, which include pulses of sinking phytodetritus, emissions from volcanic vents, large carcass-falls, turbidity currents, shifts in ocean currents and oxygen stress, as well as present and possible future human impacts such as deep-water fishing and mining (Smith, 1994; Gooday, 2002; Glover and Smith, 2003). These processes span a range of temporal and spatial scales and as such are significant on both ecological and evolutionary timescales.

Historically, ecological studies in the deep sea have often been habitat focused, while evolutionary studies have generally been taxon focused. In this review, we bring together studies from a range of habitats and taxa that address the theme of long-term (inter-annual to multi-decadal) temporal trends in benthic ecosystems. This time-scale is too short to be normally resolved in the deep-sea sediment record and yet too long to have been addressed by most ecological monitoring programmes. Whilst there have been several studies of long-term changes in shallow-water marine ecosystems (e.g. Southward *et al.*, 2005; Robinson and Frid, 2008), it is only recently that long-term sampling has started to reveal coherent trends at a number of deep-sea sites (Billett *et al.*, 2001, 2010; K. L. Smith *et al.*, 2006). Furthermore, the first data from satellite-based ocean productivity sensors only now approach decadal scales (Behrenfeld *et al.*, 2006). Thus, now is an appropriate moment to assess possible links between decadal-scale climate change and deep-sea ecosystems.

We review a range of studies addressing multi-year to multi-decadal scale changes at deep-sea chemosynthetic and non-chemosynthetic ecosystems. Although deep-sea chemosynthetic ecosystems, such as hydrothermal vents and seeps, are driven by quite different physical and chemical processes to sedimented habitats, their fauna share a relatively recent evolutionary origin (Little and Vrijenhoek, 2003) and are likely to show some of the same physiological and metabolic constraints as communities depending on sinking organic particles. New data are emerging on long-term changes at vents, highlighting how geology dynamically influences biology over decadal scales (Cuvelier *et al.*, submitted for publication; Sarrazin *et al.*, 1997). Rather than treating this ecosystem in isolation, we believe that understanding the adaptations of organisms to radical changes in temperature and water chemistry can inform our studies of how lineages and species will respond to the rapid changes predicted by some scenarios (IPCC, 2007). Our review builds on existing knowledge of seasonal variability in the deep sea (Tyler, 1988; Gooday and Turley, 1990; Beaulieu, 2002; Gooday, 2002) and places recent findings in the context of palaeoenvironmental data obtained from deep sediment cores (Discussion Section 5.2.1). However, we do not consider in detail the evidence from the palaeoceanographic record for faunal change occurring over geological time scales. Our review also touches on fisheries data only where they relate to one of our study sites (Section 3.2.1). This topic is reviewed more fully elsewhere in the context of human impacts (Koslow *et al.*, 2000; C. R. Smith *et al.*, 2008). In summary, we will evaluate the following four hypotheses:

1. Deep-sea sedimented ecosystems are subject to biologically driven forcing events induced by climate change or climate variability in recent decades.
2. Chemosynthetic ecosystems are subject to stochastic geological forcing events, which override climatically induced biological processes.
3. Although the drivers are different, there are commonalities in the biological responses observed in these contrasting settings.
4. The deep-sea benthos embodies the influences of climatic changes that have occurred over both geological (evolutionary) and decadal (ecological) timescales.

2. THEORETICAL FRAMEWORK

The last century saw a revolution in our understanding of the deep ocean, and the animals that live in it. Among the key technical developments that facilitated this new vision was our ability to actually observe deep-sea organisms in their natural habitat (Fig. 1.1). These included first-hand observations through the windows of deep-sea submersibles and the more recent use of remotely operated vehicles (ROVs) and free-vehicle 'landers' equipped with cameras and other useful sensors. In two very different environments, direct visual observation was the vital clue to paradigm-shifting discoveries. At the hydrothermal vents of the Galapagos

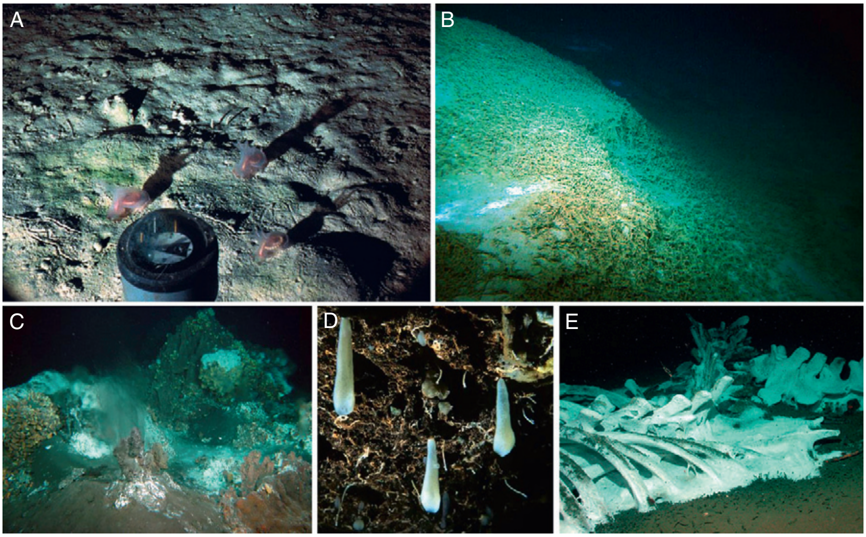

Figure 1.1 Direct visual observation of deep-sea habitats, and shallow-water deep-sea analogs. (A) The Porcupine Abyssal Plain in the north-east Atlantic (4800 m) with visible (green) phytodetritus and three individuals of the elasipodid holothurian *Amperimsa rosea*, with a coiled gut visible through the transparent bodywall. (B) A field of siboglinid tube worms on the Haakon Mosby Mud Volcano, a 1 km^2 construct associated with methane seepage, located at 1255 m depth on the Barents Sea continental slope (C) 'Lucky Strike' hydrothermal vent on the Mid-Atlantic Ridge (1690 m). (D) Deep-sea glass sponges (*Oopsacas minuta*) found in a shallow-water marine cave at 15–25 m depth in the Mediterranean, where habitat conditions are analagous to those in the deep sea. (E) a 'whale-fall' (the remains of a dead whale) on the seafloor of the Santa Cruz Basin (NE Pacific; 1600 m depth). Images courtesy of the National Oceanography Centre, Southampton (A), Vicking Cruise 2006 ©Ifremer (B), MoMARETO Cruise 2006 ©Ifremer (C), Jean-Georges Harmelin, CNRS (D) and Craig R. Smith, University of Hawaii (E).

Rift, the first observations of large clam shells clustering around a venting region were made using a towed video system (Lonsdale, 1977). On the deep abyssal plain of the north-east Atlantic, the first direct observations of the seasonal input of green 'phytodetritus' from surface waters were made using a free-vehicle lander with a time-lapse camera (Billett *et al.*, 1983). Both of these discoveries contributed to a new acknowledgement that the deep sea is not quiescent, and that environmental perturbations over different temporal scales are likely to be very important in structuring the deep-sea biological community. In this section, we outline a theoretical framework that deals with change over these temporal scales, and in particular the relative roles of biologically driven and geologically driven processes.

2.1. Biological processes and temporal scaling

Space and time form convenient dimensions upon which to classify natural phenomena, ranging from the diurnal migration of zooplankton, the seasonal impact of hurricanes, the climatic shifts of the Quaternary to the mass extinctions recorded in the deep geological record. In the past, the deep sea was often viewed as a quiescent habitat; the vast, sedimented plains of the abyss undisturbed over millions of years (e.g. Menzies, 1965). This generalisation has been firmly rejected. We now know that the ocean floor is subjected to a variety of disturbances that operate across very broad temporal scales. In this sense, the deep sea can be thought of as encompassing two end-members, namely the abyssal sediments underlying the oligotrophic gyres, where sedimentation is often virtually zero, and the highly dynamic hydrothermal vents, where organism growth rates may be amongst the highest ever recorded.

The types of disturbances (or drivers) that impact the deep sea can be arranged on a temporal scale (Table 1.1). Benthic storms (temporally variable periods of high current speeds) can resuspend sediments on daily timescales (Thistle *et al*., 1991). Food availability can lead to recruitment pulses on intra-annual, seasonal scales (Tyler, 1988; Gooday, 2002). Inter-annual shifts in production can cause migrations or changes in the local abundance of some species (Billett *et al*., 2001). Over decadal scales, changes in oceanic temperature patterns, such as the El Niño Southern Oscillation (ENSO), may cause widespread changes in abyssal food supply (e.g. Levin *et al*., 2002; Arntz *et al*., 2006; Ruhl *et al*., 2008). Also over decadal scales, hydrothermal vents may change in their activity patterns, with consequences for the fauna dependent on them (Van Dover, 2000). Human-induced climate change, acting over periods of 50–100 years (IPCC, 2007), is also thought to be capable of impacting on the deep seafloor, although data are still insufficient to demonstrate this (C. R. Smith *et al*., 2008; K. L. Smith *et al*., 2009). Over geological time, orbital periodicity on 100,000-year timescales is probably largely responsible for the glacial/interglacial climatic shifts of the Pleistocene. At the 1–100-My scale, large climatic shifts, continental drift, and episodes of widespread deep-ocean anoxia are believed to have had global-scale impacts on the deep-sea fauna (e.g. Jacobs and Lindberg, 1998).

These deep-sea drivers can also be plotted using a range of estimates for both their temporal and spatial impact (Fig. 1.2). Plotted in log–log space, a positive relationship is found between the temporal spacing (i.e. the timescale) of the events and their spatial impact, which for the very large events is limited by the size of the planet. Although the errors are large, and the number of disturbance types limited, the data suggest a predictable power-law relationship between the frequency and the severity of the disturbance, and a degree of scale-invariance (i.e. the relationship does not change across spatial or temporal scales). Such power-law relationships can be commonly

Table 1.1 Temporal scales of deep-sea environmental drivers of change, estimated severity and frequency and relevance to ecological and evolutionary scale processes

Temporal scale (years)	Spatial scale (km^2)	Driver	Impact	Relevance
0.01	1×10^{-6}	Local predation, disturbance	Local disturbance	Ecology
0.1	1–100	Benthic storms, down-slope or canyon sediment transport	Resuspension of sediments, organic enrichment, disturbance	Ecology
0.5	1×10^4–1×10^6	Seasonal food supply, phytoplankton blooms	Food availability, growth, recruitment pulse, seasonal migration	Ecology
1–5	1×10^5–1×10^7	Inter-annual variability in food supply driven by surface processes or geological stochastic events	Food availability, growth, long-term migration	Ecology
10–20	1×10^5–1×10^7	Decadal shifts including geological stochastic events, trends in surface processes (ENSO, NAO, MEI)	Long-term shifts in community structure and abundance	Ecology - Evolution
50–100	global	Anthropogenically induced rapid climate change	Range shifts, local extinction	Ecology - Evolution
100–100,000	global	Climate change caused by orbital periodicity, solar activity	Extinction and speciation	Evolution
1×10^6–1×10^9	global	Continental drift, formation of spreading centres	Speciation and adaptive radiation (e.g. at vent sites)	Evolution

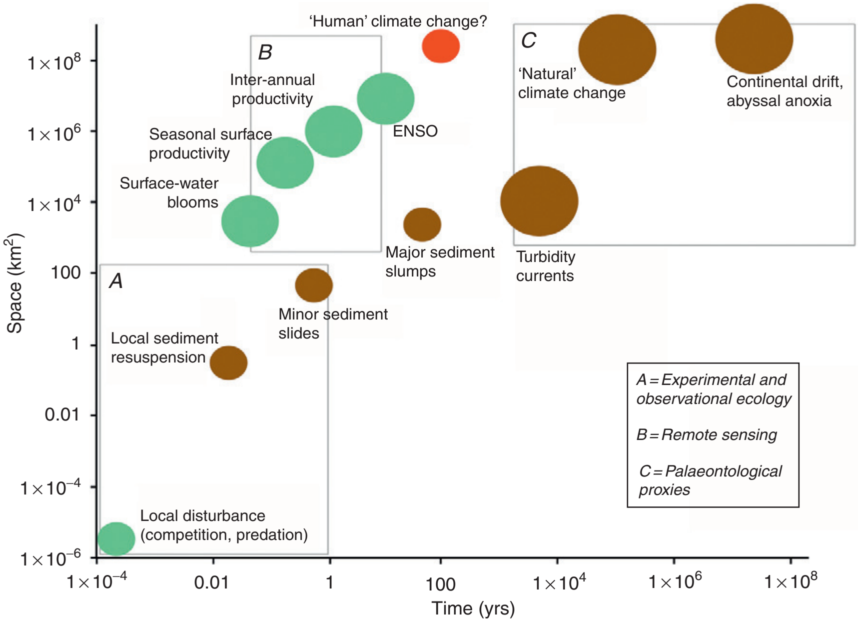

Figure 1.2 Deep-sea environmental forcing factors (biological as green circles, geological as brown circles) plotted against space (km^2 of potential impact) and time (frequency of occurrence) in log–log space. A scale-invariant power-law relationship is evident until the spatial extent of the forcing factor reaches a maximum at the total size of Earth's marine environment. The time–space scales for human measurement methods are observational and experimental ecology (Box A), remote sensing, for example, satellite ocean colour, (Box B) and palaeontological proxies from deep-sea sediment records and ice cores (Box C). The temporal scale of human-induced climate change (red circle) potentially lies between B and C in a region difficult to monitor using existing technologies.

found in natural systems such as earthquake frequency (Bak and Tang, 1989) and in ecological communities (Pascual and Guichard, 2005).

The space–time plot also serves as useful template to assess the human ability to measure these drivers and their impacts (Fig. 1.2—boxes). Measurement methods could include either experimental and observational ecology, remote sensing or the use of palaeontological and geochemical proxies preserved in the sediment record. It is significant that there is little overlap on the space–time plot between these methods. In particular, there is a temporal gap between the time scale for remote sensing, and that for the resolution of palaeontological proxies. Most remote sensing data—for example, ocean colour—are available only for the last 10–15 years (Behrenfeld *et al.*, 2006). With a few exceptions, notably varved sediments in hypoxic basins such as the Cariaco Basin (Black *et al.*, 2007; Section 3.1.3), marine sediments yield temporal records with a resolution in excess of 250 years. Within this gap lies the forcing factor of human-induced climate change, where most models forecast significant global changes over the next 50–100 years (IPCC, 2007).

It is clear that long-term datasets are required in order to understand the impacts of current warming trends, and projected models. It is no surprise that rather few studies have been conducted in the deep sea, the planet's remotest and least-accessible ecosystem. Yet it is surprising that few long-term ecological time series studies are available even for shallow-water settings. The best are from the continuous plankton surveys of the North Atlantic (Richardson and Schoeman, 2004) and the north-east Pacific (Roemmich and McGowan, 1995), which have run for over 50 years and show trends that co-vary with recent climatic shifts. For non-pelagic ecosystems, rather little is known on the 50–100 year scale. The longest concerted time series that involve sampling soft-bottom (sediment) communities in coastal and shallow-water settings span shorter periods, for example, 36 years in the North Sea off the Northumberland coast (Frid *et al.*, 2008). Fisheries biologists have collected quantitative data on the benthos in some areas since the 1920s, and qualitative information can be derived from historical sources over centennial time scales (e.g. Jackson *et al.*, 2001; Holm, 2005; Robinson and Frid, 2008). Monitoring of intertidal habitats in SW England since the 1950s has revealed striking changes in the distribution and abundance of barnacle species (Southward *et al.*, 2005). The majority of shallow-water studies, however, fall within the decadal or sub-decadal range, where the influence of climate change is hard to separate from other climatic variations such as ENSO and stochastic shifts in new production and food supply. Even for major variables, such as global ocean productivity, there are currently no more than about 10 years of analysed remote-sensing data (Behrenfeld *et al.*, 2006).

2.2. Biological drivers

With few exceptions, the deep sea is a food-limited environment. The sedimented abyssal plains, which constitute the most widespread deep-ocean environment, are dependent on an allochthonous supply of food in the absence of sunlight and new production. It is therefore a central hypothesis that benthic density and biomass are correlated with the amount of organic material raining down from the surface waters, or transported in by ocean currents (Fig. 1.3). A number of studies support this idea (Thiel, 1979; Rowe, 1983; Sibuet *et al.*, 1989; Gooday and Turley, 1990; Thurston *et al.*, 1994; Rex *et al.*, 2006). Over spatial scales, benthic abundance is expected to be highest where surface productivity is highest. Likewise, changes in surface productivity over time should lead to changes in benthic abundance. But this relationship may be obscured by variations in the

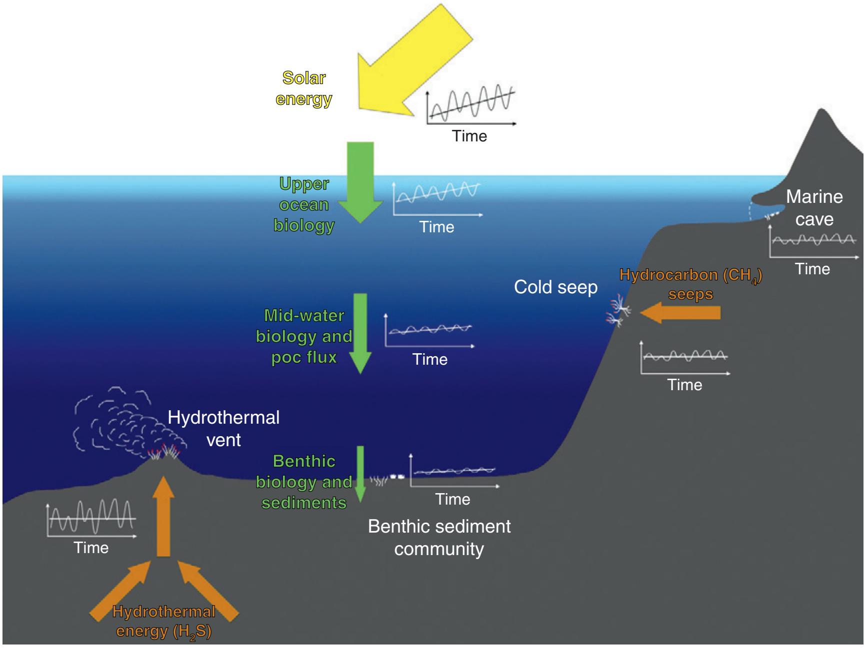

Figure 1.3 Schematic cross-section of the ocean floor, with vertical scale exaggerated, illustrating the typical location of soft-sedimented abyssal plains, regions of hydrothermal venting and cold seep habitats. Shallow-water marine caves, buffered from the effects of solar radiation and shifting temperatures, can provide habitats that are deep-sea analogs. Major energy fluxes illustrated by arrows (yellow—solar radiation, green—biologically mediated processes, brown—geologically mediated processes). For sedimented environments, stochastic shifts, seasonal shifts, inter-annual shifts and climatic trends (illustrated by the graphs of generalised environmental change over time) are transmitted to the upper ocean through atmosphere–ocean dynamics, these shifts are then transmitted through benthic–pelagic coupling to the seafloor several km below, where stochastic variation and climatic trends may be evident in the benthos, albeit muted in response relative to the surface. At hydrothermal vents and hydrocarbon seeps, the energy sources are geological, and temporal changes are stochastic and less influenced by climatic trends. POC refers to Particulate Organic Carbon.

efficiency of export to the deep-sea floor. Quantifying export production using sediment traps and benthic proxies is essential to understanding deep-sea benthic–pelagic coupling, which in turn underpins our understanding of how surface-water climate and 'biological forcing' drives deep-sea processes over the temporal scales associated with climatic shifts.

Studies of export production have usually relied on measuring the amount of particulate organic carbon (POC) flux to the seabed using mid-water moored sediment traps. When reviewed, these data suggest that there is a link between POC flux and surface water productivity, but at high levels of production other variables may be more important (Lampitt and Antia, 1997). Thus an increase in primary productivity, over both spatial and temporal scales, may not always be reflected in an increase in POC flux. Likewise, increased POC flux may not necessarily coincide with a peak in surface productions (e.g. Lampitt *et al.*, in press). This is because of the nature of primary production, the efficiency of the biological pump, the great distance the organic material has to sink (over 4 km in the abyss) and the resulting action of mid-water variables such as horizontal transport caused by currents and consumption by pelagic animals.

The settling particles are of four main types: (1) fine particulates, (2) visible macroaggregates of microscopic plant and animal remains known as phytodetritus (Fig. 1.4), (3) large plant remains such as macroalgae, seagrasses, and wood of terrestrial origin, and (4) large animal remains such as vertebrate carcasses (see Section 4.3). Down-slope transport, submarine slides, and turbidity currents may also inject organic materials into the deep sea (Carey, 1981). Phytodetritus accounts for much of the organic input to the deep seafloor. It generally comprises a wide variety of planktonic remains, including diatoms, coccolithophores, dinoflagellates, foraminferans, and faecal pellets embedded within a gelatinous matrix (Thiel *et al.*, 1989). Intact specimens of the diatom *Rhizosolenia* sp., recorded in box cores from 4400 m depth in the central Pacific, could be directly correlated with an observed bloom of this species in surface waters (C. R. Smith *et al.*, 1996). On both the Atlantic and Pacific seafloor, phytodetritus has been observed accumulating

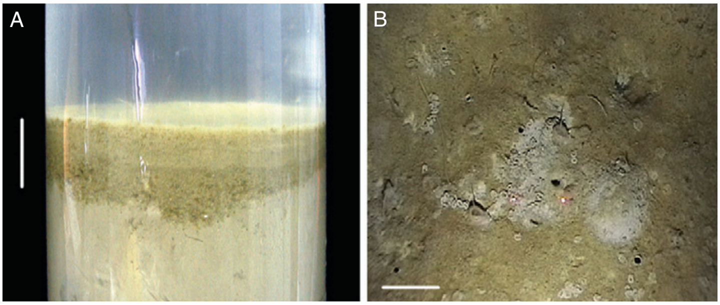

Figure 1.4 In deep-sea sedimented environments, food for benthos on the seafloor arrives in temporally variable pulses of green-tinted phytodetritus, macro-aggregates of microscopic plant remains and biological detritus produced in the upper water column. (A) Image of a 2.5 cm layer of intact phytodetritus recovered from a multi-core tube in 600 m water depth from the Southern Ocean (B) Seafloor at 600 m, Southern Ocean, showing thick layer of phytodetritus and evidence of phytodetritus consumption by surface deposit feeders. Scale bars (A) 2.5 cm, (B) 10 cm. Photos A and B courtesy of Craig R. Smith, University of Hawaii.

in biogenic depressions, tracks, and holes leading to a patchy distribution of the material (Billett *et al.*, 1983; C. R. Smith *et al.*, 1996). Phytodetritus is eventually consumed by motile surface deposit feeders, incorporated into the sediment through bioturbation, or washed away by deep-sea currents. Time-lapse imagery has shown that the residence time for phytodetritus is on a scale of days to months (Rice *et al.*, 1994; Smith and Druffel, 1998).

The best evidence for a direct link between surface waters and the deep sea has come from studies of the impact of seasonal phytodetritus deposition in the northeast Atlantic and central and northeast Pacific (Gooday and Turley, 1990; Gooday, 2002; Smith *et al.*, 2009). Holothurians may actively select and consume phytodetritus (Billett *et al.*, 1988). Echinoids may exhibit seasonal to interannual reproductive strategies in response to phytodetrital input (Tyler, 1988; Booth *et al.*, 2008). Benthic abundance is higher in phytodetritus-rich sites compared to those without phytodetritus (Paterson *et al.*, 1994a,b; Sibuet *et al.*, 1989; Glover *et al.*, 2001, 2002).

