

8 Responses of marine benthos to climate change

Silvana N. R. Birchenough*, Steven Degraer*, Henning Reiss*, Ángel Borja, Ulrike Braeckman, Johan Craeymeersch, Ilse De Mesel, Francis Kerckhof, Ingrid Kröncke, Nova Mieszkowska, Santiago Parra, Marijn Rabaut, Alexander Schröder, Carl Van Colen, Gert Van Hoey, Magda Vincx, and Kai Wätjen

*Joint first authors.

8.1 Introduction

Benthic communities are especially suited for long-term comparative investigations because many of the constituent species are sessile or have low mobility, are relatively long-lived, and integrate the effects of environmental change over time (e.g. dredged material, organic enrichment, aggregate extraction, and climate change; Rachor, 1990; Frid *et al.*, 1999; Birchenough *et al.*, 2006; Rees *et al.*, 2006; Foden *et al.*, 2009; Birchenough *et al.*, 2010). Furthermore, the macrobenthos has an important functional role in the reworking of sediments (i.e. bioturbation and bio-irrigation activities), provides nutrients/food to other higher trophic groups, and also creates habitats through habitat-engineering species (Figure 8.1; e.g. Tsuchiya and Nishihira, 1986; Ragnarsson and Raffaelli, 1999; Callaway, 2006; Hendrick and Foster-Smith, 2006; Van Hoey *et al.*, 2008).

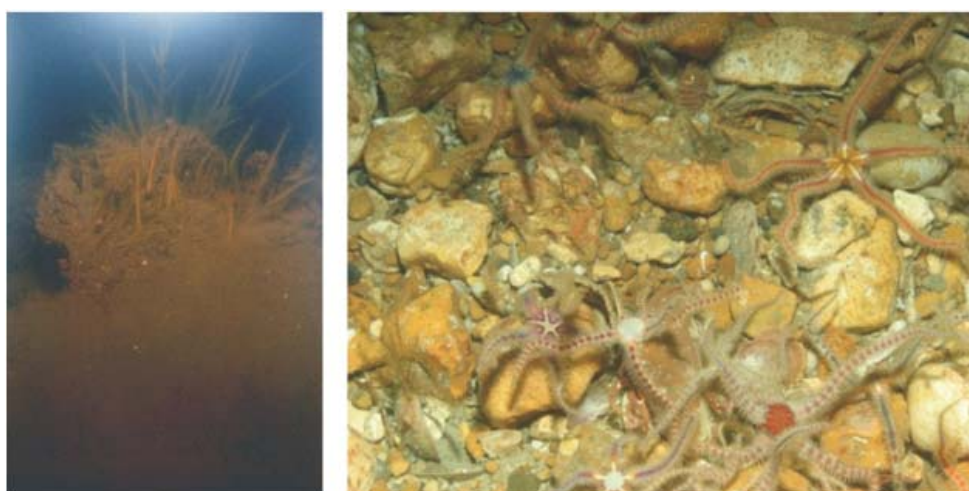


Figure 8.1. Examples of different benthic habitat types: (left) image of reefs formed by the tube polychaete *Sabellaria spinulosa* collected with Sediment Profile Imagery (SPI), and (right) photo of *Ophiothrix fragilis* beds over coarse substratum. Images are used to show the different types of benthic habitat with high levels of biodiversity in marine ecosystems. (Images courtesy of Cefas.)

Descriptions of benthic variability and its relation to climate change and other effects are subjects that are still evolving as more evidence and time-series observations become available. Climate change may modify population dynamics over time and space, phenology, and the geographical distribution of communities (and species; Dulvy *et al.*, 2008). These modifications could result in habitat loss and species extinctions over time, with repercussions for biogeochemical fluxes, ecosystem functioning, and biodiversity.

The need to assess and monitor benthic changes in relation to a wide range of stressors, including climate change, has prompted researchers to collect information over a long time-scale. Long-term studies of the macrobenthos have been carried out at a number of sites in the ICES region over the past 100 years (ICES, 2009a). For the

eastern Atlantic, these sites include the North Sea (Rees *et al.*, 2002), western English Channel (Southward *et al.*, 1995, 2005), Bay of Biscay (Alcock, 2003), Bristol Channel (Henderson *et al.*, 2006) and the Wadden Sea (Beukema, 1992; Beukema *et al.*, 2009), and, for the western Atlantic, Chesapeake Bay (Seitz *et al.*, 2009) and Boston Harbor (Diaz *et al.*, 2008).

Assessment of effects over larger areas (i.e. the North Sea) in relation to climate change is based on localized studies, with some exceptions (e.g. Bay of Biscay and the UK; Alcock, 2003). Efforts to document the status and change of the benthos have involved collaboration, via ICES, in a number of initiatives: the North Sea Benthos Project (NSBP), Benthic Ecology Working Group (BEWG) and Study Group on Climate-related Benthic Processes in the North Sea (SGCBNS). These collaborative projects have allowed scientists to assess the structure and dynamics of the benthic assemblages inhabiting the North Sea between the 1980s and 2000s.

Current requirements under international legislation (Water Framework Directive (WFD), Habitats and Bird Directives, EU Marine Strategy Framework Directive (MSFD), US Clean Water Act (CWA), US Oceans Act, etc.) focus on the quality and status of the marine environment (see Borja *et al.*, 2008, 2010, for an overview). However, under the new MSFD, climate change is included under Descriptor 1. Possible effects are, at present, an unquantified pressure on species and ecosystems. Little is known about the robustness and sensitivity of the proposed “Good Environmental Status” (GES) descriptors that will be used to support future assessments (see also additional information provided in Borja *et al.*, In press). Benthic systems have been studied by employing a suite of indices as tools to characterize community status (e.g. Borja *et al.*, 2000; Rosenberg *et al.*, 2004; Muxika *et al.*, 2007). Although there is merit in these approaches, there is still a need to fully understand the function and mechanisms that are altering these processes; such studies will lead to a better knowledge of benthic responses and a more targeted tool for the environmental management of marine systems (Birchenough *et al.*, In press).

Climate change and variation could affect all components of marine and coastal ecosystems, including habitats, benthos, plankton, fish, mammals, seabirds, and the presence of non-native species. Such effects have implications for physiological responses, biogeochemical processes, and higher trophic groups, with repercussion for overall ecosystem biodiversity and function. Some examples of complex interactions within the benthic–pelagic environment in relation to climate change are summarized in a conceptual model (Figure 8.2). The model illustrates the complex linkages between various environmental factors (effects of storms, sea-level rise, turbidity, currents, stratification, and salinity) and biotic effects (e.g. benthos and pelagic systems). The left panel shows the influence of increased CO₂ and temperature, and how these factors could directly affect biotic and abiotic components.