Data from these short intra-annual studies of seasonality, or inferences based on spatial patterns, strongly suggest that changes in surface-water biology associated with climatic perturbations, such as the North Atlantic Oscillation (NAO), ENSO, and human-induced climate change, will influence deep-sea benthic abundance and diversity. Temporal shifts in benthic parameters (e.g. abundance patterns, sediment respiration, and inventories of organic matter) almost certainly will reflect changes in the upper water column. As surface production changes as a result of ocean–atmosphere processes and climate change, benthic parameters may act as a useful measure of longer-term (inter-annual to decadal) shifts in surface-water production caused by climate change (K. L. Smith *et al.*, 2006). The majority of studies have examined only short-term, seasonal trends. As some studies now have data spanning a decade or more we are now in a position to assess the longer-term, decadal-scale changes that may reflect climatic influences.

2.3. Geological drivers

In contrast to the sedimented ecosystems that make up most of the deep seafloor, hydrothermal vents found at mid-ocean ridges are dependent on a geologically controlled supply of chemically enriched fluids. In this sense, temporal processes at vents are ‘geologically forced’ (Fig. 1.3). Whilst vents make up only a tiny fraction of the deep-ocean environment, they are sites of remarkable biological activity and concentrated biomass relative to the sedimented plains that surround them (Fig. 1.1C).

The discovery of rich biological communities on hydrothermal vents in 1977 was a surprise as hitherto, nobody had considered geologically derived sulphide as an energy source for the production of organic carbon. The conversion of inorganic to organic carbon by chemical means (i.e. chemosynthesis) was already known from studies of shallow-water microbial sulphur cycles. But in shallow-water systems, the sulphide is created from the degradation of organic materials and there is no net gain of organic carbon. At hydrothermal vents, a geochemical interaction between seawater and hot rocks in the Earth's crust creates the sulphide, resulting in a net gain of organic carbon (Van Dover, 2000).

Hydrothermal activity in the deep sea is associated with spreading centres on mid-oceanic ridges, back-arc basins, arc and fore-arc volcanoes, as well as active intra-plate seamounts. The hydrothermal habitat is characterised by strong environmental variables that influence the composition, distribution, and dynamics of associated communities (Tunnicliffe, 1991). These factors include the spatially irregular distribution of active vent sites, the temporal variability of hydrothermal activity and, at smaller scales, the local physical and chemical conditions experienced by vent fauna (Juniper and Tunnicliffe, 1997). In terms of chemistry, time-series measurements show the relative stability of the pure hydrothermal fluid composition within a site over decadal scales. It is only when eruptive or intrusive catastrophic events occur that large changes in hydrothermal systems are triggered and cause temporal variability (reviewed by Von Damm, 1995).

Along continental margins and subduction zones, the seepage of hydrocarbons (especially methane) upwards and along fault planes can create cold-seep habitats, usually in deep-water environments along continental slopes. Sulphate-reducing bacteria produce sulphide using methane as a carbon substrate (Van Dover, 2000). Rich biological communities of chemosynthetic organisms have been found in these habitats, utilising both methanotrophic and thiotrophic microbes (Levin, 2005). Although the majority of seep-dwelling species are distinct from those at vents, they are usually phylogenetically closely related, and utilise similar symbiotic or free-living bacteria as a source of energy.

Although not all vent and seep animals rely on chemosynthesis directly, it has long been recognised that the communities are highly dependent on the ephemeral nature of chemical fluid venting (Van Dover, 2000). In theory, the creation and cessation of vents over time should have drastic consequences for the associated communities and their successional processes. The very first discoveries of hydrothermal vent ecosystems showed how the cessation of vent flow could cause the death of these localised habitats (Corliss *et al.*, 1979). It was quickly realised that the ephemeral hydrothermal vents, in particular, may exist in a non-equilibrium successional state (Hessler *et al.*, 1988). The first hypotheses were based around an ordered succession from initial colonisation by opportunistic tubeworms, followed by clams and finally mussels. More detailed studies involving the mapping of assemblages on vent edifices over time has suggested that vent ecosystems conform to a chronic disturbance model, where one assemblage may be replaced by another without intermediary stages (Sarrazin *et al.*, 1997; and Section 4.1).

Over time, evidence suggests that changes in the chemistry of vent fluids, or in the amounts of pore-water methane at cold seeps, will drive changes in the structure of chemosynthetic ecosystems in the same way that changes in POC flux drive shifts in sedimented environments. Some vent sites, in particular those underlying high productivity regimes and those in shallower water, may host a range of species that utilise heterotrophy of photosynthetically derived food in addition to chemosynthesis. Such environments will experience a combination of geological and biological forcing mechanisms. Although the drivers may vary, the common evolutionary heritage and ecological constraints of deep-sea faunas, whether from vents or sediments, will create commonalities in the response to changes.

3. CASE STUDIES: SEDIMENTED ENVIRONMENTS

Muddy, deep-sea sediments represent the most widespread habitat on the Earth's solid surface, occupying approximately 96% of the ocean floor (Glover and Smith, 2003). With an average ocean depth of 3800 m, they are also one of the least accessible of habitats. Modern quantitative deep-sea biology only started in earnest during the 1960s with pioneering studies on the small infauna of the deep north-west Atlantic (Hessler and Sanders, 1967). The majority of these and subsequent studies have not included a long time-series element. Proxy records from long deep-sea sediment cores have yielded a large body of data on long-term change on the planet (Section 5.2.1), but on shorter ecological time-scales rather little is known.

Deep-sea sedimented environments are found in bathyal, abyssal, and hadal (trench) settings (Fig. 1.5). Bathyal environments, which are closer to land and often characterised by steep slopes, irregular topography, greater sediment heterogeneity, and a more complex water-mass architecture, are subject to a broader range of drivers. These include highly variable POC fluxes, down-shelf cascades, sediment slumps, turbidity currents, benthic storms, and organic inputs from river and canyon systems. In contrast, abyssal sites are usually (but not always) less influenced by horizontal transport and are more closely linked to the surface waters directly above them. Since nothing is known about temporal change in trenches, they are omitted from consideration in this review.

3.1. Bathyal sites

The bathyal region of the deep sea, being close to land and the home ports of nations actively involved in deep-sea work, has been better sampled than the abyss or hadal regions. However, the majority of sampling programmes have focussed on expanding our ecological or biogeographic knowledge

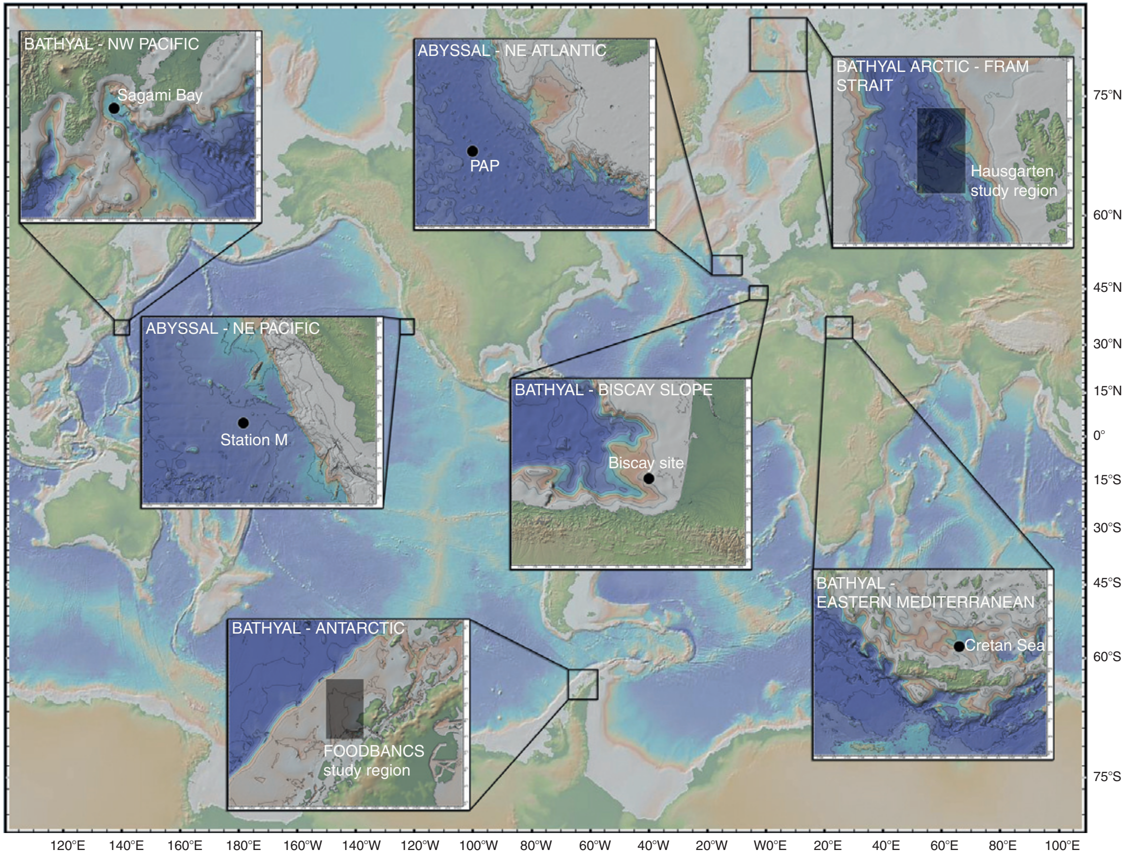

Figure 1.5 Geographic and bathymetric localities for known deep-sea sedimented environments with benthic time-series data. All bathymetric contours are 500 m interval. Data from GeoMapApp (http://www.geomapapp.org).

through broad spatial coverage rather than repeat visits. We have identified only 7 bathyal sites for which benthic biological time-series data is available.

3.1.1. HAUSGARTEN

The Alfred Wegener Institute for Polar and Marine Research in Germany has established the deep-sea long-term observatory 'HAUSGARTEN' west of Svalbard (Soltwedel *et al.*, 2005a). One of the main goals of the study is to measure the impact of large-scale environmental changes over time on a deep-sea ecosystem, and to determine experimentally factors that influence deep-sea biodiversity. The observatory includes 16 permanent sampling sites along a depth transect from 1000 to 5500 m and a latitudinal transect following the 2500 m isobaths for approximately 125 km (Fig. 1.5). The central HAUSGARTEN station at 2500 m water depth serves as an experimental area for *in situ* biological experiments (e.g. Premke *et al.*, 2003, 2006; Kanzog *et al.*, 2008; Gallucci *et al.*, 2008a,b). Multidisciplinary research activities at HAUSGARTEN started in 1999 and cover almost all compartments of the marine ecosystem from the pelagic zone to the benthic realm, with some focus on benthic processes.

The HAUSGARTEN observatory is located in Fram Strait, the only connection between the central Arctic Ocean and the Northern North Atlantic where exchanges of intermediate and deep waters take place. The main topographic features in the area are the Vestnesa Ridge, a submarine projection from the Svalbard continental margin (1000–2000 m water depth), and the Molloy Hole, a deep depression with a maximum depth of 5669 m, adjoining the ridge to the west. The hydrography is characterised by the inflow of relatively warm and nutrient-rich Atlantic Water into the central Arctic Ocean. The advection of these waters exerts a strong influence on the climate of the Nordic Seas and the entire Arctic Ocean (Hassol, 2004). HAUSGARTEN is also located in the highly productive Marginal Ice Zone (MIZ), where the dramatic decrease in the extent of summer sea-ice observed over the last decades causes an ongoing northward shift of the ice-edge related primary production.

Water column studies at HAUSGARTEN include the assessment of physico-chemical parameters as well as flux measurements of particulate organic matter to the deep seafloor. Water temperatures in the Fram Strait have increased significantly in recent years. Between the summers of 2003 and 2004, a relatively large temperature increase of 0.6 °C was observed within the upper 500–1000 m of the water column. At the central HAUSGARTEN site, temperature records covering the years 2000 through 2008 exhibited small seasonal variations, and an overall slight temperature increase, even at 2500 m (Fig. 1.6). Between 2000 and 2005, settling particulate matter at HAUSGARTEN showed seasonal patterns with elevated fluxes during May/June and at the end of the growth season (Bauerfeind *et al.*, 2009). The export flux of POC was rather low suggesting

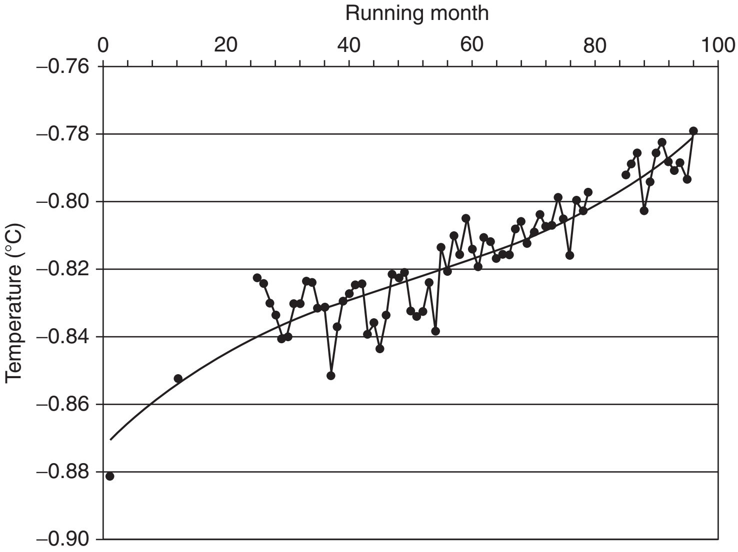

Figure 1.6 Bottom-water temperature (2 m above seafloor) at the central HAUSGARTEN site (2500 m) between the summers of 2000–2008.

a large retention and recycling of particulate organic matter in the water above 300 m. Based on the composition of the settled matter, the working hypothesis is that export of organic carbon is mainly governed by non-calcareous organisms. Furthermore, variations in the surface currents and ice regime appear to trigger changes in the patterns and composition of settling matter in the eastern Fram Strait.

Benthic investigations at HAUSGARTEN include analyses of biogenic sediment compounds to estimate organic matter input to the deep seafloor (using sediment-bound pigments as indicators of phytodetrital matter) as well as the activity, biomass, numerical abundance, and diversity of the benthic fauna from bacteria to megafauna. Biochemical analyses between the summers of 2000 and 2004 revealed a generally decreasing flux of phytodetrital matter to the seafloor, and subsequently, a decreasing trend in sediment-bound organic matter and the total microbial biomass in the sediments (Fig. 1.7). Over the spatial depth transect, mean metazoan meiobenthic (mainly nematode and copepod) densities ranged from 149 to 3409 individuals per 10 cm^2 (Hoste *et al.*, 2007). Although there was a significant correlation between meiobenthic densities, microbial exo-enzymatic activity (esterase turnover), and phytodetrital food availability (chlorophyll *a* and phaeophytines), there was no consistent relationship between nematode or copepod densities and measures for organic matter input. However, significant inter-annual variations in meiofaunal abundance were observed.

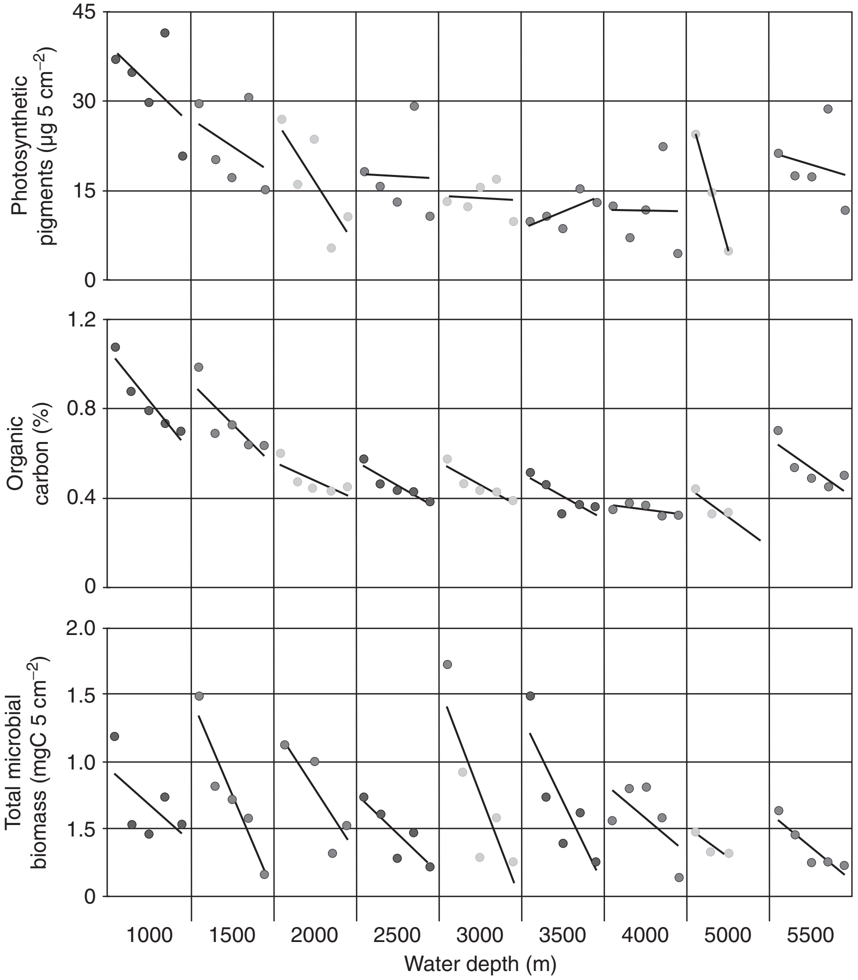

Figure 1.7 Temporal changes in sediments at the HAUSGARTEN site. Decreasing concentrations of photosynthetic pigments (top), organic carbon (middle) and total microbial biomass (bottom) recorded over the 2000–2005 time series are associated with increasing bottom water temperatures (Fig. 1.6). Figure adapted from Soltwedel *et al.* (2005a).

The species composition of nematode communities was studied along the complete HAUSGARTEN bathymetric gradient for the year 2000, and three stations (1200, 2500, and 4000 m) were sub-sampled for detailed species-level analysis over the 5-year time series. Although depth-related changes were more prominent than shifts according to sampling year, inter-annual variability in nematode community structure was clearly apparent.

Between-sample variability tended to increase with increasing water depth, and inter-annual variability was most pronounced at 2000 and 2500 m for nematode abundance (Hoste *et al.*, 2007). The 4000 m station was characterised by the highest variation within the same year, suggesting high spatial patchiness. However, parallel observations at several water depths indicate that most of the variation over the time series was the result of real temporal shifts in food availability as measured by sediment-bound phaeopigment and chlorophyll *a* concentrations (Hoste *et al.*, 2007). Nematode genera such as *Microlaimus*, *Dichromadora,* and *Tricoma* likewise seemed to be related to high food availability as they were present in the year 2000 and replaced, especially at 4000 m, by more typical deep-sea taxa such as Monhysteridae, *Cyartonema*, *Theristus*, *Halalaimus,* and *Acantholaimus*. One explanation for the high interannual variability at 4000 m is sediment disturbance caused by the steep slope (up to 40° inclination, Soltwedel *et al.*, 2005a) between the 4000 and 5000 m stations.

For the larger organisms, the abundance and distribution of epifaunal megafauna were assessed over the time-series using a towed camera system, taking seafloor images at regular intervals 1.5 m above the seafloor. A comparison of footage taken in 2002 and 2004 demonstrated a significant decrease (from 8.6 to 4.2 individuals per square meter) in megafauna densities at 2500 m (Soltwedel, unpublished data). Lower values in 2004 for the vagile megafauna (e.g. holothurians, gastropods, isopods) might reflect horizontal migrations of organisms. However, as densities of the sessile megafauna (i.e. poriferans, crinoids, and anthozoans) were also clearly lower in 2004 (a drop of 46.5%), this may be a general trend related to decreased food availability and higher bottom temperatures at the deep Arctic seafloor. Similar observations of decreasing megafaunal densities were made by other scientists in the nearby Kongsfjord during roughly the same period (J.M. Weslawski, personal communication). Studies of meiofaunal changes at HAUSGARTEN are ongoing.

3.1.2. Eastern Mediterranean

The Eastern Mediterranean deep sea is characterised by relatively high bottom temperatures (~14 °C) and recent notable changes in its thermohaline properties observed by time-series studies (Theocharis *et al.*, 1999; Danovaro *et al.*, 2004). During the period 1991–1995 the bottom temperature dropped by around 0.4 °C, and subsequently increased from 1995 to 1999 by about 0.2 °C (Danovaro *et al.*, 2004). Because the deep sea is normally characterised by very stable temperatures over long periods (although data are scarce for the Mediterranean; Lejeusne *et al.*, 2010), some benthic biotic response might be expected. Nematode abundance and diversity data from seven cruises between 1989 and 1998 revealed an increase in diversity during the 1990–1994 cooling period and a subsequent decrease during the ‘re-warming’ that followed (Danovaro *et al.*, 2004).

The degree of background stochastic variation in nematode diversity at these sites is unknown, so it is difficult to know whether this represents a long-term trend or a normal level of spatial or temporal variation. However, the potential link between hydrographic conditions, bottom-water temperature and benthic diversity is intriguing and merits continued monitoring.

In the seas to the south of Crete, long-term monitoring has been undertaken for the last 20 years in the Ierapetra Basin at 2500–4500 m. Data on pigment concentrations in surface sediments indicate that the Eastern Mediterranean, normally a highly oligotrophic area, may occasionally experience periods of very high organic-matter input (Fig. 1.8). Unusually, high concentrations of phytopigments have been reported in sediments (Tselepides *et al.*, 2000). These events could be linked to hydrographic shifts such as an increasing outflow of nutrient rich water masses into the Levantine Basin (Roether *et al.*, 1996; Klein *et al.*, 1999; Theocharis *et al.*, 1999), resulting in enhanced biological productivity and organic matter flux to the seabed. In 1993, this enhanced flux caused significant changes in the abundance and composition of the meiobenthic assemblages (Tselepides and Lampadariou, 2004; Lampadariou *et al.*, 2009). It also affected the planktonic (Weikert *et al.*, 2001) and the macrobenthic (Kröncke *et al.*, 2003) communities. These large changes in the physiochemical characteristics of the eastern Mediterranean (Roether *et al.*, 1996) provide a striking example of how large-scale, ocean-climate changes may abruptly convert a deep-sea ‘desert’ into an ‘oasis’ or a monoculture of opportunistic species, such as the polychaete *Myriochele fragilis* or the crustacean *Chaceon mediterraneus*. These species were once known only from the western Mediterranean basin, but are now found in high numbers also in the deep eastern basin (Sardà *et al.*, 2004).

3.1.3. Peru and Chile margin

Time-series studies at bathyal depths off the Peru and Chile margin have focused on how interactions between the well-developed oxygen minimum zone (OMZ) and decadal-scale ENSO impact the benthic fauna (Sellanes *et al.*, 2007; Arntz *et al.*, 2006). OMZs are layers of the water column, typically located between ~50 and 1000 m depth, where dissolved oxygen (DO) concentrations fall below 0.5 ml L^{-1} ($<22\ \mu$M). They are major oceanographic features on the eastern margins of ocean basins, notably the Pacific, as well as in the northern Indian Ocean (Kamykowski and Zentara, 1990; Paulmier and Ruiz-Pino, 2008). OMZs persist over geological time scales and are maintained by a combination of factors, particularly high surface productivity and water-column stratification. Where they intersect the seafloor on the outer shelf, upper slope, and oceanic seamounts (Helly and Levin, 2004), OMZs strongly influence the abundance, diversity, and composition of benthic faunas, mainly as a result of oxygen depletion and organic matter enrichment (Levin, 2003; Murty *et al.*, 2009; Gooday *et al.*, 2009).

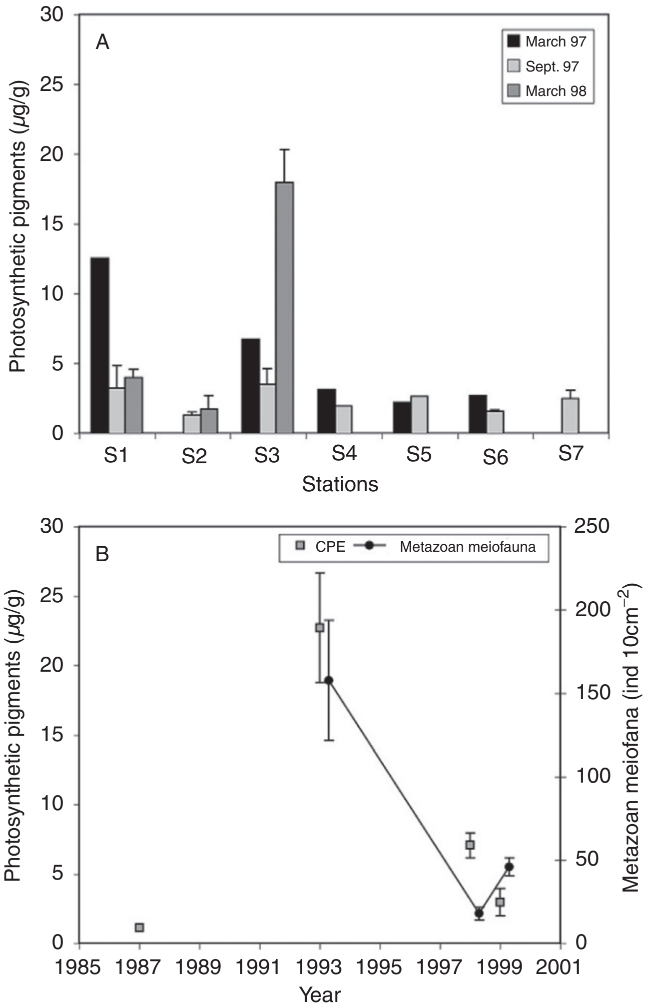

Figure 1.8 Temporal changes in sediments at the Eastern Mediterranean Ierapetra Basin sites over the 1987–1999 period: (A) photosynthetic pigment concentrations in surface sediments measured at three time points, indicating large inter-annual shifts in food flux to the seafloor, (B) changes in metazoan meiofaunal abundance associated with changes in food availability at the deep seafloor.

Of particular interest in the context of this review is the impact of ENSO on the OMZ upper boundary. This boundary is depressed during warm El Niño (EN) events on the Peru-Chile margin (Helly and Levin, 2004). Off Concepçion (central Chile), the upper OMZ boundary was located ~80 m between May 1997 and August 1998 (EN period) compared to ~30 m between November 2003 and March 2003 (non-EN period) (Sellanes *et al.*, 2007). The cooler non-EN period was further characterised by a higher total organic carbon and phytodetritus content of the sediment compared to the EN period. These environmental changes were accompanied by a decrease in the abundances of total macrofauna and certain polychaete species, the disappearance of an ampeliscid amphipod, and a shallowing of the macrofaunal living depth (Sellanes *et al.*, 2007). The 1997–1998 EN was also associated with changes among the meiofauna off Peru and Chile (reviewed by Arntz *et al.*, 2006).

Although EN-related oxygenation is felt most strongly on the shelf, it also extends deeper. On the Peru margin (~12°30′ S), the 1982–1983 EN event depressed the upper boundary of the OMZ from the shelf (50–100 m) onto the upper slope (nearly 300 m) (Arntz *et al.*, 1991). The 1997–1998 event lowered the boundary to ~200 m and is believed to have led to a slight increase in oxygen levels to 300 m depth (Levin *et al.*, 2002). Although rises in oxygen concentrations during EN periods probably do not penetrate below the upper slope, the associated reduction in surface productivity leading to a decline in carbon flux will have consequences for deeper benthic communities as well as those in shallower water. Arntz *et al.* (2006) conclude that 'it is likely that large areas of the margin below the OMZ should respond to ENSO-related changes in hydrography and productivity.'

3.1.4. Bay of Biscay

At temperate slope sites, a pronounced seasonal signal may also be accompanied by inter-annual variability in surface production. Oscillations in the strength of this seasonal and inter-annual production are quickly transmitted to the bathyal seafloor. A time-series study in the Bay of Biscay has identified a spring-bloom related increase in chlorophyll *a* concentrations in the sediments. The response of the 'live' benthic foraminifera (63–150 and $>150\ \mu$m size fractions) to this bloom was analysed in multi-year time-series samples from two bathyal sites, located at 550 m (October 1997–April 2000) and 1000 m (October 1997–April 2001) (Fontanier *et al.*, 2003, 2006). Although total foraminiferal densities varied considerably between cores at 550 m, a principal component analysis suggested that temporal variability was more important than spatial variability, even in the finer (63–150 μm) fraction. At both sites, a pronounced spring bloom led to phytodetritus deposition to the seafloor, which induces strong seasonal fluctuations among foraminifera, particularly small opportunistic species living close to the sediment surface. However, although there are some inter-annual differences, there is no evidence for longer-term trends at these two bathyal localities.

3.1.5. Sagami Bay

A permanent bathyal station (1430 m water depth) in Sagami Bay, a deep-water embayment on the Japanese margin near Tokyo, has been sampled repeatedly for foraminifera since 1991 (Kitazato and Ohga, 1995; Ohga and

Kitazato, 1997). Data on surface productivity, fluxes through the water column, and dynamic processes at the sediment–water interface, were gathered regularly since 1996, the 1997/1998 period being studied in particular detail (Kitazato *et al.*, 2000, 2003). The area is characterised by a seasonal deposition of fresh phytodetritus, which causes changes in the thickness of the oxygenated layer of the sediment. Corresponding to these annual cycles, there are clear fluctuations in the population densities of foraminifera (Kitazato *et al.*, 2000), changes in the vertical distributions of harpacticoid copepods and kinorhynchs (Shimanaga *et al.*, 2000), but no obvious seasonality in the species composition and diversity of copepods (Shimanaga *et al.*, 2004). Thus, as on the Biscay margin, this intensively studied deep-water embayment is dominated by seasonal processes with no evidence to yet emerge for longer-term faunal changes.

3.1.6. Rockall Trough

Another bathyal site with long-term temporal data is the Rockall Trough off the west coast of Scotland. The site was established in 1973 and includes the Scottish Association for Marine Science Permanent Station at 2990 m and a Station 'M' on the Hebridean Slope (Gage *et al.*, 1980; Tyler, 1988). The main focus of these studies was not the investigation of long-term change, but the impacts of seasonality, which required sampling over several years. The results from many studies indicate that there is an obvious seasonal response that manifests itself in seasonal reproductive patterns of species such as the ophiuroids *Ophiura ljungmani*, *Ophiocten gracilis*, echinoid *Echinua affinis*, asteroid *Plutonaster bifrons*, the bivalves *Ledella messanensis* and *Yoldiella jeffreysi* (Lightfoot *et al.*, 1979; Tyler and Gage, 1980; Tyler *et al.*, 1982), variation in recruitment in the ophiuroid *Ophiomusium lymani* (Gage and Tyler, 1982) and differences in breeding intensity in isopods (Harrison, 1988). In a similar pelagic time series, Gordon (1986) studied fish reproductive cycles in the Rockall Trough reporting that *Nezumia aequalis*, *Trachyrhynchus murrayi* and *Lepidon eques* showed seasonal reproduction spawning in spring. The majority of these species have synchronised their breeding cycles to coincide with the annual increase in surface production; and food supply from surface waters was thought therefore to be a key factor in these life histories. Such observations indicate a close link between reproduction, recruitment and survivorship and variations in surface production. Although these data were not collected with climate change in mind, it is clear that changes in climate affecting surface production are likely to impact on organisms that show such close benthic–pelagic coupling.

3.1.7. West Antarctic Peninsula

A final 'bathyal' site of interest is located on the West Antarctic Peninsula continental shelf; we classify it bathyal owing to the greater depth of the Antarctic shelf (500–1000 m) caused by the ice-loading of the Antarctic continent. The region to the west of the US Palmer Station is targeted as a Long-Term Ecosystem Research site (the LTER programme, funded by the US National Science Foundation) and has been subject to 12 years of upper-ocean monitoring (C. R. Smith *et al.*, 2006). Sediment-trap monitoring of POC flux to the seafloor has revealed intense seasonal pulses of food input, as might be expected given the pronounced variation in photoperiod and sea-ice cover in high latitude marine environments (C. R. Smith *et al.*, 2006). Benthic studies in the form of the 'Food for Benthos on the Antarctic Shelf' (FOODBANCS) programme only commenced in 1999, but have already revealed that the seasonal pulse in food is strongly buffered in benthic sediments by the presence of a persistent 'food bank' that allows detritivores to continue feeding and reproducing year-round (Mincks and Smith, 2007; Glover *et al.*, 2008; Sumida *et al.*, 2008). However, over the study period (1999–2001), strong inter-annual variability in the quantity of phytodetritus was observed at the ocean floor, hinting at major shifts occurring on potentially decadal scales (C. R. Smith *et al.*, 2006). Ongoing sampling over inter-annual scales (FOODBANCS 2) is expected to provide a new decadal-level benthic dataset in the Southern Ocean.

3.2. Abyssal sites

The abyssal plains are the most extensive of deep-sea habitats. Their distance from land, and great depth, creates major sampling problems in terms of technical and financial logistics. Even with modern winches, it requires over 4 h to take a simple spade box core in 5000 m of water. An abyssal trawl usually takes at least 8–12 h and the majority of ROVs are unable to reach such depths. Nevertheless, long-term monitoring has been carried out in two principal abyssal settings. The Porcupine Abyssal Plain (PAP) is centred in the north-east Atlantic and has been the focus of mainly British oceanographic cruises. The second, 'Station M', is in the north-east Pacific and has been sampled mainly by US cruises. Both these sites have been sampled, mainly on a semi-regular basis, by researchers over the last two decades. Government funding for such cruises has been intermittent, and it is only recently that the value of these long-term datasets has been fully realised. The PAP and Station M are now considered 'observatories' and as such are key sites for the study of long-term change in the abyss.

3.2.1. Porcupine Abyssal Plain sustained observatory

The PAP site lies at 4850 m water depth in the north-east Atlantic (Fig. 1.5). This important site has been studied in different ways and at various frequencies over a period of more than 20 years. The most complete benthic datasets are for invertebrate megafauna (1989–2005) and fish (1977–1989 and 1997–2002) collected using a semi-balloon otter trawl. From 1989 to 2002, there was a threefold increase in megafaunal abundance and major changes in species composition (Fig. 1.9; Billett *et al.*, 2001, 2010). Evidence from time-lapse photography indicates that the increase was even more dramatic than suggested by the trawl samples (Bett *et al.*, 2001). The most obvious changes were seen among holothurians, notably *Amperima rosea* and *Ellipinion molle*, small species that both showed rapid abundance increases in 1996/1997 followed by a decline that was particularly precipitate in the case of *E. molle*. This period (1997–1999) has been termed the '*Amperima* event' (Fig. 1.9D). *Amperima* densities underwent a second 'boom-bust' cycle in 2002–2005. Two larger holothurian species (*Psychropotes longicauda* and *Pseudostichopus aemulatus*) exhibited more modest increases during the *Amperima* event, while a third (*Oneirophanta mutabilis*) underwent a significant decrease over the entire time series. Tunicates and actiniarians increased in abundance at the same time as *Amperima* and maintained higher densities after the *Amperima* event; pycnogonids showed a sharp increase during the *Amperima* event, but no significant trend over the time series as a whole. The increases in densities of holothurians, in particular *A. rosea*, led to an increase in the extent to which surface sediments, and particularly phytodetritus deposits, were reworked during the *Amperima* event (Bett *et al.*, 2001). Probably as a result of these activities, there was little sign of phytodetritus on the seafloor between 1997 and 1999.

Changes in other elements of the benthic fauna, the foraminifera, metazoan meiofauna and macrofaunal polychaetes, were also observed during the 1990s at the PAP. Foraminiferal densities (0–1 cm sediment layer, >63 μm fraction) were significantly higher in 1996–2002 compared to 1989–1994 (Gooday *et al.*, 2010). Over the same period, species richness and diversity decreased and dominance increased, although not significantly. Species-level multivariate analyses revealed three assemblages represented by samples collected in 1989–1994, September 1996–July 1997 and October 1997–October 2002 (Fig. 1.10). These reflected temporal changes in the densities of higher taxa and species. The abundance of Trochamminacea, notably a small undescribed species, increased substantially. Species of Hormosinacea and *Lagenammina* also tended to increase in density from 1996/1997 onwards. Rotaliida, dominated by *Alabaminella weddellensis* and *Epistominella exigua*, showed a bimodal distribution over time with peak densities in May 1991 and September 1998 and lowest densities in 1996–1997. Short-term responses to seasonal phytodetritus inputs probably explain the relative abundance of *E. exigua*, and to a lesser extent *A. weddellensis*, in 1989 and 1991 when phytodetritus was present. A qualitative change in the phytodetrital food, repackaging of food by megafauna, increased megafaunal disturbance of the surficial sediment, or a combination of these factors, are possible explanations for the dominance of trochamminaceans from 1996 onwards. Horizontally sliced box-core samples (0–5 cm, >250 μm fraction) revealed that the miliolid *Quinqueloculina* sp. was more abundant in March 1997, and also concentrated in

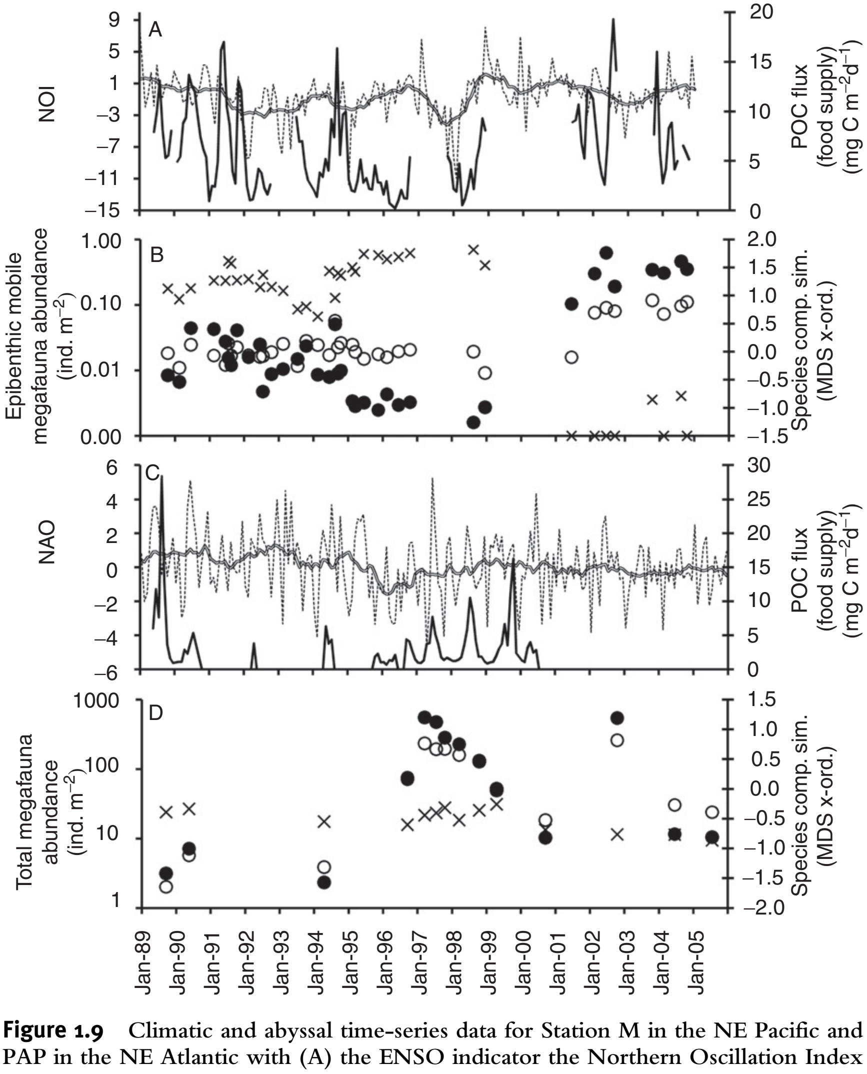

Figure 1.9 Climatic and abyssal time-series data for Station M in the NE Pacific and PAP in the NE Atlantic with (A) the ENSO indicator the Northern Oscillation Index (NOI) with monthly (light dashed line) and 13-month running mean (compound line), and POC flux to 4050 m depth at Station M; (B) mobile megafauna variation at Sta. M including *Elpidia minutissima* abundance (crosses), *Echinocrepis rostrata* abundance (open circles), and an index of species composition similarity of the top ten most abundant megafauna (solid circles); (C) the NAO index with monthly (light dashed line) and 13-month running mean (bold dashed line), and POC flux to 3000 m depth at the PAP; and (D) total megafauna variation at Station M including *Oneirophanta mutabilis* abundance (crosses), *Amperima rosea* abundance (open circles), and an index of species composition similarity of the benthic megafauna (solid circles).

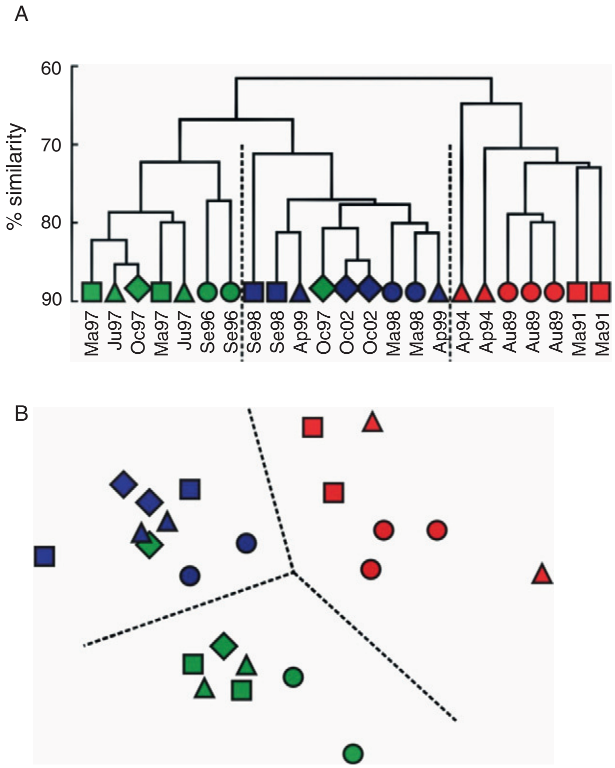

Figure 1.10 Cluster analysis (A) and non-metric multi-dimensional scaling ordination (B) based on square root transformed abundance (density) for foraminiferal assemblages from the Porcupine Abyssal Plain. Different symbols indicate different cruises. Note the change in assemblage composition over time. Figure from Gooday *et al.*, 2010.

deeper sediment layers, than in September 1996. This species apparently migrated to the sediment surface in response to a 1996 flux event, grew and reproduced, before migrating back into deeper layers as the phytodetrital food became exhausted. These time-series samples therefore suggest that decadal-scale changes have occurred among shallow-infaunal foraminifera at the PAP site, more or less coincident with changes in the megafauna, as well as indications of shorter-term events related to seasonally pulsed phytodetrital inputs.

Densities of metazoan meiofauna (32–1000 μm) increased significantly between 1989 and 1999, driven mainly by the dominant taxon, the nematodes, and to a lesser extent the polychaetes (Kalogeropoulou *et al.*, 2010). Ostracods showed a significant decrease while most other taxa, including the second-ranked group the copepods (harpacticoids and their nauplii), did not exhibit significant temporal changes in abundance. MDS ordination of higher taxon composition showed a significant shift at this taxonomic level in meiofaunal species composition from the pre-*Amperima* to the *Amperima* periods. There were also significant increases in the proportion of total meiofauna, nematodes, and copepods (but not polychaetes) inhabiting the 0–1 cm layer over time. In addition, seasonal changes in the vertical distribution patterns of total meiofauna and nematodes within the sediment were apparent during the intensively sampled period (1996–1997).

Macrofaunal polychaetes exhibited a more muted response to changes at PAP. Soto *et al.* (2010) found that the abundance of the whole assemblage increased significantly before and after the *Amperima* event. These differences were localised to the upper 3 cm of the sediment and the increase in the assemblage density was less than that of the megafauna. Analyses of the polychaete faunal composition indicated that only certain taxa and trophic groups responded. The families Cirratulidae, Spionidae, and Opheliidae had significantly higher abundances during the *Amperima* event that before, while others, such as the Paraonidae, showed no obvious change during this time. The Opheliidae response was characterised by an influx of juveniles, probably all of the same species (Vanreusel *et al.*, 2001). Significant increases were also detected in two trophic groups, surface deposit feeders and predators.

Although polychaete assemblages exhibited an overall change at the higher taxon and functional group level at the PAP during the period 1989–1998, the response was much less obvious at the species level (Soto, 2008). The same dominant species occurred throughout the study period, with the exception of the Paraonidae, where the dominant species of the genus *Aricidea* declined prior to the *Amperima* event and was replaced by two other species. While the 12 most abundant species all exhibited some interannual variation, only 6 showed a significant response during the *Amperima* event. All had the highest abundance in July 1997 and September 1998 corresponding to the highest values of phytopigment fluxes, carbon and nitrogen in the water column. The increase in abundance of these species, however, was quite low and often only slightly higher than pre-*Amperima* event densities. The fact that only some polychaete species responded may be related to greater foraging efficiency by megafaunal deposit feeders that sequestered and repackaged nutrients, with the result that fewer nutrients reached smaller organisms. Surface deposit-feeding polychaetes increased during the *Amperima* event, at the same time as disturbance of the surficial sediment by holothurians and ophiuroids was presumed to be increasing.

The extent to which the above-mentioned changes in the benthic community affect the associated fish communities remains unclear. As described above, the main factor driving change in abyssal communities is temporal variability of food availability. A study of muscle tissue RNA and protein content for abyssal fishes caught in spring suggested lower growth rates than conspecifics caught during the preceding autumn (Kemp *et al.*, 2006). This suggests that temporal changes in benthic food availability could potentially affect fish, as growth rates were highest just after the summer peak in POC flux. As most fish do not feed directly on phytodetritus, any trophic link would depend on changes to prey animal availability or composition as a result of these animals feeding on phytodetritus. Such changes were not observed in previous studies in the Pacific (see Section 3.2.2), but the greater seasonal variability in primary productivity in the North Atlantic could explain this (Kemp *et al.*, 2006). Cyclic changes in the melatonin content of the isolated pineal glands of the bathyal eel *Synaphobranchus kaupii* indicate that these fish may have retained a biochemical rhythm linked to monthly tidal-cycle variations (Wagner *et al.*, 2007). Such a time-keeping system might allow a fish to schedule its growth and reproduction to times when food is most available, or even migrate to areas where seasonal increases in food occur.

Like the invertebrate fauna, the abundance and composition of the fish community of the PAP and the adjacent slope (Porcupine Seabight, PSB) have been subject to studies using trawling (Merrett, 1992; Collins *et al.*, 2005). They have also been studied with baited landers (Bailey *et al.*, 2007). These studies have told us much about the spatial distribution and behaviour of these fishes, but as yet very little about natural temporal change. Commercial fisheries landing data for the upper slopes of PSB reveal declines in the abundance of target species (Basson *et al.*, 2002) but we know little about natural drivers of temporal change in these fishes, or about changes at lower bathyal and abyssal depths. A recently studied long-term dataset of 161 trawls at depths of 800–4800 m, conducted from 1977 to 2002, reveals a decline in fish abundances between 800 and 2500 m, but no changes deeper than this (Bailey *et al.*, 2009). Changes were observed in both fisheries target and non-target species, as long as a portion of their range fell within the fishing grounds (<1500 m). This may reflect fishing on the upper slope preventing these fish from spreading down-slope to populate deeper areas (Bailey *et al.*, 2009). In this way fishing effects are transmitted down-slope, effectively removing fish from areas tens of kilometres from the fishing grounds themselves. However, the PAP site is well below the depth at which these effects are visible. The dataset for PAP consists of only 35 research trawls targeting fish at >4000 m over the period 1978–2002. We have not discerned any temporal patterns in these data. If changes have occurred they may be obscured by the low numbers of fish caught in most of these trawls, gaps in the dataset and the difficulty in accurately estimating the area sampled. If there is a role for seasonal changes in food availability in the ecology of these fishes (Kemp *et al.*, 2006) it is reasonable to assume that longer-term changes in food inputs could affect fish numbers and community structure in the same way as has been seen in the invertebrates.

3.2.2. North-east Pacific

Station M, in the north-east Pacific has been monitored since 1989. This site is located 220 km off the coast of Point Conception, California in 4100 m of water. The region has been shown to exhibit pronounced seasonal and interannual climate variability (Smith and Druffel, 1998). The site is also in the vicinity of the California Current Oceanic Fisheries Investigations (CalCOFI), a programme of biological oceanographic research that has been conducted seasonally in surface waters since 1949. A partner programme to CalCOFI, operating in the same vicinity since 2004, is California Current Ecosystem Long-Term Ecological Research (LTER) programme (Ohman and Hsieh, 2008).

The Station M time-series programme has revealed substantial variations in mega and macrofaunal abundance and size from the species to community level, along with shifts in ecosystem functions such as bioturbation rate and sediment community oxygen consumption (SCOC) (Drazen *et al.*, 1998; Ruhl, 2008; Ruhl *et al.*, 2008; Vardaro *et al.*, 2009; Fig. 1.9). It is believed that these changes are linked to fluctuations in the availability of food at the seafloor. The data suggest that changes in food supply influence the smaller fauna more rapidly. Over a period of nearly 2 years, beginning in June 1989, significant seasonal variations in macrofauna were observed (Drazen *et al.*, 1998). Protozoans (especially agglutinating foraminifera) and major metazoan groups including nematodes, polychaetes, harpacticoids, tanaids, and isopods retained on a 300-μm sieve, exhibited seasonal variations with maximum abundances following peaks in food supply. Also, the arrival of a pulse of phytodetritus on the seafloor was followed within weeks by a significant increase in protozoan densities (Drazen *et al.*, 1998). A longer-term (1989–1998) analysis of metazoan macrofaunal data also revealed that metazoans first responded after ~3–4 months in terms of density and after 7–8 months in terms of total biomass and individual biomass. This would be expected if the dominant faunal response was reproduction and recruitment followed by individual increases in body size (Ruhl, 2008; Ruhl *et al.*, 2008).

Given that abyssal fauna are thought to be food-limited (Johnson *et al.*, 2006; C. R. Smith *et al.*, 2008; K. L. Smith *et al.*, 2009), it has been hypothesised that inter-annual and longer-term variation in food supply would have implications for abundance and community structure similar to those observed in the seasonal studies. Longer-term analysis indicates that, in addition to the seasonal trends, the observed variations in metazoan abundances extended to interannual periods where food supplies were higher or lower (Ruhl *et al.*, 2008). For example, the food supply in 1991 was approximately twice that in 1992, with comparable differences in metazoan macrofaunal abundance. This change is similar to that observed for macrofaunal polychaetes at the PAP site. Furthermore, there were significant changes in dominance and community structure, even at the phylum level. Community changes were seen in the relative abundance of specific phyla, as well as in the rank abundance distributions, a biodiversity indicator of relative abundance and evenness. The changes included a switch from dominance by the larger annelids during periods (e.g. 1991) of higher food supply to dominance by smaller arthropods when food was scarcer (e.g. 1992). So, even though the total abundance of the metazoan macrofauna increased both in terms of biomass and density, the response was not consistent across phyla, with larger fauna apparently gaining competitive advantage during higher food flux conditions.

For several species of mobile megafauna, abundance was correlated with food supply over the 1989–2004 study period (Ruhl and Smith, 2004; Ruhl, 2007). Shifts in species composition, and the relative evenness of species abundances, were also noted. The elasipod holothurian *Elpidia minutissima* grew in abundance from 1989 to 1998 to almost 1 indiv. m^{-2}, but then showed a precipitous decline to nearly 1 indiv. ha^{-1} (Fig. 1.9B). Another elasipod, *Peniagone vitrea*, showed a similar trend. Other species (e.g. the irregular urchin *Echinocrepis rostrata*) exhibited the opposite tendency, occurring in relatively lower abundances over the early part of the time series, but showing an order of magnitude increase during the 2001–2004 period. The larger holothurian *Psychropotes longicaudata* showed a similar, albeit less variable trend.

As with the metazoan macrofauna, the abundance of many dominant epibenthic megafaunal species was linked to the food supply. However, the echinoderms exhibited much larger abundance variations (up to three orders of magnitude) compared to a factor of two in the case of the macrofauna. Additionally, the megafauna had longer temporal lags (several months on average) in their apparent responses to the variable food supply. An analysis of the body-size distributions of the most abundant mobile megafauna suggested that increases in abundance were negatively correlated to decreases in the average body size in seven of the ten species (Ruhl, 2007). This increased proportion of smaller individuals suggests that reproduction and recruitment probably play an important role in abyssal population dynamics. Migration and mortality are also likely to influence the declines in abundance. However, except for *Peniagone* spp., which have been observed swimming above the seafloor, adult stages of these species are thought to move too slowly for mass migrations to be an important factor. Estimates from time-lapse photography have put the speed of megafaunal movement at 0.4–5.7 km yr^{-1} (Kaufmann and Smith, 1997). A more detailed investigation of the size distribution dynamics of the ophiuroids did not reveal any seasonal trends, although there were significant correlations between the body-size distribution shifts and food supply (Booth *et al.*, 2008). The lack of a detectable correlation at the seasonal scale may reflect the fact that the interannual variation in food supply observed at Station M is greater than in the Rockall Trough, where seasonality in ophiuroid recruitment was frequently observed.

Recent data have suggested that there are temporal trends among abyssal Pacific fish populations, although the reasons behind them are not fully understood. The behaviour, abundance, and biochemical composition of abyssal fish change temporally, over both seasonal and interannual timescales. Baited camera observations suggest that grenadier swimming activity at Station M vary between seasons (Priede *et al.*, 1994a), while seasonal changes in size frequency were observed in the Central North Pacific (CNP) (Priede *et al.*, 2003). These observations led Drazen (2002) to test for seasonal differences in the body compositions of three grenadier species. After examining a whole suite of biochemical indicators of nutrition and growth, Drazen (2002) concluded that seasonal changes in productivity have no measureable effect on the fish, perhaps because fish are able to switch between prey types, and eat mid-water fish or squid. Interestingly, there were indications of interannual variability in biochemical composition, which might indicate changes in food availability, or a spawning cycle.

A camera sled has also been used to estimate benthopelagic fish abundance in the Station M region (Bailey *et al.*, 2006). Only fish within ~2 m of the seafloor were visible, and the majority of these were grenadiers (*Coryphaenoides* spp.). The numbers of these fish more than doubled over the period 1989–2004 (Bailey *et al.*, 2006). Fish numbers also correlated with the abundances of benthic echinoderms but with changes in the fish lagging behind changes in echinoderms by 9–20 months (Bailey *et al.*, 2006). Although echinoderms are not normally considered a major source of food for grenadiers, a predator–prey relationship is the simplest explanation for the correlation. However, recent dietary studies based on stomach contents, stable isotope analysis (Drazen *et al.*, 2008) and fatty acid profiles (Drazen *et al.*, 2009) seem to show that these abyssal fish are much more dependent on carrion than was previously thought, and do not feed primarily on echinoderms. These findings lead to the intriguing idea that abyssal fish communities might be affected strongly by sinking fish carrion derived from stocks in the photic zone.

On an ecosystem level, the broad faunal changes noted above could have consequences for ecosystem function, such as organic matter remineralisation rates and sediment bioturbation. Shifts in ecosystem functioning could have important impacts on the proportion of organic carbon that is either remineralised or becomes buried in marine sediments. Research into ecosystem function at Station M has focused on a few key areas, including SCOC, bioturbation, and links between biodiversity and ecosystem function. SCOC is indicative of food demand and also is an indicator of organic carbon remineralisation. After the initial 10 years of measurements at Station M (1989–1998), two features of SCOC variability became apparent. There were distinct seasonal cycles in SCOC that were less variable between years relative to POC flux, and the ratio of POC flux to SCOC declined over time, suggesting that there was a trend towards less food availability to support the demand implied by the SCOC measurements (Smith and Kaufmann, 1999; K. L. Smith *et al.*, 2001). These studies hinted at a potential long-term change in community structure and/or function, even if some food derived from high flux pulses remained in the sediment. Although the food supply did increase in the more recent 2001–2006 period, POC flux:SCOC ratios in the limited data collected during that period still showed a deficit (K. L. Smith *et al.*, 2008). Nevertheless, SCOC is positively correlated to POC flux with no discernable time lag (Ruhl *et al.*, 2008). Because the detrital aggregates may have represented an underestimated part of the POC flux input, an empirical estimation of aggregate POC flux was also made with the available data. Even including the occasional intense pulses of POC seen in the aggregate coverage data, there is still an overall deficit (K. L. Smith *et al.*, 2008). Over the same period, the metazoan community did change (as described above) but there was no correlation between the synoptically observed SCOC and macrofaunal abundance or biomass. Thus, the microbial, meiofaunal, and protistan community are likely to dominate abyssal SCOC dynamics with macrofauna, like the megafauna, having a primary functional role of bioturbation.

4. CASE STUDIES: CHEMOSYNTHETIC ECOSYSTEMS

Whilst the sedimented abyssal plains and bathyal slopes are dependent on a steady 'rain' of organic detritus from surface waters, chemosynthetic ecosystems can utilise *in situ* energy sources of reduced compounds, most often hydrogen sulphide or methane. These chemicals may have a geological source (e.g. at hydrothermal vents and cold seeps) or a biogenic origin—such as the carcass of a dead whale, a sunken log or even a shipwreck with an organic-rich cargo. The considerable similarities between these ecosystems in terms of the chemical habitat have created taxonomic affinities, functional similarities and in some cases species overlap between habitats that may initially appear quite different.

Whilst chemosynthetic ecosystems are globally widespread (Fig. 1.11 illustrates those that are discussed in this review), they are often relatively isolated from each other, creating habitat 'islands' on the deep seafloor. A number of faunistic compositional and biogeographical paradoxes have emerged with the recent study of chemosynthetic ecosystems that must to some extent be explained by their geographic isolation and unique habitat conditions. The dramatic differences in species composition may also reflect differing scales of temporal change that depend on the geological or biological drivers that are prevalent.

Studies of chemosynthetic ecosystems, in particular those with hard-substrates, was more or less impossible prior to the invention of deep-water

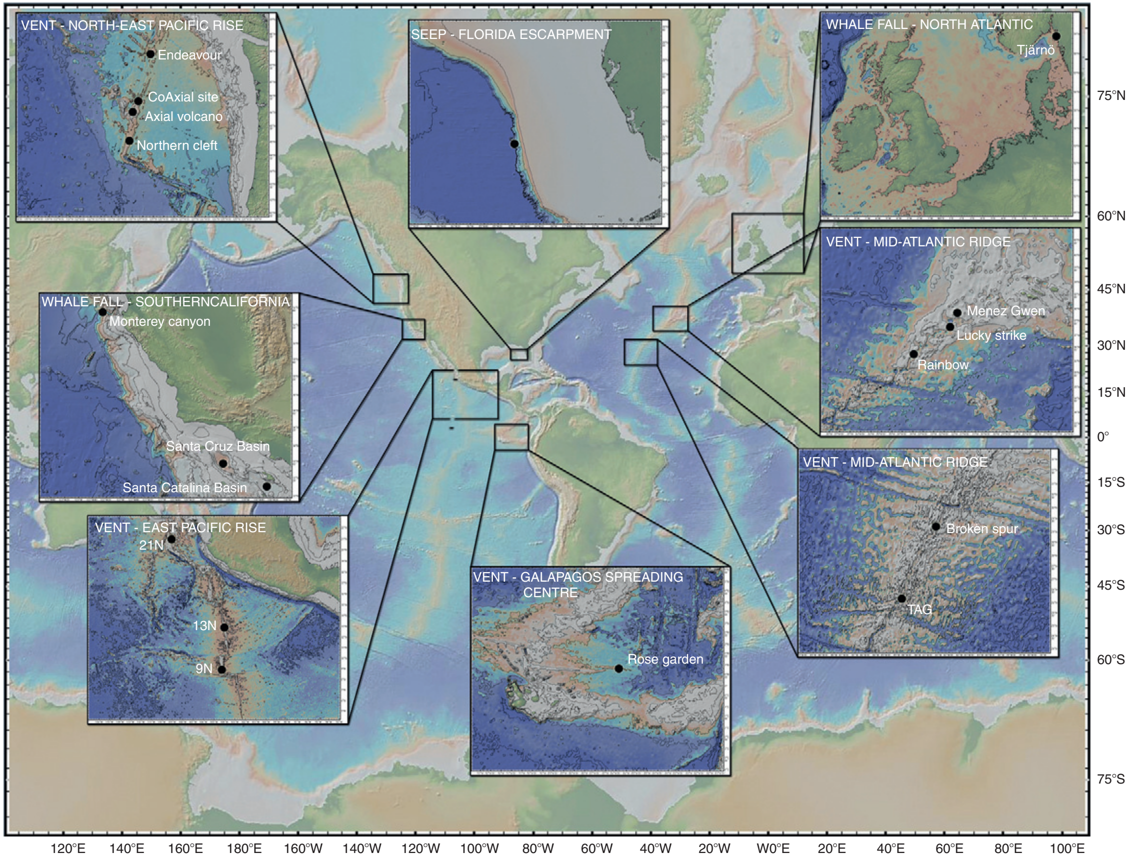

Figure 1.11 Geographic and bathymetric localities for known deep-sea chemosynthetic ecosystems with benthic time-series data. Bathymetric countours are 500 m interval (or 1000 m in some instances for clarity). Data from GeoMapApp (http://www.geomapapp.org).

video systems, submersibles and most recently ROVs. For these reasons, it is a young and constantly shifting scientific field. Entire ocean basins remain almost completely unstudied, and our knowledge of temporal patterns comes from the relatively few sites described here, the majority of them hydrothermal vents.

4.1. Hydrothermal vents

When hydrothermal vents were first discovered it was quickly realised that, although biologically rich, they were likely to be ephemeral both in space and time. In particular, the fields of dead clams first noticed near the Galapagos in 1977 suggested that cessation of fluid flow, or eruptions, may periodically wipe out entire local populations. However, it has proved difficult to mount expeditions with a sufficient temporal resolution to truly study successional processes at vents. This has been achieved at only a handful of better-known sites. There has always been a trade-off in terms of the allocation of ship-time between repeat visits and searching for new vents, especially as vent fauna exhibit such intriguing biogeographic patterns.

In general, time-series data has been obtained from cruises that were launched in response to a major eruption (e.g. the famous 1991 eruption at 9° N), or by piecing together data from a series of discrete cruises that were not originally designed for temporal studies. In almost all cases, biological data is in the form of video surveys, with only small samples being taken for the obvious reason that major sampling would severely impact on the studied community. Major problems with such image sampling include the difference between videos taken from manned submersibles and ROVs. In the former case, the video is often secondary to the personal notes and observations of the observer. In the latter case, the video is the basis for all observations. Additional problems include locating the same vent edifices and communities after major geological changes.

Despite the many recent vent discoveries in the west Pacific, Indian Ocean and southern Atlantic, the only real long-term study sites are in the East Pacific and North Atlantic.

4.1.1. East Pacific Rise

The East Pacific Rise (EPR) is a mid-oceanic ridge that extends continuously along the floor of the Pacific Ocean (Fig. 1.11). It lies 2–3 km below sea level and rises above the surface to form Easter Island and the Galapagos Islands. This divergent tectonic plate boundary separates the Pacific Plate from the North American, Rivera, Cocos, Nazca, and Antarctic Plates. The EPR was the site of the first hydrothermal vent discovery in 1977, at the Galapagos Spreading Centre (GSC) 'Rose Garden' (Lonsdale, 1977). Since that time, several more vent fields have been discovered and named for the degree of latitude that they lie closest to. The best studied are at 21°, 13°, and 9° N.

Rose Garden (GSC): This famous 'textbook' vent site was visited in 1979, 1985, 1988, 1990, and 2002. It represents a typical low-temperature site with community zonation from the vent to the periphery (Van Dover, 2000). During the two first visits, no major venting fluctuations were observed but the *Riftia pachyptila* tube-worm population, which was luxuriant in 1979 (and thought to be the first coloniser) had been outcompeted by *Bathymodiolus thermophilus* mussels (Hessler *et al.*, 1985). These mytilid mussels harbour a mixotrophic type of symbiosis. In 1988, the population of *Calyptogena magnifica* clams had grown dramatically and surrounded the mussel beds probably due to a decrease in fluid flow (clams are able to insert their foot in cracks to pump the sulphide). In 1990, the peripheral fauna (anchored siphonophores, serpulids, anemones) had moved into the active area and the whelk (*Phymorhynchus* sp.) and squat lobster (*Munidopsis* sp.) populations increased. In 2002, the community was buried by fresh basaltic sheet flow and a nascent site 'Rosebud', which includes an assemblage of young vent animals (Shank *et al.*, 2003), was discovered ~300 m northwest of the last known position of the Rose Garden site.

21° N: This vent field is characterised by tall sulphide mounds and is dominated by large fields of clams (Van Dover, 2000). The site was visited in 1979, 1982, and 1990. Beds of dead clams indicate that the segment has been active for at least 300 years based on the dissolution rates of the clam shells (Kennish and Lutz, 1999). The comparison of venting patterns and community distribution between 1979 and 1990 demonstrates temporal stability on at least a decadal scale (Desbruyères, 1998; Hessler *et al.*, 1985).

13° N: This complex set of seven active vent sites, dominated by tubeworms, mussels, and alvinellid polychaetes, was visited in 1982, 1984, 1987, 1991, 1992, 1996, and 2002. Between 1984 and 1987, a rearrangement of subsurface circulation led to the collapse of two active sites and the reactivation of a previously dead area. Conversely, some sites situated 100 m north of this field were not affected. The reactivated site 'Genesis' was previously visited in 1984 and showed no measurable temperature anomaly. The fauna was composed of only a small clump of small-sized mussels and some groups of rusty and empty tubes of the siboglinid *Tevnia jerichonana*. By 1987, warm water (~23 °C) venting covered an extensive area and whitish microbial mats and deposits were observed around the vent openings. The fauna was dominated now by the vent crab *Bythograea thermydron* and widespread populations of *T. jerichonana* mixed with young individuals of *Riftia pachyptila* (Desbruyères, 1998). In 1990, diffuse emissions were concentrated at several points at the Genesis site. The extensive population of *T. jerichonana* had collapsed and was replaced by small clumps of *R. pachyptila*. Active chimneys up to 5 m high developed and were colonised by large alvinellid populations dominated by *Alvinella pompejana*. During the following decade, no major large-scale changes occurred and the site was stable.

9° N: This site comprises multiple black smokers and low-temperature vents within an axial valley, and is the site of a long-tem monitoring transect (the BioGeoTransect) established after the April 1991 eruption. This event covered a large proportion of the ridge crest with a fresh basaltic sheet and wiped out some of the established vent communities. Nevertheless, in some places, clumps of worms and mussels survived the eruption and the lava flow. These cruises led to the first documentation of surprisingly fast rates of temporal succession in vent communities (Shank *et al.*, 1998; Fig. 1.12). Nascent hydrothermal vents and adjacent glassy basalts were covered by an extensive and patchy white bacterial 'floc' and the water was cloudy with apparent 'floc' (Desbruyères, personal observation and Haymon *et al.*, 1993). Large populations of *Bythograea thermydron* and other mobile species, probably feeding on increased biological production, were observed. Nine months later, the microbial coverage had decreased (~60%) and the venting focused on restricted areas; the level of hydrogen sulphide decreased by almost half. Numerous venting fissures were occupied by dense populations of *T. jerichonana* (Desbruyères, 1998) with tubes up to 30 cm long. Less than 32 months after the eruption, dramatic changes in the vent community were observed at the same location (Shank *et al.*, 2003). Large clumps of *R. pachyptila* had settled, reaching lengths of 1.5 m, suggesting that individuals reached maturity in less than 20 months. The smokers had grown rapidly and their walls were colonised by alvinellid polychaetes. Fifty-five months after the initiation of venting, *Bathymodiolus thermophilus* colonised the seafloor around the live vestimentiferan clumps.

4.1.2. North-East Pacific

The Juan de Fuca Ridge (JdF) in the north-east Pacific has hosted several decades of hydrothermal vent research. This ridge is bordered by the Explorer Ridge to the north and by Gorda Ridge to the south (Fig. 1.11). It is formed of seven different segments, most of them harbouring active vent sites (Baker and Hammond, 1992). These segments appear to be at different stages of magmatic and tectonic evolution, resulting in differences in hydrothermal activity (Delaney *et al.*, 1992; Embley *et al.*, 1990, 1991). The vents are linearly distributed along the ridge axis (Tunnicliffe, 1991) and their depths vary from ~1500 to 2400 m. while individual vents can be separated by a few metres or kilometres within a single vent field, vent fields may be separated by tens to hundreds of kilometres on one segment (Tsurumi and Tunnicliffe, 2001).

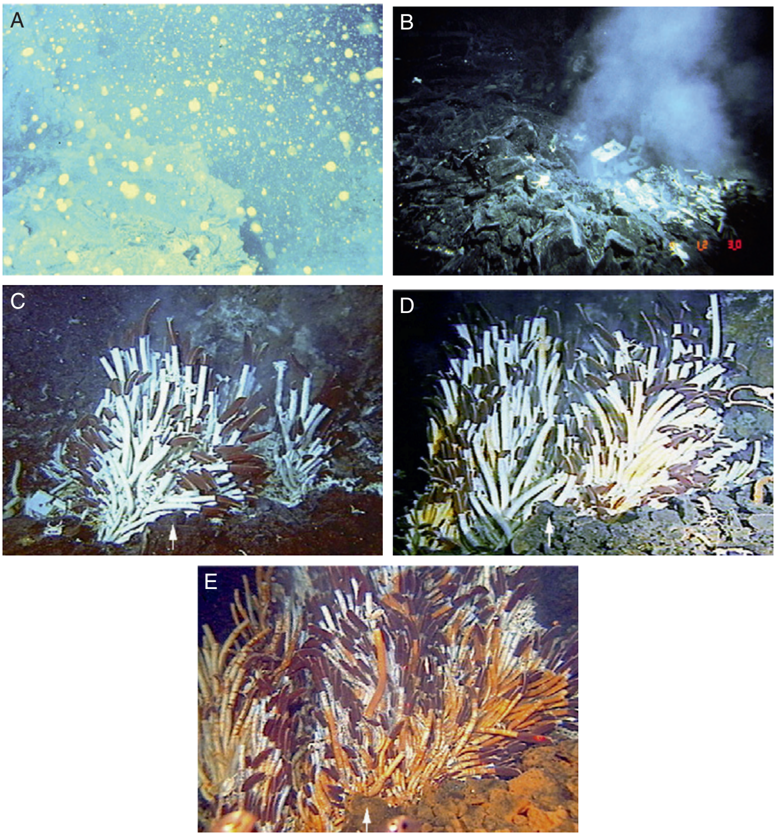

Figure 1.12 Five years of community change at a specific hydrothermal vent (Biomarker #9) following the April 1991 eruption at 9° N on the East Pacific Rise. (A) April 1991, flocculent bacterially generated material visible in the days/weeks after the eruption; (B) March 1992, biomarker is in place and tubeworms (*Tevnia jerichonana*) colonising the fissure; (C) December 1993, the giant tubeworm *Riftia pachyptila* has colonised, overgrowing the population of *Tevnia*; (D) October 1994, the *R. pachyptila* population has recruited and continues to grow; (E) November 1995, the population of *R. pachyptila* is now over 2000 individuals and the tubes are stained with rust-coloured ferrous oxide precipitate. Arrow in C, D and E indicate a common reference point. Image courtesy of Tim Shank, Woods Hole Oceanographic Institution and adapted from Shank *et al.* (1998).

In the north-east Pacific, several studies have assessed the temporal variability of hydrothermal ecosystems, most of them related to catastrophic events on the seafloor. The first identified eruption on mid-ocean ridges occurred in 1986 on the northern Cleft segment of the Juan de Fuca (JdF) (Baker *et al.*, 1989). It initiated a 6-year study of successional patterns at vents (Tsurumi and Tunnicliffe, 2001). Additional studies at NEP sites followed different eruption events: two on the Axial Volcano after the 1986 (Tsurumi *et al.*, 1998) and 1998 eruptions (Levesque *et al.*, 2006) and one on the CoAxial segment after the 1993 eruption (Tunnicliffe *et al.*, 1997). Finally, a 4-year study was initiated on the Endeavour segment to assess the dynamics of a sulphide edifice and its inhabitants through repeated visits (Sarrazin and Juniper, 1999; Sarrazin *et al.*, 1997). As on the EPR, most of these time-series studies are based on discrete annual or sub-annual observations, not on continuous temporal monitoring.

North Cleft segment: The 1986 eruption on the Cleft segment led to the formation of an extensive megaplume whose characteristics suggested a sudden expulsion of fluids from an ancient hydrothermal system, initiated by an episode of seafloor extension (Baker *et al.*, 1989; Embley and Chadwick, 1994). Following the disturbance, new lava flows and vigorous hydrothermal activity were observed. This eruption provided the opportunity to observe potential successional patterns of vent fauna from 1988 to 1994 (Tsurumi and Tunnicliffe, 2001). The communities found at Cleft in 1988 were characteristic of those found 2 years after an eruption on CoAxial segment (Tunnicliffe *et al.*, 1997) and Axial Volcano (Tsurumi *et al.*, 1998): extensive microbial mats, large *Ridgeia piscesae* tube worm bushes, abundant and well dispersed *Paralvinella pandorae* polychaetes and 'floc' particulates within the cracks (Tsurumi and Tunnicliffe, 2001). Between 1988 and 1990, the microbial coverage decreased, the siboglinid and alvinellid polychaetes changed and flocculated particles disappeared. Within 5 years, most diffuse habitats were lost and the whole community became extinct probably due to the progressive decline in hydrogen sulphide concentrations (Butterfield and Massoth, 1994). On the other hand, areas of focused flow on high-temperature chimneys remained active on the Cleft segment but were only colonised by a limited number of species. The extreme unevenness of the Cleft community reflects dominance patterns that may be observed in frequently disturbed habitats, suggesting that the Cleft fauna appears to be 'adapted' to episodic eruptive events (Tsurumi and Tunnicliffe, 2001).

Coaxial segment: Extensive accumulation of microbial-mineral 'floc' in association with abundant diffuse venting on new lava flows were observed after an eruption at this site in July 1993 (Juniper *et al.*, 1995). This eruption was the third to occur on this segment since 1981 (Embley *et al.*, 2000). At the Floc site, rapid colonisation was observed despite the lack of adjacent vent communities (Tunnicliffe *et al.*, 1997). Seven months after the eruption, several species had colonised the active sites, *Ridgeia piscesae* tube worms, alvinellid polychaetes (*Paralvinella pandorae*) and nemertean worms (*Thermanemertes valens*) being the most abundant. The greatest faunal recruitment occurred in the area where the microbes were most abundant (Tunnicliffe *et al.*, 1997). The sulphide concentrations and temperature increased during the 1993–1995 interval. In July 1995, the biomass had increased and more polynoid predators, copepods, and gastropods were observed. At least 16 species colonised the site, most of them living in *R. piscesae* bushes (Tunnicliffe *et al.*, 1997). A possible competitor of *P. pandorae*, *Paralvinella palmiformis* (Levesque *et al.*, 2006), appeared in 1995. One-third of the NEP species had arrived within 2 years.

Axial Volcano: Axial Volcano is an active volcano located at 1800 m depth on the central part of the JdF (Johnson and Embley, 1990). In 1990, the summit was colonised by a few sessile animals and also by white microbial mats and crabs, indicating the presence of venting activity, whilst the vertical walls of the caldera were supporting a normal deep-sea fauna dominated by suspension feeders (Tunnicliffe *et al.*, 1990). In 1986, a time-lapse camera was deployed over periods of 1, 5, and 26 days on the Mushroom vent. The most striking phenomenon was the rapid growth and collapse of anhydrite spires, which may have caused the mortality of 44% of the *Ridgeia piscesae* tube worms studied within the 26-day period (Tunnicliffe, 1990). Mass removal of animals by falling chimney fragments or landslides may be common in these vent habitats and significantly impact on the vent communities (Tunnicliffe, 1990; Sarrazin *et al.*, 1997). A volcanic eruption occurred in 1998 on the South Rift Zone covering most of this 2 km^2 areas with new lavas (Fig. 1.13). New venting activity of warm hydrothermal fluids (80 °C) attracted a suite of hydrothermal species (Embley *et al.*, 1999) and the basaltic seafloor was covered with white microbial mats. In June 1999, *R. piscesae* tube worms and additional consumer species had colonised the site (Levesque and Juniper, 2002; Fig. 1.13). A recent study, based on the 1998 eruption, proposes a general model of post-eruption succession for JdF macrofaunal communities at diffuse flow vents (Marcus *et al.*, 2009). The model identifies six successional stages that are driven, on the one hand, by fluid conditions, and on the other hand, by biotic factors such as the provision of space by tube worms and intra- and inter-specific competition. This study further highlights the ability of the vent communities to rapidly colonise newly formed sites (Marcus *et al.*, 2009).

Endeavour segment: At Endeavour, vent communities are found either on the large sulphide edifices or in diffuse flow areas emanating from cracks in the basaltic seafloor (Tunnicliffe, 1990; Sarrazin *et al.*, 1997). The edifices are colonised by mosaics of faunal assemblages where alvinellid and siboglinid polychaetes are important key-species (Sarrazin and Juniper, 1999; Sarrazin *et al.*, 1997). The basaltic seafloor communities are dominated by *Ridgeia piscesae* tube worm communities (Urcuyo *et al.*, 2003; Tsurumi and Tunnicliffe, 2003). The Sarrazin *et al.* model (Sarrazin *et al.*, 1997, 1999, 2002; Sarrazin and Juniper, 1999) recognises six distinct faunal assemblages that form a mosaic community on the large

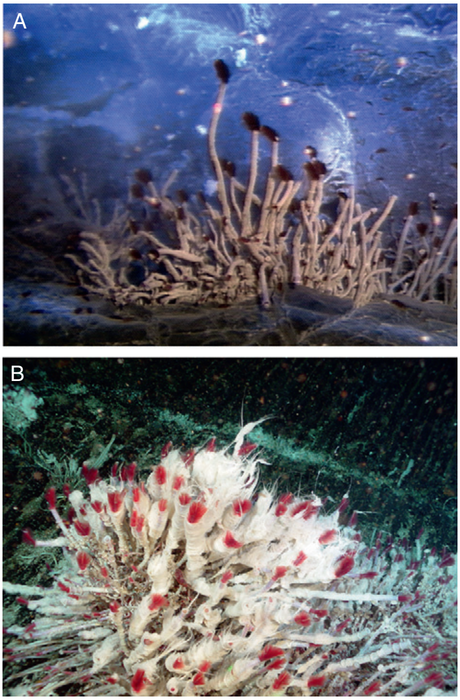

Figure 1.13 Clusters of the tubeworm *Ridgeia piscesae* photographed on the Axial Volcano caldera hydrothermal vent. (A) Image taken shortly after the 1998 eruption (B) image taken 6 years after the eruption. Both images taken by ROV ROPOS and courtesy of the NOAA VENTS programme and Canadian Scientific Submersible Facility.

hydrothermal edifices of the Main Endeavour field. These assemblages appear to be representative of different successional stages that are primarily initiated by variations in hydrothermal fluid flow and substratum porosity. Thus, the progressive mineralisation of hydrothermal edifices contributes to fluid-flow modification at small spatial scales and faunal succession proceeds as the substratum matures (Sarrazin *et al.*, 2002). Moreover, biotic processes such as particulate food diversification, growth of structuring species, or facilitation interact with abiotic conditions in driving successional patterns (Sarrazin *et al.*, 1997, 2002). As mineralisation and succession progress on the edifice, the influence of other biotic factors such as predation and competition, becomes stronger. While abiotic factors appear to predominate in earlier successional stages, biotic factors modulate later successional stages such as the *R. piscesae* tube worm assemblages. Recent observations suggest that the hydrothermal activity of the southern part of this vent field may be waning substantially

(K. Juniper, personal communication). Because of the dynamics of this fast-spreading ridge, most vent communities probably fail to reach stable or equilibrium conditions (Juniper and Tunnicliffe, 1997).

4.1.3. Mid-Atlantic Ridge

The Mid-Atlantic Ridge (MAR) is a long mountain range extending for about 16,000 km in a curving path from the Arctic Ocean to the southern extremity of Africa (Fig. 1.11). The ridge is equidistant between the continents on both sides. It mostly runs under the water but portions of it extend above sea level, forming the archipelago of the Azores and the Ascension and St. Helena islands, among others. The spatial frequency of venting on the MAR is on the order of one field every 100–350 km while in the Pacific Ocean, it can be as high as one active vent field every 5 km of ridge axis (Haymon *et al.*, 1991; Murton *et al.*, 1994; German *et al.*, 1996).

Mid-ocean ridge spreading rate exerts a geological control on the temporal variability of hydrothermal activity at the vent field scale. The interannual to decadal-scale ecological dynamics observed at several hydrothermal vent communities on the fast-spreading East Pacific Rise are associated with local interruptions of hydrothermal activity or disruption by volcanic events (Desbruyères, 1998). In contrast, tectonic and volcanic events that can disrupt the pathways for vent fluids are less frequent on the slow-spreading Mid-Atlantic Ridge, resulting in greater temporal stability in the location and activity of vent fields.

A large part of the northern MAR (15–35° N) has been monitored for 2 years for seismic events (D. K. Smith *et al.*, 2003) and some variability in event rate along the MAR axis was observed. Groups of neighbouring segments appeared to behave similarly, producing an along-axis pattern with high and low levels of seismic activity (D. K. Smith *et al.*, 2003). Moreover, due to differences in water depth, the geology of source rocks, and to hydrothermal deposits, vent habitats among MAR fields vary in their fluid chemistry and the distribution of minerals (Desbruyères *et al.*, 2000). Stochastic disturbance events (e.g. eruptions) are certainly less frequent on the MAR than in the Pacific. However, in 2001 a dike intrusion caused the largest teleseismic earthquake swarm recorded at Lucky Strike in more than 20 years, an one of the largest ever recorded on the northern MAR (Dziak *et al.*, 2004). There were no obvious catastrophic consequences for the hydrothermal edifices, but independent observations reported an increase in the extent of microbial mats and diffuse venting, the latter especially along the sides and base of black smoker mounds, 3 months and 1 year after the dike intrusion (Dziak *et al.*, 2004).

Two groups of vent communities at different water depths are presently recognised among the hydrothermal vent fields of the Mid-Atlantic Ridge (Desbruyères *et al.*, 2001; Van Dover *et al.*, 2002). The shallower vent fields include 'Lucky Strike' and 'Menez Gwen' on the plateau south of the Azores, while the other spans the deeper vent fields (> 2500 m) located further to the south (TAG, Broken Spur; Fig. 1.13). In general, the shallower vent fields are dominated by *Bathymodiolus azoricus* mussels, with the deeper more southerly sites dominated by swarming shrimps, *Rimicaris exoculata*.

TAG mound: The TAG site is a large hydrothermal sulphide mound and black smoker complex in the deep Mid-Atlantic (3600 m) and is the longest-studied vent community on the MAR (Rona *et al.*, 1986). A quantitative comparison between 1994 and 2004 of the distribution and abundance of the fauna that occupies the central chimneys and the periphery on the upper terrace of the mound shows decadal-scale constancy in community structure at TAG (Copley *et al.*, 2007). No significant difference in the coverage and abundance of the shrimp *Rimicaris exoculata* and the sea anemone *Mariactis rimicarivora* were observed over that period. Although not quantified, similar distributions of these species were noted in 1985 (Rona *et al.*, 1986), suggesting these patterns may have persisted over two decades. In addition, TAG exhibits consistency in physical parameters on decadal timescales. The rise height of the hydrothermal plume, which is indicative of heat flux, appears to have been invariant over 10 years (Wichers *et al.*, 2005), along with the geochemistry of high-temperature vent fluids (Parker *et al.*, 2005). At the within-vent-field spatial scale and on shorter timescales, following Ocean Drilling Project (ODP) drilling at TAG in 1994 and a rise in seafloor temperature, dense aggregations of vent shrimps appeared over the 9 months that a time-lapse video camera was deployed, while the distribution of sessile species remained more or less the same (Copley *et al.*, 1999). However, this change was transient and the central black smoker complex remained the focal point of high-temperature hydrothermal discharge at TAG. The NE quadrant had returned to relative quiescence, with aggregations of shrimp no longer present, by 2004 (Copley *et al.*, 2007).

Broken Spur: Initial submersible dives at the Broken Spur vent field (3100 m) found *Rimicaris exoculata* to be present but not in the dense aggregations seen at the TAG and Snake Pit sites. Subsequent observations at Broken Spur, including the discovery of sulphide structures with differing morphologies (Copley *et al.*, 1997) and the evolution of single chimneys into structures with flanges (Allen Copley *et al.*, 1998), suggest that aggregations of *R. exoculata* require substratum that is exposed to hydrothermal fluid flow (Ravaux *et al.*, 2003). At individual chimneys, where most vent fluid is expelled from the summit, such habitat is not available and shrimp aggregations are reduced or absent, as confirmed by observations at other hydrothermal fields within the same province such as Logatchev (Gebruk *et al.*, 2000). Dense aggregations of shrimp appear when accretion of sulphides on a single edifice leads to the production of over-flowing flanges. This geological control on shrimp populations operates over the timescale corresponding to the evolution of edifice morphology (Allen Copley *et al.*, 1998).

Menez Gwen, Lucky Strike, and Rainbow: In contrast to the deep Atlantic vent sites (e.g. TAG), the shallower vent fields of Menez Gwen (850 m) and Lucky Strike (1700 m) are dominated by *Bathymodiolus azoricus* mussel assemblages (Fig. 1.14). Rainbow vent field (2300 m) could be regarded as intermediate between deep and shallow MAR fields. Hence, it harbours

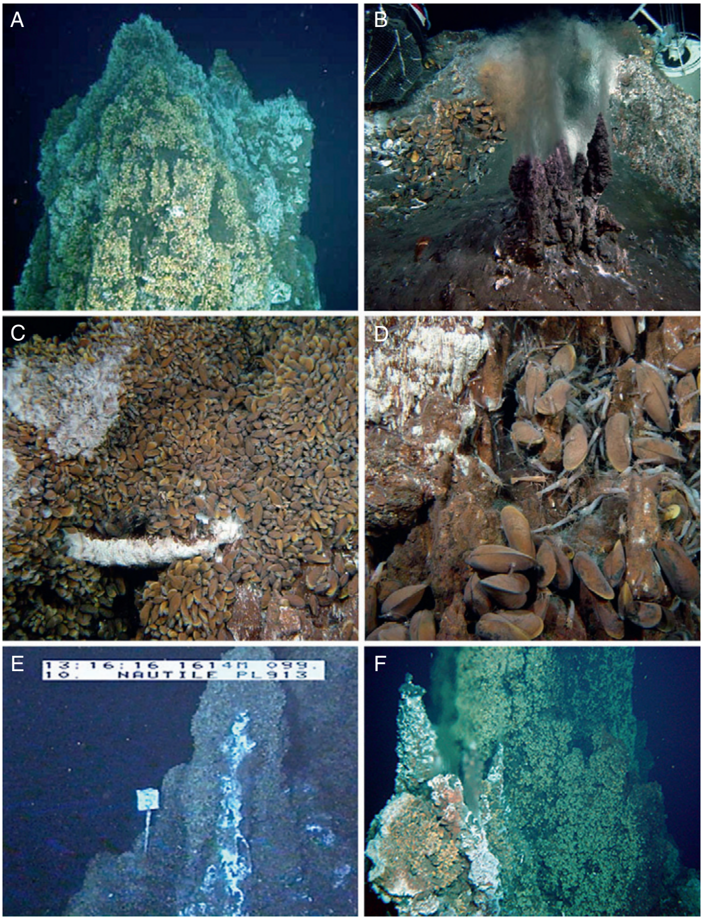

Figure 1.14 Spatial and temporal heterogeneity at the Lucky Strike hydrothermal vent field, Mid-Atlantic Ridge. This vent is characterised by a high degree of patchiness (A), including bare rock surrounding the hot fluid exits (B), abundant populations of *Bathymodiolus* (C, D), and patches of vent shrimps and bacterial mats (D). It is thought that the vents on the Mid-Atlantic Ridge are more stable over long time periods than those of the East Pacific; here abundant mussel populations can be seen on the same region of the vent edifice during a dive in 1994 (E) and 2008 (F) suggesting stability over 10–15 year time periods. Images all ©Ifremer.

tall sulphide chimneys that host *B. azoricus* assemblages and *Rimicaris exoculata* aggregations, but both in lower densities than in respectively shallower and deeper hydrothermal vent sites. No detailed micro-distribution or temporal evolution studies have been published on Menez Gwen or Rainbow. However, at Rainbow vent field, changes in the form of broken chimneys have been observed between cruises, which might be caused by stochastic geological events (see Section 5.2.6), or the normal evolution and development of the spire chimneys.

Lucky Strike is one of the largest known vent fields and one of the most visited in the Atlantic Ocean. It features several well-defined and active edifices, one of which, 'Eiffel Tower', is considered representative for the entire vent field (Desbruyères *et al.*, 2001). Faunal assemblages visibly dominated by either *Bathymodiolus azoricus* mussels or by alvinocaridid shrimps (*Mirocaris fortunata* and less abundant *Chorocaris chacei*) are distributed according to their access to resources, their tolerance and a viable position on the edifice (Cuvelier *et al.*, 2009; Fig. 1.14). Change in any of these factors might shift the local equilibrium and induce a reorganisation or mortality. Von Damm *et al.* (1998) showed that short-term (3-year scale) changes in fluid composition and temperature at Lucky Strike were probably a result of the geological history (formation, age) of the seafloor and longevity of the current period of hydrothermal activity. Despite 17 international cruises to the Lucky Strike vent field, there has been a lack of synthesis on the temporal evolution of this site compared to the similarly well-visited north Pacific vent sites. A recent study has been undertaken of 14 years of temporal data from Lucky Strike. At a decadal-scale, the vent edifice is in general quite stable, while on shorter time-scales as well as at the smaller assemblage and patch-dynamic scales, changes do occur (Cuvelier *et al.*, submitted). This first long time-series quantification of the rate of change at a slow-spreading MAR ridge supports the hypotheses that community dynamics are effectively slower compared to faster-spreading ridges such as those on the EPR (Cuvelier *et al.*, submitted).

4.2. Cold seeps

Cold seep and vent communities share many taxonomic and functional attributes, reflecting their similar evolutionary histories and use of chemoautotrophic symbioses. Like vents, the processes creating the seeps are predominantly geological, and hence we consider seeps to be 'geologically forced'. However, the geological and chemical milieu in which they exist is quite different. Unlike vents, cold seeps are formed by a variety of different processes and have been recorded from a wide range of tectonic settings, including both active and passive margins (Levin, 2005; Sibuet and Olu, 1998). Furthermore, most of the methane and sulphide that sustain seep communities is ultimately of biological origin, although the proportion may vary between seeps. In addition to soft sediments, the precipitation of authigenic carbonate to form pavements, chimneys, and other constructs is a feature of many seeps (Foucher *et al.*, 2009).

Cold-seep communities were first discovered at the base of the Florida Escarpment, a dramatically steep slope in the Gulf of Mexico (Paull *et al.*, 1984; Fig. 1.11). These communities were feeding on sulphide, methane, and ammonia-rich hypersaline brines that seep out of the base of the escarpment (Van Dover, 2000). In recent years, mud volcanoes and pockmarks associated with fluid and gas discharges on continental margins have also attracted a considerable research effort (e.g. Foucher *et al.*, 2009; Vanreusel *et al.*, 2009). Cold-seep communities include characteristic chemosynthetic taxa such as vestimentiferan siboglinids, vesicomyid clams, bathymodiolid mussels and alvinocarid shrimp, as well as polychaetes, nematodes and foraminifera among the smaller size classes (Sibuet and Olu, 1998; Levin, 2005; Vanreusel *et al.*, 2009). Species are often congeneric with those found at vents, although rarely conspecific. Unfortunately, there are no real ecological time-series studies at seeps, and we must rely on inferences based on other lines of evidence to understand temporal trends.

Fluid flow at cold seeps is variable, which results in a temporal variation in availability of methane, sulphide, and other porewater constituents (Levin, 2005). The seep fauna responds to this fluid flow variability with behavioural and physiological adaptations that either limit the exposure to toxic compounds or that enhance access to required compounds. Functional responses, such as small-scale migration (e.g. vertical movement within sediment) or numerical responses, including reproduction, recruitment, colonisation, and succession, are expected in the mobile or opportunistic taxa. Changes in diet, as reflected by carbon and nitrogen isotopic signatures, have also been observed in seep mussels (Dattagupta *et al.*, 2004). The meso-timescale history of the fluid discharge at cold-seep sites can be reconstructed from the barium to calcium (Ba/Ca) ratio in vesicomyid clam shells. Hydrogen sulphide discharge is recorded as an enrichment in the Ba/Ca ratio in clam shells collected live from cold seeps in Monterey Canyon and the Cascadia margin. For the Monterey canyon site, a 2-year episode of high fluid flow centred on 1993 was inferred from coherent changes in the Ba/Ca profiles of three *Calyptogena kilmeri* shells (Torres *et al.*, 2001).

4.2.1. Gulf of Mexico

The hydrocarbon and saline seeps of the Gulf of Mexico contain some of the best-described seep communities in the world. Cordes *et al.* (2009) proposed a theoretical framework for seep community succession based on hypotheses generated from the seeps on the upper Louisiana slope between 500 and 1000 m depth prior to the year 2000, and tested in a series of subsequent studies (Fig. 1.15). The earliest stage of a cold seep is characterised by a high seepage rate and the release of large amounts of biogenic

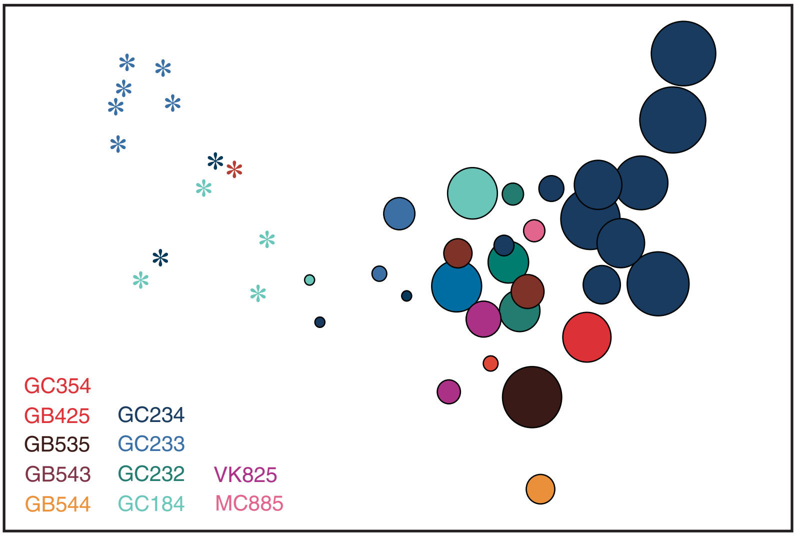

Figure 1.15 Successional processes at Gulf of Mexico cold seeps inferred from community composition plotted using multi-dimensional scaling and ages of tubeworm aggregations (size of the circles). Seeps are initially colonised by mussel-dominated assemblages (asterisks), followed by tubeworm-dominated assemblages (circles), as the seeps age the tubeworms get larger and the community composition shifts. Figure modified from Cordes *et al.* (2009).

and thermogenic methane and oil (Sassen *et al.*, 1994). As authigenic carbonates start to precipitate, they provide the necessary hard substrate for the settlement of vestimentiferans and mussels (Tyler and Young, 1999). These communities begin with mussel (*Bathymodiolus childressi*) beds containing high biomass communities of low diversity and high endemicity (Bergquist *et al.*, 2003). Individual mussels live for 100–150 years, whereas mussel beds may persist for even longer periods (Nix *et al.*, 1995).

The next successional stage consists of vestimentiferan tubeworm aggregations dominated by *Lamellibrachia luymesi* and *Seepiophila jonesi* (Bergquist *et al.*, 2003). Young tubeworm aggregations often overlap in time with, and normally persist past, mussel beds. These tubeworm aggregations and their associated faunas go through a series of successional stages over a period of hundreds of years. Declines in seepage rates result from ongoing carbonate precipitation (Sassen *et al.*, 1994) as well as the influence of *L. luymesi* on the local biogeochemistry. In older tubeworm aggregations, biomass, density, and number of species per square meter, decline in response to reduced sulphide concentrations (Cordes *et al.*, 2009). Once habitat space is made available, more of the non-endemic background species, such as amphipods, chitons, and limpets, are capable of colonising the aggregations. Due to the lower concentrations of sulphide and methane, the free-living microbial primary productivity is reduced. The number of associated taxa is positively correlated with the size of the tubeworm-generated habitat, so diversity in this stage remains fairly high although the proportion of endemic species is smaller in the older aggregations. This final stage may last for centuries, as the vestimentiferan tubeworms can live for over 400 years (Cordes *et al.*, 2009).

Once the seepage of hydrocarbons has declined, the authigenic carbonates of the relict seeps may provide a substrate for cold-water corals. The scleractinians *Lophelia pertusa* and *Madrepora oculata*, several gorgonian, anthipatharian, and bamboo coral species form extensive reef structures on the upper slope of the Gulf of Mexico (Schroeder *et al.*, 2005). They also harbour distinct associated assemblages consisting mainly of the general background fauna, but also contain a few species exclusively associated with the corals and a few species that are common to both coral and seep habitats (Cordes *et al.*, 2008). Unfortunately, in the absence of time-series studies at cold seeps, the reconstruction of the community succession proposed by Cordes *et al.* (2009) remains hypothetical.

4.2.2. Haakon Mosby Mud Volcano (HMMV)

In addition to successional sequences driven by changes in seepage rates and biological interactions, temporal changes at seeps probably arise from physical processes associated with the fluid discharges. These are likely to be particularly prevalent on large mud volcanoes, such as the well-studied HMMV, located on the Barents Sea continental slope at 1270 m water depth (Fig. 1.1B). This structure is characterised by a central muddy area devoid of chemosynthetic organisms and with strong concentrations of methane, a rather flat inner zone with variable densities of the filamentous bacterium *Beggiatoa*, and a hummocky outer zone with variable densities of siboglinid polychaete tubes, sometimes accompanied by *Beggiatoa* (Gebruk *et al.*, 2003; Soltwedel *et al.*, 2005b). A moat-like feature encircles the mud volcano. High-resolution microbathymetry of the HMMV has revealed flat features, interpreted as recent mud flow, that protrude into peripheral hummocky areas, which are believed to represent old mud flows (Jerosch *et al.*, 2007). The HMMV is a highly active mud volcano characterised by high rates of discharge of methane-laden mud, fluid, and gas (Sauter *et al.*, 2006). These discharges cause mudflows on a time-scale of a few years (Foucher *et al.*, 2009) that are likely to severely disturb the benthic communities occupying the outer parts of the mud volcano. Indeed, preliminary evidence suggests that changes occurred in the distribution of microbial mats and siboglinids between 2003 and 2006 (Vanreusel *et al.*, 2009). Similar processes may occur on other mud volcanoes, for example, in the eastern Mediterranean (Foucher *et al.*, 2009).

4.3. Whale-falls

When whales die they sink to the seafloor, creating ‘whale-falls’ that provide enormous point-sources of organic carbon in an otherwise food-poor deep sea. The huge size of the great whales has led many to speculate on their final fate, and the organisms that may consume them (Smith and Baco, 2003). This debate has become even more relevant since we now understand that pre-whaling whale population sizes (and hence whale-fall habitats) were likely orders of magnitude greater than previously thought (Roman and Palumbi, 2003). The first species found associated with a whale-fall was a small mytilid mollusc, *Idas simpsoni*, found clinging to a whalebone trawled up by a Scottish fisherman (Marshall, 1900). This species is now known to belong to a genus of mytilids that use chemosynthesis to gain energy (Distel *et al*., 2000). In 1987, the remains of a large balaeonopterid whale were discovered by scientists in the DSV *Alvin* in 1200 m of water in the Santa Catalina Basin (Smith *et al*., 1989). In the 1990s and more recently, several studies have been undertaken of temporal succession on whale-carcasses in both deep and shallow-water, mainly using dead stranded whales that are deliberately sunk at a known location. Unlike a hydrothermal vent, a whale-fall habitat can be artificially created (by sinking a whale) and as such they are amenable to temporal studies, especially as the time point of origin is known.

4.3.1. Southern California whale-falls

Studies conducted over a period of more than a decade, mainly of implanted whale remains in southern California (Fig. 1.11), have shown that large whale-falls may be extremely persistent in the deep sea, and support quite long-lived faunas that are partly heterotrophic and partly chemosynthetic (Smith and Baco, 2003). The initial scavenging stage of whale-fall succession may take between 6 and 18 months, during which time the remains are skeletonised mainly by the actions of scavenging hagfish (*Eptatretus deani* and *Myxine circifrons*), sleeper sharks (*Somniosus pacificus*) and lithodid crabs (e.g., *Paralomis multispina*). The scavenging stage is followed by a period where opportunistic species may consume the highly enriched sediments and organics leaching from the bones. This includes large numbers of the well-known opportunistic polychaete *Ophryotrocha* sp., as well as very high numbers of ‘carpet worms’ (Chrysopetalidae, *Vigtorniella flokati* and *Vigtorniella ardabilia*) (Wiklund *et al*., 2009). The enrichment opportunist stage is then followed by a relatively long period where chemosynthetic organisms can take advantage of hydrogen sulphide flux from the bones and enriched sediments around the bones, known as the ‘sulphophilic’ stage (Smith and Baco, 2003). These include vesicomyid clams and vestimentiferan siboglinids, some conspecific with those found at vents and seeps.

During both the enrichment opportunist stage and the sulphophilic stage, the whale bones of most whale-falls are consumed by *Osedax* sp., a clade of heterotrophic siboglinid polychaetes that has only recently been discovered (Rouse *et al.*, 2004; Glover *et al.*, 2005; Fujikura *et al.*, 2006). These animals possess symbiotic bacteria housed within a root system that dissolves and penetrates the bone itself, possibly using lipids and/or bone protein as an energy source (Goffredi *et al.*, 2007). It might be expected that the prevalence of *Osedax* sp. on whale-falls would result in the bones becoming rapidly eaten and the whale-falls relatively short-lived (e.g. Braby *et al.*, 2007). But experiments based on radioisotope dating of bones suggest that bones from natural whale-falls may have been on the seabed for 40–80 years (Schuller *et al.*, 2004). The degree of *Osedax* sp. consumption may be quite different depending on the ecological setting of the whale fall, and other factors such as the degree of bone calcification. In a deep shelf (120 m) environment of the west coast of Sweden, a small minke whale has been supporting a specialist whale-fall fauna (including *Ophryotrocha* sp., *Vigtorniella* sp., and *Osedax* sp.) for over 5 years, despite the location being hydrodynamically complex, subject to a high degree of sedimentation and an extensive benthic scavenging fauna (Fig. 1.16; Dahlgren *et al.*, 2006; Dahlgren and Glover unpublished observations).

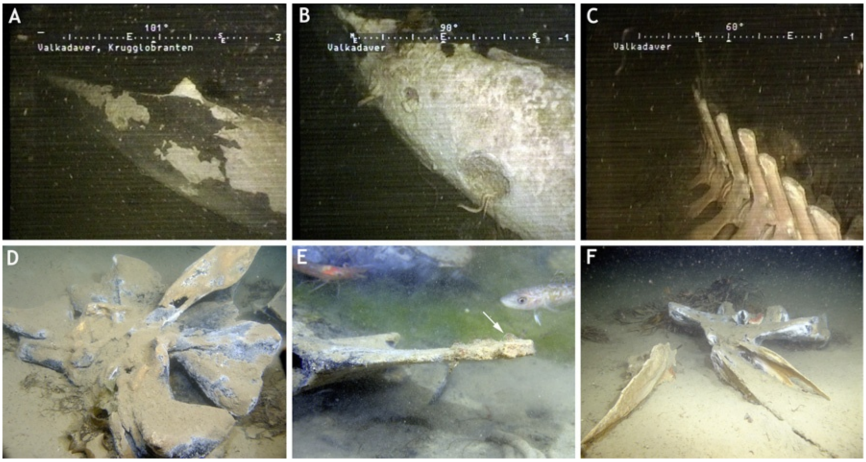

Figure 1.16 Temporal change over 6 years at a single whale-fall site in Kosterfjord, Sweden: (A) remains of a dead 5 m long minke whale at 125 m at time of implantation; (B) 2 weeks following implantation, hagfish (*Myxine glutinosa*) and shark bites visible; (C) 6 months following implantation, complete skeletonisation and first colonisation by *Osedax mucofloris*; (D) 3 years since implantation, skeleton starting to become covered by sediment, still supporting *Osedax* population; (E) 4 years since implantation, bone processes becoming degraded by *Osedax* activity (arrowed specimens); (F) 5.5 years since implantation, skull and mandibles partially covered by sediment, *Osedax* still growing on underside of skull. All images courtesy of Thomas Dahlgren, Göteborg University and Dahlgren *et al.* (2006).

5. DISCUSSION

The deep sea is isolated from us by a thick layer of water, opaque to almost any instruments we deploy in space, the atmosphere or on the surface of the ocean. This simple fact made it impossible to appreciate the dynamic nature of most deep-sea environments until very recently. Images of the deep seafloor did not become available until the 1960's, and time-series studies did not start until the mid 1970s. Even these studies were not designed for long-term monitoring. In most cases they were located at the most convenient area of deep ocean to reach from a ship's home port, and were hence subject to repeat opportunistic sampling. There has been a constant trade-off between the need to increase spatial coverage of sampling with the need to take repeat measurements at a single site. The fact that in the Earth's largest habitat—the abyss—there are only two sites with more than 10 years of benthic data suggests that in general our efforts have been greater with regard to geographic coverage. However, vast areas of the abyss (e.g. the entire south Pacific Ocean) still remain essentially unexplored. Chemosynthetic ecosystems, such as hydrothermal vents, are so isolated and difficult to find that in many cases repeat visits have been made for reasons unrelated to time-series analysis, such as analyses of local species diversity and ecology. These early repeat visits, to sites such as 9° N and Lucky Strike, have since evolved into more directed long-term programmes.

Climate change has forced ecological researchers to look again at what long-term data are available for ecosystems. The deep sea is no exception. As a major carbon sink, and a potential repository for carbon dioxide via bio- or geo-engineering schemes, it is clear that improved understanding of natural benthic processes is needed. In particular, it has become apparent that benthic processes are tightly coupled to pelagic ones, and that the deep-sea should not be ignored in the crucial science of ocean–atmosphere interactions (C. R. Smith *et al.*, 2008; K. L. Smith *et al.*, 2009). Here, we consider first the long-term responses seen in deep-sea ecosystems driven by biology and geology. We then discuss the potential impacts of climate change, and finally the role of stochastic and successional processes in shaping the deep-sea biology that we observe.

5.1. Biological responses to environmental change

The science of environmental change uses a variety of terms which can be confusing, and refer to conceptual ideas that inevitably overlap. For example, there is a distinction made between climate change and climate variability, the former referring to a secular trend over time, the latter to changes that exhibit some periodicity on a particular scale. In the science of climate-change impacts, the crucial question is usually whether a change observed is a 'real' change or just a snapshot of natural variability about a mean, or variability associated with some periodic driver (e.g. ENSO). The term variability is often applied to short-term fluctuations (daily, monthly, or inter-annually), and change is used to describe long-term change (decades to millions of years) (Murray, 2000). The temporal perspective of observation is crucial. It is hard to think of the change from a Pleistocene glacial to an inter-glacial as anything other than a significant, large scale change over thousands of years, but on a scale of millions of years, such glacial-scale change can appear as variability (albeit with periodicity) around a mean. Likewise, the 'variability' we associate with ENSO events on decadal scales are in fact a series of changes over interannual time periods with major, global-scale consequences for ecosystems and human activities. More important than the difference between short-term change and long-term change is whether the change is stochastic, cyclic or progressive (Fig. 1.17). Volcanic eruptions are stochastic, although with a predictable power-law frequency. Both ENSO events and glacial–interglacial events are cyclic; human-induced climate change is (at present) a progressive trend. However, any cyclic event includes periods that are progressive trends, such as the warming of the planet as it comes out of a glacial period.

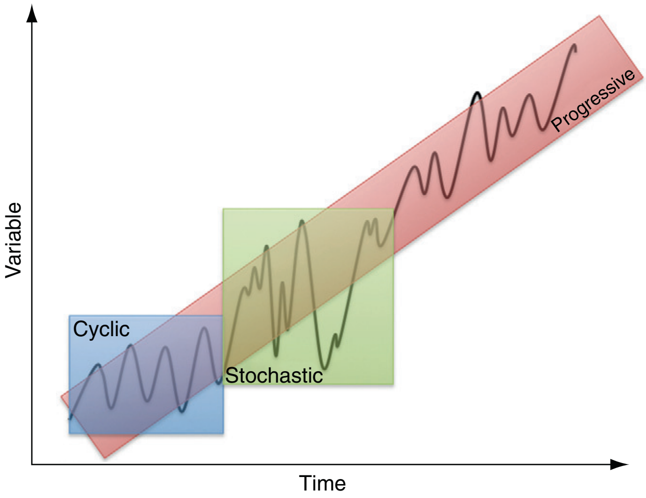

Figure 1.17 Changes in a variable over time viewed as cyclic (blue), stochastic (green) or progressive (red) dependent on the scale of observation.

We discuss here the published data for changes observed at sedimented ecosystems and chemosynthetic ecosystems. We focus on examining whether the changes are significant, whether they are likely to be progressive, cyclic or stochastic and if a specific driver can be identified.

5.1.1. Biological responses at sedimented ecosystems

We identified 11 sites where data on recent long-term change were available (Table 1.2, Fig. 1.5). The earliest time point was 1973 (for the Rockall Trough), and the longest time series are for the PAP (16 years) and Station M (20 years). Apart from these two sites, only three sites have more than 5 years of data, and the remainder less than 5. There is only a single site in the southern hemisphere, and it has only 3 years of temporal data (although studies are ongoing).

The sites for which there is some evidence for progressive trends are HAUSGARTEN, the Cretan Sea, PAP, and Pacific Station M (Table 1.2, and references therein). HAUSGARTEN provides the clearest evidence yet that bottom waters are warming in response to climatic change (Fig. 1.6). This warming trend is associated with a decrease in deep POC flux, and hence food availability, at the seafloor. However, the evidence for a dramatic change in benthic biology (e.g. community structure) in response to this change is so far inconclusive.

For the Cretan Sea site, significant changes in bottom-water temperature were recorded that were correlated with significant changes in nematode species diversity. A cooling period was associated with an increase in diversity and a warming period with a decrease in diversity (Section 3.1.2). However, for the cooling period, the diversity change is only based on two measurement periods (1989 and 1994), while for the warming period, the change is very small. These data therefore represent only preliminary evidence for a change in benthic biology in response to a climate variable.

At PAP, the time series is much longer (16 years) and based mainly on megafaunal abundance surveys derived from trawl samples, supplemented by core material for smaller faunal groups. A progressive trend from 1989 to 2002 involved a marked increase in the abundance of several key megafaunal taxa—the '*Amperima* event' (Section 3.2.1, Table 1.2 and references therein). Later analysis of video data, and samples from other taxa (fish, polychaetes, nematodes, and foraminifera) have supported the view of a long-term change in community structure at PAP, possibly in response to changes in food supply linked to the NAO index (Fig. 1.9). However, the apparent reversion in more recent samples of the community composition to levels closer to those in 1989 suggests that the observed changes may be either stochastic or cyclic. Only longer-term data will resolve this question.

For the Pacific Station M site, a long (17 years for Booth *et al.*, 2008; K. L. Smith *et al.*, 2008; Smith *et al.*, 2008c) time series is also available, again

Table 1.2 Summary of data availability and key identified parameters and long-term temporal trends at sedimented ecosystems

Habitat	Site	Latitude	Longitude	Depth (m)	Key Oceanographic data	Key Benthic biological data	Temporal scale	Key identified long-term trend and forcing factor	Type of long-term change	Key references
Bathyal–Abyssal Arctic sediment	HAUSGA-RTEN	79° N	4° E	1200–5500	Pelagic and benthic POC flux and composition; temperature	Sediment pigments; nematode and megafaunal abundance and diversity	2000–2008 (temperature); 2000–2005 (sediment flux); 2002–2004 (megafauna)	Decrease in deep POC flux driven by increase in temperature; potential shift in community structure	Progressive trend?	Soltwedel *et al.* (2005a); Hoste *et al.* (2007); Bauerfeind *et al.* (2009)
Bathyal Mediterranean sediment	Cretan Sea	35°76′ N	25°10′ E	1540	Bottom-water temperature	Nematode abundance and diversity	1989–1998	Increase in nematode diversity during cooling (1990–1994), decrease during re-warming	Progressive trend?	Danovaro *et al.* (2004)
Bathyal–Abyssal Mediterranean sediment	Ierapetra Basin	33°44′ N 34°30′ N	26°08′ E 26 °11′ E	2500–4500	POC flux (inferred from hydrographic context)	Sediment phytopigments; meiofauna	1987–1999	Increase in opportunistic species in response to stochastic shifts in POC flux	Stochastic shifts	Tselepides and Lampadariou (2004); Lampadariou *et al.* (2009)
Bathyal oxygen minimum zone sediments	Globally distributed along margins	n/a	n/a	∼50–1000	Surface production, benthic oxygen, temperature,	Faunal abundance and diversity across the OMZ region (spatial)	Inferences based on change in OMZs; 1997–2003 ENSO shift	Shift in foraminferal species composition driven by hypoxia; decrease in macro and megafaunal	Stochastic shifts	Levin (2003); Gooday *et al.* (2009)
Bathyal Atlantic sediment	Bay of Biscay	43°50′ N	2°23′ W	550	Surface production inferred from SeaWIFS	Sediment oxygen profiles, foraminiferal abundance	1997–2001	No obvious long-term trend (seasonal only)	No change	Fontanier *et al.* (2003, 2005)
Bathyal Atlantic sediment	Rockall Trough: 'Station M' Permanent Station	57°18′ N 54°40′ N	10°11′ W 12°16′ W	2200–2900	Limited hydrographic and sediment data	Macrofauna and megafauna abundance, reproductive condition	1973–1984 (sporadically thereafter)	Initial analyses indicated interannual variation but analyses of longer time series needed.	Stochastic shfits	Gage *et al.* (1980), Tyler (1988)

(*continued*)

Table 1.2 (*continued*)

Habitat	Site	Latitude	Longitude	Depth (m)	Key Oceanographic data	Key Benthic biological data	Temporal scale	Key identified long-term trend and forcing factor	Type of long-term change	Key references
Bathyal Pacific sediment	Sagami Bay	35° N	139°22′ E	1400	Surface production, POC flux	Sediment chloroplastic pigment; foraminiferal and copepod abundance	1996–1998	No obvious long-term trend (seasonal only)	No change	Kitazato *et al.* (2000, 2003)
Bathyal Antarctic sediment	FOODBANCS	65° S	65° W	500–600	Surface production (LTER data), POC flux	Video and photography; faunal abundance; microbial biomass; sediment quality; reproduction	1999–2001 (and ongoing)	Buffered seasonal signal (sediment foodbank) with major inter-annual shifts	Stochastic shifts	C. R. Smith *et al.* (2006)
Abyssal Atlantic sediment	PAP	48°50′ N	16°30′ W	4850	Surface production, POC flux	Video and photography; faunal abundance and diversity; microbial biomass; sediment quality; reproductive condition	1989–2005 (and ongoing)	Increase in megafaunal abundance and composition shift from 1989–2002 ('*Amperima* event'). Species-level shifts in foraminiferal and polychaete abundance and composition; shifts in abundance of major meiofaunal taxa.	Progressive trend, amidst stochastic variation	Billett *et al.* (2001, 2010); Gooday *et al.* (2010); Kalogeropoulou *et al.* (2010); Soto *et al.* (2010)
Abyssal Pacific sediment	Station M	34°50′ N	123° W	4100	Surface production, POC flux	Sediment community oxygen consumption; bioturbation; macro/megafaunal abundance; fish abundance and composition	1989–2004 (and ongoing)	Shifts in faunal abundance and size, and ecosystem functions—all related to availability of food at the seafloor.	Progressive trend, amidst stochastic signal	Ruhl *et al.* (2008), Ruhl and Smith (2004)

mainly covering the mobile megafauna. This faunal component exhibits significant changes in community composition that are correlated with changes in food availability at the seafloor. As with the PAP, it is not clear if the variations have a progressive trend related to long-term climate change or are part of a stochastic or cyclic variation (climate variability). The link between the ENSO index (NOI), surface production, export flux, POC flux to the seafloor, and the shifts in community composition suggest that if a trend does become apparent in surface productivity, the signal would be transmitted by POC flux to the seafloor biota. Again, longer-term data will be needed to determine if climate change will indeed alter the composition and/or functioning of abyssal communities.

Discounting seasonal signals (not discussed here), two sites (Bay of Biscay and Sagami Bay) exhibit no significant long-term changes (Table 1.2). For the remainder of the sites, changes are observed but it is very difficult to ascertain whether they represent any long-term trend owing to lack of data. For the Ierapetra Basin site, the data suggest that, at the very least, stochastic shifts in food availability occur in the abyssal Mediterranean, and that the benthic community can respond quickly. For bathyal OMZs, we can infer the type of changes that must take place based on evidence from the local impact of the hypoxia (measured in space) with our hypothesised frequency and severity of hypoxic events in the past. A level of inter-annual variability has been detected at both the Rockall Trough and FOODBANCS sites, but the time-series are either not yet long enough to have detected any progressive trends (FOODBANCS) or have been discontinued (Rockall Trough).

5.1.2. Biological responses at chemosynthetic ecosystems

Twelve hydrothermal vent sites were identified as yielding useful long-term data (Table 1.3). For cold seeps, repeat visits to the same sites are scarce, or have gone unpublished, and inferences are made based on what is known about cold seep biology. For chemosynthetic ecosystems of biogenic origin (e.g. whale-falls), time-series data are available for sites in the north-east Pacific, and fjords of the Swedish west coast.

The earliest major biological studies at a vent ecosystem took place in 1979 at Rose Garden on the EPR, not long after their discovery by geologists in 1977. Not surprisingly, this is the site for which we have the longest data set (1979–2002) but there are enormous gaps in the data (e.g. a 12-year gap between 1990 and 2002). The main reason for such gaps is the difficulty in getting funding for repeat visits as opposed to searching for new vents. Probably, the best temporally resolved dataset for a hydrothermal vent is that for the 9° N site (also on the EPR), where surveys were taken every year for 5 years following the April 1991 eruption (Shank *et al.*, 1998; Fig. 1.12). For the Mid-Atlantic Ridge sites, despite many repeat visits under different oceanographic programmes, there has been a lack of

Table 1.3 Summary of data availability and key identified parameters and long-term temporal trends at hydrothermal vents. Geographic data and geological notes from Van Dover (2000). In almost all cases, biological data is in the form of video observations from ROVs or submersibles, with faunal sampling

Habitat	Site	Latitude	Longitude	Depth (m)	Key geological features	Temporal scale	Key identified long-term trend and forcing factor	Key references
East Pacific Rise Vent	21° N	20°49′–50′ N	109°5′ W	2600	Tall sulphide edifices	1979–1990	Apparently stable over decadal scales	Hessler *et al.* (1985); Desbruyères (1998)
East Pacific Rise Vent	Rose Garden	00°48′ N	86°13′ W	2500	Absence of high-temperature vents	1979–2002	Succesion from luxuriant *Riftia* to dominance by *Bathymodiolus*, then *Calyptogena*. Buried by lava flow in 2002, with recolonisation by juveniles at nearby 'Rosebud' site.	Hessler *et al.* (1985); Shank *et al.* (2003)
East Pacific Rise Vent	13° N	12°38–54′ N	103°50′–104°1′ W	2600	Tall sulphide edifices	1982–2002	Several rapid shifts in community composition observed in response to stochastic changes in fluid flow	Desbruyères (1998)
East Pacific Rise Vent	9° N	9°45–50′ N	104°17W	2500	Black smokers and low-temp vents in a linear array within axial trough; 1991 eruption	1991–ongoing	A major eruption in 1991 led to observations of succession, from initial flocs of bacterial mat to *Tevnia*, *Riftia* and *Bathymodiolus*.	Shank *et al.* (1998); Desbruyères (1998)
North-east Pacific Vent	North Cleft	44°38–41′ N	130°23′ W	2250	Cleft centre of axial valley, large sulphide edifices	1988–1994	Successional patterns following eruption in 1986- initial observations of bacterial mats, *Ridgeia*, *Paralvinella*, followed eruption, with subsequent decrease in biological activity driven by reduction in sulphide availability.	Tsurumi and Tunnicliffe (2001)
North-east Pacific Vent	Coaxial segment	46°20′ N	129°40′ W	2200	Eruption in 1993, with diffuse venting on new lava flows following	1993–1995	Rapid colonisation following eruption by *Ridgeia*, *Paralvinella* and nemertean worms, linked to microbial abundance	Tunnicliffe *et al.* (1997)

North-east Pacific Vent	Axial volcano	45°57′ N	130°02′ W	1800	Active volcano. Noted rapid growth and collapse in anhydrite spires. Eruption in 1998.	1986–2002	On short-time scales (days) major distubances from collapsing spires. On longer-scales (years?) periodic eruptions and rapid recolonisation.	Tunnicliffe (1990); Embley *et al.* (1999); Marcus *et al.* (in press)
North-east Pacific Vent	Endeavour segment	47°57′ N	129°40′ W	2250	Large sulphide edifices, with flanges and pooled hot water	1991–1995	Successional model proposed based on variations in fluid flow and substrate porosity. Potential for Southern part of vent possibly waning.	Sarrazin *et al.* (1997, 2002)
Mid-Atlantic Ridge Vent	TAG Mound	26°08′ N	44°49′ W	3600	Large sulphide mound with black smoker complex and periphery	1994–2004	Evidence suggests decadal-scale constancy of venting and of community structure.	Copley *et al.* (2007)
Mid-Atlantic Ridge Vent	Broken Spur	29°10′ N	43°10′ W	2200	Multiple sulphide mounds	1994–1997	Aggregations of the shrimp *Rimicaris exoculata* are variable depending on the shifts in fluid flow, which are driven by the production of overflowing flanges.	Allen Copley *et al.* (1998)
Mid-Atlantic Ridge Vent	Menez Gwen	37°17.5 N	32°16′ W	1700	Small sulphide mounds on the flanks of a volcano	1994–2006	Dominance of the mussel *Bathymodiolus azoricus*. Covering the sulphides and some fresh pillow lavas.	Colaço *et al.* (1998); Desbruyères *et al.* (2001)
Mid-Atlantic Ridge Vent	Lucky Strike	37°17.5′ N	32°16′ W	1700	Multiple sulphide edifices around a lava lake	1994–2008	Synthesis of long-term temporal evolution at this site is lacking, studies are underway.	Cuvelier *et al.* (submitted)

synthesis of temporal data. This is now being addressed through a major study of the Eiffel Tower hydrothermal construct in the Lucky Strike vent field (Cuvelier *et al.*, submitted).

In summary, none of the investigated sites show an obvious progressive trend. Neither are changes apparently cyclic, for example associated with some regular and periodic switching on and off of hydrothermal fluid flow. Where changes have been observed, they appear to be stochastic shifts associated with major eruptions, seismic swarms or redirections of hydrothermal vent 'plumbing'. At two sites on the EPR (Rose Garden and 9° N) and two sites on the NEP (North Cleft and Axial Volcano) major eruptions have been observed and the successional processes following those eruptions monitored. These sites have led to a model of EPR (but not NEP) vent succession from a microbe-dominated community, to one dominated by siboglinid tubeworms, and finally by chemosynthetic molluscs. These changes are thought to occur over a period of a few years following an eruption. On a finer scale, a successional model has been proposed to account both for the spatial mosaic and temporal changes on vent edifices of the NEP (Sarrazin *et al.*, 1997, 2002). In this more complex scenario, changes at individual vent edifices can occur quite rapidly on small scales following shifts in fluid flow, substratum porosity and vent mineralisation. Changes are not thought to be in the form of linear succession, with the early dominance of abiotic factors becoming less significant as biological interactions predominate on more biologically active patches. In general, EPR and NEP vent habitats are unlikely to be in stable or equilibrium conditions.

In contrast to the Pacific sites, the Mid-Atlantic Ridge vents show little evidence for major stochastic events such as eruptions. This may be simply because they have not yet been observed. However, repeat visits to sites such as TAG mound do suggest decadal-scale constancy of venting and community structure (Copley *et al.*, 2007). On a finer scale, changes have been observed in the patch-mosaic structure of vent animals at Lucky Strike (Cuvelier *et al.*, 2009) and in the response of swarming shrimp to the changes in fluid flow associated with flanges at Broken Spur (Allen Copley *et al.*, 1998). In the more stable vent ecosystems of the MAR, biotic factors such as competition and predation may be more important than abiotic factors such as eruptions, which are more frequent on the EPR and NEP. Future studies with better sampling resolution, as well as data-mining results from previous expeditions, will greatly improve our knowledge of changes at the MAR sites.

Our understanding of temporal changes at cold seeps is rudimentary, principally because the frequency and severity of change is apparently much lower than that at vents. The model (outlined above; Section 4.2.1) recently proposed for the Gulf of Mexico seeps is based on inferences mainly derived from spatial studies and knowledge of seep fauna longevity (Cordes *et al.*, 2009). In summary, the model involves initial carbonate precipitation, followed by mussel-bed colonisation, and long-lived siboglinid tubeworm aggregations, which may last many centuries. The likely final stage of seep succession is colonisation of the remaining authigenic carbonates by hard-substrate faunas (e.g. corals). These data, and inferences based on them, would suggest that cold seeps are among the most stable of deep-sea ecosystems. However, it is likely that future studies from a wider variety of seep settings will show that the amount and periodicity of hydrocarbon flow is spatially very variable, and that the simple model proposed above is not universally applicable.

At chemosynthetic ecosystems of biogenic origin, such as whale-carcasses on the seafloor ('whale-falls'), we have quite good data on successional processes, mainly derived from experimentally implanted whales, an approach that is impossible to replicate in the case of vents and seeps. This had led to the successional model of skeletonisation by scavengers (months), feeding by opportunistic species (years), colonisation of sulphide-eating chemosynthetic species (tens of years) to a final 'reef' stage where whalebones may lie on the seabed for hundreds of years (Smith and Baco, 2003). Complicating this picture is the degree of attack by the specialist bone-eating worm *Osedax*, which in some instances has been shown to degrade whale bones over just a few years (Braby *et al.*, 2007), while in others it has been growing on bones for perhaps 50–80 years (A. Glover, personal observation). It appears that for very large carcasses, with well calcified bones, the whale-fall habitat may be persistent as a bone 'reef' for hundreds of years, and as such may be a relatively widespread habitat.

5.2. Broader context: Climate, evolution and stochastic events

The time-series studies reviewed above have provided the first datasets on actual measured change in deep-sea ecosystems within the working lifetimes of scientists. Although sparse, intriguing evidence of possible links between climatic forcing and remote deep-sea ecosystems is emerging. But these are not the only data available on long-term change in the deep sea. The deep sea is one of the best-studied palaeoenvironments, and a repository of long-term sedimentary records that contain microfaunal and isotopic proxies of past climate. These deep-sea palaeoenvironmental data have made a major contribution to our understanding of past climates, and hence the predicted impacts of future climatic change. In this section, we place recent evidence for the role of climate forcing on deep-sea ecosystems in this palaeoenvironmental context. In addition, we discuss evidence for recent climate change, examine shallow-water systems for potential analogues, and examine the role of evolutionary constraints and stochastic processes.

5.2.1. Impacts of past climate change on the deep sea

One way to address the effects of environmental change in the deep sea is to analyse microfossils recovered in long sediment cores. These records reveal faunal changes occurring over much longer (geological) time scales than can be addressed in ecological studies. They include major extinction events reflecting large-scale environmental changes, as well as subtler shifts in diversity and assemblage composition. Foraminifera, particularly the calcareous species, are usually the most abundant benthic organisms to be preserved as fossils in deep-sea sediments, the other important group being the Ostracoda. These microfossils provide indicators of important environmental variables and are widely used, together with geochemical, sedimentological, and planktonic faunal proxies, in palaeoceanographic reconstructions. As a result, an extensive body of literature exists regarding fluctuations in the abundance of foraminiferal (e.g. Gooday, 2003; Jorissen *et al.*, 2007) and ostracod (e.g. Yasuhara and Cronin, 2008; Yasuhara *et al.*, 2009) species over time, particularly during the Quaternary. These faunal oscillations and trends can be interpreted within the context of contemporary climatic and oceanographic changes, for example, in productivity and temperature, revealed by the palaeoceanographic record.

In coastal regions, where sedimentation rates are high, sediments yield a record of events occurring on time-scales as short as a few years, at least for the twentieth century (Cronin and Vann, 2003). However, in the deep sea, sedimentation rates are considerably slower and mixing of the sediment by bioturbating organisms means that the temporal resolution is usually much coarser. Thus, studies of fossil deep-sea foraminifera often document changes that took place over millions of years. For example, Thomas and Gooday (1996) showed that foraminiferal diversity declined steadily at high latitudes from about 50 to 30 million years ago (middle Eocene to early Oligocene), probably related to cooling of deep water around the Antarctic continent. Samples taken at 1.5 m intervals from an ODP core revealed that many species became extinct during a period of $<25{,}000$ years across the Palaeocene/Eocene boundary and that diversity remained low for the next 260,000 years (Thomas, 1990). It is believed that the main underlying cause of the end-Palaeocene extinctions was a global warming event, although the precise mechanism remains unclear (Thomas, 2007). Yasuhara and Cronin (2008) describe fluctuations in late Quaternary ostracod species diversity (low during glacial periods, high during interglacials) in the equatorial Atlantic, which may have been caused by climatically-induced temperature changes. In this case, the sampling resolution was ~ 5000 years.

Higher resolution of sediment records can be achieved by taking sampling cores at closely spaced intervals in areas with a high enough sedimentation rate. Hayward (2002) documented the decline and extinction of elongate, cylindrical foraminiferal morphotypes (stylostomellids and similar taxa) between the late Pliocene and middle Pleistocene at a resolution of approximately 1000 years (Hayward, 2002, Fig. 1.11 therein). The causes of synchronous stylostomellid decline and extinction events are unclear but possibly related to enhanced surface productivity or cooling and increased oxygenation of bottom water. Smart (2008) analysed subsamples extracted at 2-cm intervals along the length of a Kasten core recovered from the PAP. The subsamples spanned the last 15,000 years with a resolution of ~250–300 years. Sharp fluctuations in the taxon-specific abundance, total abundance, and accumulation rates of species known to be associated with seasonal phytodetritus inputs were observed. These were interpreted to indicate variations in the intensity of phytodetritus deposition to the seafloor, and hence seasonal variability in the upper ocean. Yasuhara and Cronin (2008) report abrupt shifts in ostracod species diversity on millennial and centennial (~300 years) time scales during the last 20,000 years, as well as over longer time scales during glacial–interglacial cycles. These changes in diversity coincided with climatic oscillations and were possibly related to corresponding fluctuations in surface productivity, with high productivity (i.e. high food supply) tending to depress benthic diversity. There is also evidence that bottom-water temperature fluctuations were important drivers of diversity over millennial time scales (Yasuhara and Cronin, 2008).

On the Pakistan margin, changes in the quantity and quality of organic matter arriving at the sea floor, and corresponding variations in the thickness and intensity of the OMZ over a period of 120,000 years spanning glacial/interglacial cycles, have been inferred from shifts in foraminiferal diversity (Den Dulk *et al.*, 1998). A multiproxy study of shorter cores (spanning the last 30,000 years) from the same hypoxic margin revealed a switch from low to high foraminiferal diversity during brief, late Quaternary to early Holocene climatic oscillations (Younger Dryas, Heinrich Events 1 and 2) believed to be characterised by unusually low surface productivity and hence a weaker development of the OMZ (von Rad *et al.*, 1999). In both studies, the temporal resolution of the samples was <1000 years for some intervals. Mediterranean sapropels also yield high resolution records of foraminiferal responses to declining oxygen concentrations (Jorissen *et al.*, 2007; Schmiedl *et al.*, 2003).

The studies reviewed above have a resolution that is at least an order of magnitude greater than the 10–20 year time scales of modern deep-sea faunal time series. The mixing of sediments by bioturbation usually makes it impossible to close further the gap between sediment records and modern time series. There are some settings, however, notably bathyal anoxic or hypoxic basins with high sedimentation rates, in which varved (laminated) sediments provide a much higher temporal resolution. Anoxic basins, such as the Guaymas and Cariaco Basins, contain laminated sediments in which each varve corresponds to a single year (Pike and Kemp, 1997; Kemp, 2003). These sediments yield highly detailed records of rapid climatic changes during the Quaternary. For example, Black *et al.* (2007) reported a proxy record with a resolution of 1–1.5 years for sea surface temperatures over the last 800 years, based on Mg/Ca ratios from planktonic foraminiferal shells in laminated sediments from the Cariaco Basin. High-resolution, temporal analyses of benthic microfossils in hypoxic basins are less common. The study most relevant to the present review is that of Cannariato *et al.* (1999). They analysed benthic foraminiferal assemblages in rapidly deposited (>120 cm ky^{-1}) late Quaternary sediments in the Santa Barbara Basin, which at present is severely hypoxic (DO < 0.1 ml L^{-1}). These authors were able to resolve events occurring on time scales as short as a few decades. Assemblages characteristic of hypoxic conditions corresponded to interstadial intervals, when ventilation on the California margin was weak, while those characteristic of oxic conditions corresponded to glacial intervals, when ventilation was strong. The switches from oxic to hypoxic assemblages occurred over a period of between 40 and 400 years. None of these changes involved extinctions. Rather, it seems that species were able to migrate rapidly from refugia to occupy habitats opportunistically as conditions changed. Laminated sediments in other California borderland basins, and elsewhere, have also yielded benthic foraminifera (e.g. Hagadorn, 1996), although these have not been analysed in the same detail as the Santa Barbara records.

These palaeoceanographic studies are important because they reveal the kinds of natural, and sometimes dramatic, faunal changes that have occurred in response to past climatic shifts leading to changes in bottom-water characteristics (notably temperature and oxygenation) and the magnitude and nature of organic matter fluxes to the seafloor. Studies such as that of Cannariato *et al.* (1999), conducted on a bathyal continental margin influenced by an OMZ, suggest that climate changes occurring over a period of decades can impact the ocean floor and lead to faunal changes on time scales similar to those of modern ecological time series. Responses were probably slower in the case of well-ventilated central oceanic abyssal ecosystems, although the evidence is lacking. Whether temporal patterns observed in the palaeoceanographic records can be extrapolated to benthic communities as a whole is an open question. Small organisms with short generation times probably responded in a similar way to foraminifera and ostracods. The responses of the larger macrofaunal and megafaunal animals may have been different, although they would undoubtedly have been affected by major oceanographic changes.

5.2.2. Impacts of recent climate change on the deep-sea benthos

Current concerns about global climate change have heightened awareness of possible climatic impacts on deep-sea ecosystems. As discussed above, it is abundantly clear from the deep-sea fossil record that major shifts, often involving extinctions, have occurred in the composition and structure of deep-sea communities, and that these were linked ultimately to climatic changes. If they persist, current trends in global warming, caused by the increasing concentration of greenhouse gases in the atmosphere, are likely to have similar major consequences for upper-ocean and deep-seafloor communities. Predicted changes include a decrease in surface productivity and decreased dominance by diatoms phytoplankton assemblages, which form fast-sinking aggregates, relative to smaller plankton (Bopp *et al*., 2005; Smith *et al*., 2008b). The net result is anticipated to be a decrease in the export flux and hence the amount of food reaching the ocean floor, particularly at abyssal depths.

Although the only firm evidence that global climate change has impacted deep-sea ecosystems comes from the fossil record, there are strong indications that, interannual-scale climatic oscillations, notably the ENSO, influence the deep-sea benthos. Estimates of net global primary production obtained from satellite measurements of ocean colour have demonstrated a link between climate variability, represented by the Multivariate ENSO Index (MEI, incorporating data on sea-level pressure, surface winds, sea-surface temperature and cloudiness) and ocean productivity represented by upper-ocean chlorophyll concentrations (Behrenfeld *et al*., 2006; K. L. Smith *et al*., 2006). Changes in ocean productivity, in turn, have been linked changes in the amount and quality of organic material reaching the deep-ocean floor (K. L. Smith *et al*., 2006).

Links between climate, food supply, and the composition and functioning of abyssal ecosystems have been explored at Station M (NE Pacific) and the PAP (NE Atlantic). At interannual scales, the food supply (POC flux) to the benthic community at Station M showed a lagged response at different time intervals with the MEI and two other ENSO-related climatic indices, the Northern Oscillation Index (NOI) and the Backum upwelling index (BUI) (Ruhl and Smith, 2004; K. L. Smith *et al*., 2006, 2008). During negative deviations in the NOI index (El Niño), wind-driven upwelling tends to decrease, resulting in less primary production and less export flux to the deep sea. Conversely, during positive phases of the NOI index (La Niña), increases in southerly winds along the coast and upwelling ultimately lead to increased POC flux to the abyssal seafloor. The atmospheric air pressure anomalies reflected in the NOI can influence surface conditions within weeks to a few months and changes in primary production export flux lead to changes in POC flux to the seafloor within 1–3 months (K. L. Smith *et al*., 2006). Changes in the NOI have been related to abyssal POC flux variation with a time lag of about 6 months (Ruhl and

Smith, 2004; K. L. Smith *et al.*, 2006). Major changes in the densities of some megafaunal species, notably the holothurians *Elpidia minutissima* and *Peniagone vitrea* and the echinoid *Echinocrepis rostrata*, were linked to the NOI with a lag of 14–18 months. Smaller organisms, the macrofauna and meiofauna, showed similar responses, albeit with shorter lag times than the megafauna, to climatic oscillations.

At the PAP, variations in the export of POC from the euphotic zone (i.e. the export flux) and hence to the seafloor, as well as in the quality (e.g. content of pigments necessary for reproduction) of the material that reaches the seafloor, appear to be linked to the NAO, a climatic phenomenon that is related to ENSO and affects winds, precipitation, and storm intensity and frequency (Smith *et al.*, 2009; Lampitt *et al.*, 2010). These changes in food quantity and quality are believed to underlie the 'boom-bust' cycles observed in *Amperima rosea* and *Ellipinion molle* (Wigham *et al.*, 2003). Vastly increased populations of these small surface-feeding holothurians may, in turn, have affected foraminiferal and meiofaunal populations through depletion of food resources and sediment disturbance.

POC flux to the seafloor, macrofaunal abundance and community structure may all be useful indicators of abyssal ecosystems responses to fluctuations in the climate as well as to more permanent climatic change (C. R. Smith *et al.*, 2008b). The conclusions of much of the research at Station M, however, come from correlations that often have important unexplained variation. More research is needed to understand this variation and the mechanisms underlying it so that robust biogeochemical models can be created and used more broadly. Clearly, the results from Station M and the PAP indicate that models assuming constant rates of almost any ecological parameter at abyssal depths are flawed. If climate change continues as projected through 2300, then changes in abyssal ecosystem function could also be occurring on timescales that approach the approximate age for water masses below 1500 m depth (Matsumoto, 2007). Even subtle changes that persist for decades to centuries could have an impact on biogeochemical dynamics in the longer term.

Long-term time series studies such as those at the PAP and Station M provide essential ecological baseline information necessary to predict ecosystem responses to climate change and human impacts in the deep sea (Glover and Smith, 2003; C. R. Smith *et al.*, 2008a; K. L. Smith *et al.*, 2008). As discussed above, temporal change includes cyclical change over seasonal to decadal time scales (environmental variability) as well as a persistent change in the mean attributes of a system over time (Fig. 1.17). Climatic oscillations such as ENSO are a form of environmental variability, while global climate change inferred from the fossil record constitutes a larger time and space scale environmental change. The shifts in deep-sea benthic ecosystems at the PAP and Station M sites seem to represent an example of interannual to decadal-scale variability. Distinguishing these fluctuations from persistent faunal change caused by contemporary global warming represents a formidable challenge requiring a shift in research frameworks.

5.2.3. Climate change at high latitudes

At high latitudes, the melting of sea ice will probably be the main mechanisms linking long-term climate change to benthic ecosystems. In the Arctic Ocean, climate models forecast rapid change, and empirical studies corroborate these projections. Since the beginning of satellite remote sensing in 1979, the Arctic summer minimum sea-ice area has decreased by 10% per decade. There is a general consensus that the reduction in the amount of Arctic sea-ice is a manifestation of global warming. Further alterations in sea-ice cover, water temperature, and primary production are expected. Although the consequences for benthic ecosystems are still unclear, it is likely that this environmental change will lead to a massive response in the Arctic (Anderson and Kaltin, 2001; Hassol, 2004). In the Antarctic, the climate-related disintegration of ice shelves, which has already happened in the case of the Larsen B ice shelf (Scambos *et al*., 2003; Domack *et al*., 2005), will undoubtedly have important consequences for the underlying benthic communities (Domack *et al*., 2007; Smith *et al*., 2007). This could come from increased scouring of tabular icebergs that can reach down hundreds of metres or through biogeochemical changes in surface production imparted by their presence.

5.2.4. Lessons from shallow-water analogues

It is clear from our review that, despite an enormous research effort, our knowledge of temporal trends on the ocean floor remains poor. The great depth and often distant location of deep-sea sites precludes time-series sampling for all but the most well-funded programmes. Even for these, the majority of funding cycles are too short to support decadal-scale studies. One solution is to use shallow-water sites that are more accessible as analogues of deep-sea environments. Most time-series studies in shallow water are from systems that are very different from the deep sea and influenced by climatic and other environmental drivers that exert little or no influence in deep-water environments. However, in recent years, a few shallow-water sites with deep-sea characteristics have been identified.

Among the most promising analogues are marine caves, some of which resemble the deep sea in the permanent absence of light, the lack of high energy currents and waves, and their oligotrophic character. In one Mediterranean cave, the allochthonous organic-matter inputs are equivalent to those at a depth of 1000 m (Fichez, 1990a). Chlorophyll *a* values further demonstrate the marked oligotrophic character of the inner parts of dark caves (Fichez, 1990b). On the other hand, marine caves have a very limited spatial extent and the water is usually much warmer than in the deep sea. However, well-studied caves located in the northwestern Mediterranean have winter water temperatures (~13 °C) similar to that of the deep Mediterranean. Of particular interest is the 3PP cave near Marseille (Vacelet, 1996; Vacelet *et al.*, 1994), the descending profile of which traps cold (ca. 13–15 °C) water year round. More caves of this type have now been discovered (Bakran-Petricioli *et al.*, 2007), all of them characterised by faunal (Fig. 1.18) and ecological parallels to the deep sea. In particular, a significant number of faunistic components are either phylogenetically related to deep-sea fauna (e.g. Iliffe *et al.*, 1984; Calado *et al.*, 2004), or are truly bathyal or abyssal species sheltered in these 'deep-sea islands' of the littoral zone. The most striking examples are the carnivorous sponge *Asbestopluma hypogea* (Fig. 1.17A) and the hexactinellid sponge *Oopsacas minuta*, both also found in the bathyal Mediterranean (Vacelet *et al.*, 1994; Vacelet, 1996; Bakran-Petricioli *et al.*, 2007). Other examples include less conspicuous taxa such as bryozoans and brachiopods. It seems therefore that the 3PP and similar caves shelter an interesting combination of successfully established true deep-sea species as well as mobile shallow-water taxa using caves as a shelter from predators (Harmelin *et al.*, 1985).

Figure 1.18 Shallow water caves of the Mediterranean as analogs to the deep sea. (A) The carnivorous sponge *Asbestopluma hypogea* belongs to the exclusively bathyal and abyssal sponge family Cladorhizidae; however, dense populations thrive at 15–25 m depth in some particular caves of the Mediterranean. (B) Marine cave Mysidacea of the genus *Hemimysis* are a unique example of a species shift potentially linked to climate warming. (C) Recent efforts conducted at caves have focused on SCUBA sampling the foraminiferan and metazoan meiobenthos living in cave sediments that are remarkably similar to deep-sea sediments. Images courtesy of Jean-Georges Hermelin, CNRS (A) and Roland Graille, CNRS (B,C).

Marine caves are tempting sites in which to conduct *in situ* experiments or temporal surveys relevant to deep-sea biology. However, faunistic studies have concentrated mostly on the hard substrate sessile invertebrates covering the walls and ceiling, and mobile fauna such as crustaceans and teleost fish, making quantitative or even qualitative comparisons with deep-sea data difficult. Recent research (Fig. 1.18) has investigated the sediment-dwelling foraminiferan and metazoan meiobenthos, mainly harpacticoid copepods, nematodes, and annelids. This effort, primarily concentrated on the 3PP cave, is directed at providing baseline data on cave-sediment taxa prior to initiating a temporal survey and later comparisons with deep-sea time series. Preliminary results show a strong gradient in meiofaunal composition between the cave's entrance and the darkest parts, with a prevalence of deep-sea components (at least families and genera) in the latter (Chevaldonné *et al.*, 2008).

Little is currently known about temporal trends in marine caves. There is no evidence for seasonal variations in the supply of food (e.g. Fichez, 1990b), which is probably introduced by the slow advection of material from outside and the movements of some mobile residents, such as fish and mysids (Fig. 1.18B; Coma *et al.*, 1997). However, it appears that some marine caves are being affected by climatic warming. Following unusually hot summers, one cave mysid species has recently been replaced by a congener in the majority of NW Mediterranean caves (Fig. 1.18B). Caves such as 3PP may act as a shelter, possibly temporary, from such episodes of warming (Chevaldonné and Lejeusne, 2003; Lejeusne *et al.*, 2010). Signs of mortality during mild winters suggests that some deep-sea taxa, particularly sponges, are probably living near their thermal limit in "cold-water" marine caves (T. Perez, P. Chevaldonné, personal observation). Temperature has been monitored in several NW Mediterranean caves since 2001 (since 1995 at 3PP, with gaps). Time-series sampling of the sediment meiobenthos, as well as measurements of additional physical and chemical parameters, would be a logical next step, particularly if caves are to serve as mesocosms of deep-sea sedimented habitats. However, although some marine cave taxa function as metapopulations (Lejeusne and Chevaldonné, 2006), true deep-sea taxa living in caves may actually follow a source-sink population model. In this case, the temporal patterns observed in caves might be misleading. These questions remain to be tested.

Other shallow-water analogues of deep-water ecosystems are located at high latitudes, where relatively stable low temperatures and a more or less isothermal water column facilitates the interchange of shallow- and deep-water species (Tyler and Young, 1999; Brandt *et al.*, 2007) and makes deep-sea animals available for study (e.g. Hessler and Strömberg, 1989). The occurrence of hexactinellid sponges, an essentially deep-sea group, within SCUBA-diving depths as shallow as 18 m in fjords around Vancouver on the Canadian Pacific coast is well-established (Leys *et al.*, 2004).

In somewhat deep water (150–250 m) in the same area, hexactinellids form massive reefs (Conway *et al.*, 2001).

The western side of McMurdo Sound (Antarctica) is another interesting area. This part of the Ross Sea has a semi-permanent ice cover, a very stable physical regime including uniformly low temperatures, and is influenced by nutrient-depleted water originating to some extent from under the Ross Ice Shelf. Water column and benthic primary production, rates of heterotrophic microbial activity, and densities of benthic macro- and megafauna, are all relatively low compared to the much more productive eastern side of McMurdo Sound (reviewed by Gooday *et al.*, 1996). Dayton and Oliver (1977) noted similarities in macrofaunal densities at western Sound sites and the deep Ross Sea shelf (500 m) and the bathyal NW Atlantic, as well as 'striking visual parallels' between seafloor features and faunas in the western Sound and the bathyal deep sea. Benthic foraminifera have been intensively studied since the 1980s in Explorers Cove, a coastal embayment of the western Sound (e.g. DeLaca *et al.*, 1980; Bernhard, 1987; Gooday *et al.*, 1996). This is a relatively tranquil area where the food supply, derived mainly from under-ice, water-column, and benthic production, is highly seasonal, as in parts of the deep sea subject to pulsed inputs of phytodetritus. The foraminiferal assemblages include large agglutinated species, some of them resembling species from sublittoral to bathyal, fjordic, deep shelf and upper slope settings in the Northern Hemisphere (Gooday *et al.*, 1996). Because it is accessible to SCUBA divers, Explorers Cove is a good area in which to study the ecology of benthic communities similar to those living in deeper water. However, important environmental differences exist, notably under-ice and benthic primary production, as well as organic inputs from meltpools that lead to localised, nearshore oxygen depletion. Moreover, longer-term temporal patterns in Explorers Cove are probably strongly influenced by periodic breakouts of the ice cover. These occur every 5–7 years and result in peaks of primary production superimposed on the normal seasonal cycle (Gooday *et al.*, 1996). Like caves, high latitude sites have their own peculiarities and do not provide perfect analogues of deep-sea environments. Results obtained from them therefore must be treated cautiously.

5.2.5. Evolutionary constraints on faunal responses

Long-term time-series studies can reveal how species assemblages and ecosystems change over time in relation to environmental perturbations. We know very little, however, about the physiological mechanisms underlying these changes, or about how they are influenced by the evolutionary history of species. Taxonomic and phylogenetic studies have provided insights into the evolutionary origin of species at vents, seeps, and whale-falls. With some exceptions, these species share relatively recent ancestors with species from shallow-water settings. Among polychaetes, the dominant family at Pacific vents (Siboglinidae) are also found on seeps, whale-falls (as *Osedax*) and in shallow-water organic-rich muds (e.g. *Siboglinum* in the North Sea). The family falls within a globally-distributed clade of polychaetes that includes the Oweniidae and Sabellidae, ubiquitous tube-dwelling worms in all marine environments. Among molluscs, the Bathymodiolinae clade, which includes all the vent, seep, and whale-fall molluscs, is closely related to shallow-water mytilids, including the edible mussel *Mytilus edulis* (Distel *et al.*, 2000). Among crustaceans, the hydrothermal vent shrimp *Mirocaris fortunata* is closely related to the shallow-water species *Palaemonetes varians* (Distel *et al.*, 2000). The overlapping of depth tolerance ranges of the first stage larvae of the two species (Mestre and Thatje, unpublished data; Tyler and Dixon, 2000) suggests that they originated from a common ancestor that was physiologically tolerant to a wide range of pressures (Mestre *et al.*, 2009). Thus, whilst all of these species and clades have evolved unique adaptations to the sulphide-rich settings of vents, seeps, and whale bones, their common evolutionary heritage with shallow-water species is likely to be important in determining their physiological responses to external drivers.

Ideas about species' radiations are still based mainly on biogeographic patterns, in recent years supported by molecular analyses. It is becoming increasingly evident, however, that the radiation and speciation of deep-sea benthic taxa reflects the submergence of species from continental shelf depths into slope and deeper waters, as well as the emergence of taxa into shallower waters (Thatje *et al.*, 2005; Raupach *et al.*, 2009). Tolerance differences among life-history stages in shallow-water species suggest that the restriction of adult bathymetric distributions reflects ecological rather than physiological limitation. When environmental conditions (e.g. temperature) change, ecological limitations may relax, allowing greater bathymetric penetration (Tyler and Young, 1998). Studies of deep-sea invertebrates such as *Mirocaris fortunata* have demonstrated comparable patterns; adults have defined hyperbaric distributions but the larvae exhibit greater tolerance to lower pressures equivalent to the surface waters where they feed (Pond *et al.*, 1997; Tyler and Dixon, 2000). The ability of deep-sea species with shallow-water evolutionary origins to respond to rapid climate change therefore may be influenced by the preservation of physiological tolerances beyond those required by the ecological niche that they currently occupy in the deep ocean (Mestre *et al.*, 2009). These physiological and evolutionary considerations highlight the importance of pressure and temperature tolerance studies, and physiological studies in general, for understanding the capacity of some deep-sea species to respond to possible future environmental changes (Mestre *et al.*, 2009).

5.2.6. Stochastic events and successional processes

Like their counterparts in shallow water, deep-sea communities are controlled by the basic mechanisms of energy availability, biological interactions, heterogeneity, and stochastic disturbances, the latter ranging in scale from the very small (e.g. Jumars and Eckman, 1983; Grassle and Morse-Porteous, 1987; Grassle and Maciolek, 1992) to the very large (e.g. Levin *et al.*, 2001). Larger stochastic events include food falls (e.g. whales), episodic benthic storms and strong near-bottom currents, down-slope cascading of shelf water, mass sediment movements (turbidity currents, submarine slumps and slides) and volcanic eruptions or ashfalls. Violent disturbances, such as mass movements (Masson *et al.*, 1996) and volcanic eruptions, can eliminate most benthic life over large tracts of the seafloor. The re-establishment of a new community involves the processes of colonisation and succession. Smaller-scale disturbances can lead to changes in the structure and composition of benthic faunas and influence their dynamics. In some cases, this may take the form of a ‘regime’ or ‘state shift’ (Pascual and Guichard, 2005), a phenomenon often proceeded by a loss of resilience (Scheffer *et al.*, 2001).

Although the sedimented deep ocean is generally quiescent, some areas are subject to periods of high current activity that strongly affect benthic communities (reviewed in Levin *et al.*, 2001). Where the currents are strong enough, for example, in the HEBBLE area on the Nova Scotia continental rise, periodic erosion of the seafloor removes much of the benthic fauna, repeatedly creating fresh habitats that are available for recolonisation by opportunistic species. This process is believed to maintain communities in a constant early successional state. Similarly, dense shelf-water cascading (DSWC) can transport large volumes of water and sediment. This climatically-induced phenomenon reshapes submarine canyon floors and impacts deep-sea environments (Canals *et al.*, 2009) and communities (Boetius *et al.*, 1996; Tselepides and Lampadariou, 2004; Tselepides *et al.*, 2007). DSWC has been linked to population collapses of the commercially important deep-sea shrimp *Aristeus antennatus,* as well as to enhancement of its longer-term recruitment (Company *et al.*, 2008).

Strong current flow often characterises the upper reaches of active submarine canyons (Tyler, 2009). In the Nazare´ Canyon on the Portuguese margin, upper-canyon currents erode sediments and deposit them to the middle part of the canyon (De Stigter *et al.*, 2007). Intermittent gravity flows, occurring about once per year, and much rarer major turbidity currents, are the main agents transporting sediment through the lower section of the canyon and onto the adjacent abyssal plain. Gravity and turbidity flows and strong currents must impact on the benthos and lead to a succession of recolonising species. There is evidence for recolonisation and successional processes occurring at bathyal depths in the upper Nazaré

Canyon (Koho *et al.*, 2007) and the Cap Breton canyon (Anschultz *et al.*, 2002). In the latter case a succession of foraminferal species was observed over a 16 month period following the deposition of a turbidite. A much older turbidite, emplaced ~1000 years ago on the Madeira Abyssal Plain (MAP, NE Atlantic), seems to have had a lasting impact on polychaete and nematode assemblages (Glover *et al.*, 2001; Lambshead *et al.*, 2001), possibly because of its granulometric characteristics.

Turbidity currents grade into other types of catastrophic gravity-driven mass movements of sediments, such as slumps, slides, and gravity flows, which occur periodically on continental margins (reviewed in Levin *et al.*, 2001). Some of these events, for example, the series of Holocene (~7000 years BP) slides in the Storegga area on the Norwegian margin, were enormous and must have wiped out the benthic biota over large areas of seafloor. Presumably, the devastated areas were recolonised over time by species from adjacent areas of seafloor. This process has never been documented, although large-scale in situ experimental studies, reviewed by Thiel (2003), provide some indication of how it might proceed. The DISCOL (DISturbance and reCOLonisation of a manganese nodule area in the South Pacific) experiment, in which 11 km^2 of seafloor were disturbed, suggested that recovery from disturbance may take years, particularly for the megafauna. In the case of the composite Storegga slide, which covers an area of 90,000 km^2 (Canals *et al.*, 2004), recolonisation must have taken much longer. Volcanic ash falls are another kind of sudden event with the potential to wipe out or seriously disturb benthic communities over wide areas. The recovery of foraminiferal communities following the deposition by the 1991 Mt Pinatubo eruption of an ash layer over large areas of the South China Sea is well documented (Hess and Kuhnt, 1996; Hess *et al.*, 2001). Samples collected between 1994 and 1998 revealed a succession of species and increasingly diverse assemblages following this disturbance event.

At hydrothermal vents, the relative roles of environmental drivers, biological interactions and random processes remain poorly understood (Desbruyères, 1995, 2001; Juniper and Tunnicliffe, 1997; Mullineaux *et al.*, 2003; Sarrazin and Juniper, 1999; Sarrazin *et al.*, 1997; Shank *et al.*, 1998). Nevertheless, the ephemeral and unpredictable nature of the habitat is clearly responsible for sequences of extinction and rapid colonisation (Tunnicliffe, 1991; Thiébaut *et al.*, 2002). The mixing of sea water and hydrothermal fluids exposes the vent fauna to strongly fluctuating physicochemical conditions (Johnson *et al.*, 1986; Luther *et al.*, 2001), while small-scale variations in hydrothermal fluid discharges influence faunal distributions by altering the supply of primary food sources to microbial communities. Over longer timescales, changes in fluid flow resulting from the rearrangement of subsurface plumbing by tectonicism or clogging, as well as submarine volcanic eruptions, can lead to the creation of new venting areas or to the cessation of venting activity (Hessler *et al.*, 1985; Tunnicliffe, 1991; Haymon *et al.*, 1993; Grehan and Juniper, 1996; Tunnicliffe *et al.*, 1997; Sarrazin *et al.*, 1997; Shank *et al.*, 1998; Desbruyères, 1998; Tsurumi and Tunnicliffe, 2001; Embley *et al.*, 2006). These processes lead to major changes in community composition and distribution over months and years. However, the frequency of episodic tectonic and volcanic disturbances varies according to spreading rates (Fornari and Embley, 1995). Catastrophic perturbations occur on time scales of years to decades on fast-spreading mid-ocean ridges, but are far less common on the more stable slow-spreading ridges (Lalou, 1991; Desbruyères *et al.*, 2001). Tectonic events and heat convection through the oceanic crust may also induce a fast faunal turnover on fast-spreading ridges (Thiébaut *et al.*, 2002). In contrast, community structure and faunal distribution at the TAG site on the Mid-Atlantic Ridge exhibits a decadal-scale constancy that may be enhanced by the resilience of a single large mound (Eiffel Tower) to total clogging of vent fluid conduits by mineralisation. This hypothesis could be tested by comparing the decadal-scale ecological dynamics of TAG with those of other deep Mid-Atlantic vent fields, where venting is associated with smaller constructs, such as at Broken Spur, Snake Pit or Logachev. Unfortunately, no relevant data are yet available from these sites.

5.3. Temporal change in shallow-water versus deep-water settings

Historically, there has been much greater interest in temporal change at shallow-water habitats compared to those in the deep sea. This has been partly because of the huge economic and societal importance of the continental shelf compared to the inaccessible deep ocean. A large literature exists on the impact of global industrialised fisheries both on fish stocks (e.g. Pauly *et al.*, 1998) and on the entire shelf ecosystem (e.g. Worm *et al.*, 2006). There is no doubt that enormous changes have taken place in shelf ecosystems over the temporal scales considered in this review. However, the majority of these changes have been driven by fisheries and other human activities in the littoral or riverine zone (Table 1.4). Ironically, it is the fisheries themselves that generate most of the data on long-term change in shallow-water, as well as driving the changes that the data reveal. If we are to consider changes brought about by possibly ‘natural’ cycles (e.g. climate cycles), or the regional influences of global rises in carbon dioxide and associated temperature, the results may be much more subtle, and possibly hidden by fisheries or land use impacts (Table 1.4). At abyssal settings, still not directly impacted by commercial fishing, oil and gas exploration or mining (Glover and Smith, 2003), the impacts of these more subtle drivers of temporal change may be much clearer.

Table 1.4 Dominant drivers of inter-annual to decadal-scale temporal change in marine benthic habitats

	Intertidal	Sub-tidal	Bathyal	Abyssal	Hadal
Hard substrate habitats	Human land use Fisheries Climate forcing	Fisheries Human land/resource use Climate forcing	Stochastic down-slope processes Climate forcing	Unknown	Unknown (Drivers may include stochastic down-slope processes, (e.g. sediment mass movements)
Sedimented habitats	Human land use Fisheries Climate forcing	Fisheries Human land/resource use Climate forcing	Stochastic down-slope processes Fisheries Climate forcing	Climate forcing Stochastic down-slope processes	Unknown (Drivers may include stochastic down-slope processes, (e.g. sediment mass movements)
Cold seep habitats	Unknown	Unknown	Stochastic events (e.g. Grand Banks turbidite) Methane hydrate release?	Unknown	Unknown
Hydrothermal vent habitats	Unknown	Unknown (possible drivers include periodic changes in fluid flow)	Fluid flow and chemistry Biological succession Volcanic eruptions	Fluid flow and chemistry Biological succession Volcanic eruptions	Unknown
Large organic-fall habitats	Biological succession (scavenging)	Biological succession (scavenging)	Biological succession (scavenging)	Biological succession (scavenging)	Unknown

It is an intriguing thought that the regions of the worlds oceans that are most insulated from change may be the best settings in which to detect it. Just as deep-sea sediment cores have revealed past shifts in the Earth's climate, modern time-series studies in the deep sea are revealing current changes (K. L. Smith *et al.*, 2009). Summarising the drivers of temporal change reveals four important points (Table 1.4). Firstly, the impacts of the main human drivers (not including climate) are reduced with increasing depth and increasing habitat speciality (i.e. more rare and ephemeral habitats such as vents and seeps). Secondly, the impacts of natural climate cycles and climate change may be a more significant driver of change in the abyss compared to shallow water. Thirdly, it is abundantly clear from this review that deep-sea ecosystems are highly variable over inter-annual, decadal, and centennial scales, both in sedimented regions and those dependent on locally-sourced chemosynthesis. Finally, if climate change does indeed significantly alter the amount or distribution of the POC fluxes that feed most deep-sea areas, then related changes in deep-sea systems would likely occur with a delay that is comparable with most other habitats globally.

6. CONCLUSIONS

6.1. Hypotheses

Four hypotheses were put forward at the start of this review. These can now be revisited and assessed, based on the literature reviewed above.

Deep-sea sedimented ecosystems are subject to biologically driven forcing events induced by climate change or climate variability in recent decades: We find some support for this hypothesis in the case of the two abyssal plain sites for which we have data for a period longer than 10 years. It is clear that deep-sea benthic sedimented environments are being impacted by changes in upper-ocean processes linked to interannual to decadal-scale oscillations. However, it is not yet clear to what extent human-induced climatic changes are impacting on the deep sea. This is largely because we have not been collecting data for long enough to distinguish a long-term, warming-induced trend from natural stochastic and cyclic changes.

Chemosynthetic ecosystems are subject to stochastic geological forcing events which override climatically induced biological processes: It is a widely held view that chemosynthetic ecosystems such as hydrothermal vents are unstable, ephemeral habitats that are subject to frequent stochastic disruptions, such as volcanic eruptions. However, the data available suggest that, although this may sometimes be the case at fast-spreading centres such as the East Pacific Rise, vent ecosystems at slow-spreading centres such as the Mid-Atlantic Ridge may be quite stable over decadal to century scales. Data are lacking at cold-seeps, but inferences based on the longevity of cold-seep organisms suggest that these environments may be stable for many hundreds of years, except where they are disturbed by sediment flows. For other chemosynthetic ecosystems such as whale-falls, the stability of the habitat may be highly variable depending on the ecological setting and the size of the carcass and bones. We find no evidence for climate-induced temporal change at chemosynthetic ecosystems.

Although the drivers are different, there are commonalities in the biological responses observed in these contrasting settings: New data have emerged which suggest a relatively recent ancestry of organisms from vents, seeps, and deep-sea sediments. Species that now inhabit high-sulphide vent sites may have evolved from deep-sea or even shallow-water sediment-dwelling species, and exhibit some similar physiological constraints. Organisms at vents are likely to respond to a waning sulphide supply in the same way as detritivores in sediments respond to reduced organic carbon flux. However, chemosynthetic ecosystems that are driven by geology may be independent of changes in surface waters associated with climatic change, and therefore insulated from these impacts to some degree.

The deep-sea benthos embodies the influences of climatic changes that have occurred over both geological (evolutionary) and decadal (ecological) timescales: Traditionally, climate change studies in the deep sea were concerned only with the long-term sediment record revealed in cores. However, the 'ecological-scale' studies at PAP, Station M and other sites are now beginning to suggest that we can identify climate-induced changes in the communities of animals living at the seafloor some 4–5 km below the surface. Given that the palaeoceanographic record yields abundant evidence for climate-change impacts on deep-sea biota, we believe it is essential to determine whether current climatic change is leading to ecological-scale faunal change at deep-sea sites. In addition, as the deep-sea benthos is to some extent 'buffered' from seasonal, inter-annual and human (e.g. fisheries) effects in the overlying water column, climate-induced changes may be easier to detect on the ocean floor than in shallow-water marine environments.

6.2. Future directions

Our knowledge of temporal changes in the deep sea is extremely poor, to a large extent reflecting our inability to directly observe deep-sea habitats through remote sensing. Surface waters and the terrestrial environment can be observed from satellites capable of enormous and rapid spatial coverage. In contrast, even a short series of oceanographic cruises to a single site such as that on the Porcupine Abyssal Plain is a major effort and provides only limited spatial coverage. The observation of the Earth from space, and the ability to measure change over global scales, has been a key factor in our gradual realisation of the significance of human impacts on the Earth's terrestrial and surface-water ecosystems. An even greater level of observational detail is needed for the deep sea, which covers the other two-thirds of the planet's surface.

Technologies are now arriving that will allow us to make the necessary broader-scale observations. The development of autonomous underwater vehicles (AUV's), freed from the need to be tethered to the surface, will allow us to image for the first time vast tracts of the seafloor at a resolution sufficient to relate spatial and temporal change across a range of scales. Access to ROVs has also improved, allowing for more creative and experimental approaches to deep-sea research. At the same time, ocean observatories are developing world-wide in major programmes, for example, the US NSF-Ocean Observatories Initiative, the Canadian NEPTUNE programme, and various European (EuroSITES, the European Seas Observatory NETwork (ESONET), and the European Multidisciplinary Seafloor Observatory programmes) and Japanese (DONET) initiatives. Data from these observatories can either be cabled to the shore, using existing fibre-optic networks from industry or by laying new cables, or sent via satellite-based telemetry from buoys. In this way, researchers can monitor oceanographic and biological variables in real-time. These systems, especially when used together in a Global Earth Observation System of Systems (GEOSS), will provide an unprecedented opportunity to examine science questions across disciplines as well as spatial and temporal scales more effectively than ever before. By producing, for example, transformative maps of the deep sea, such developments will improve significantly our ability to gather scientific data and herald a new era of public understanding of the deep ocean.

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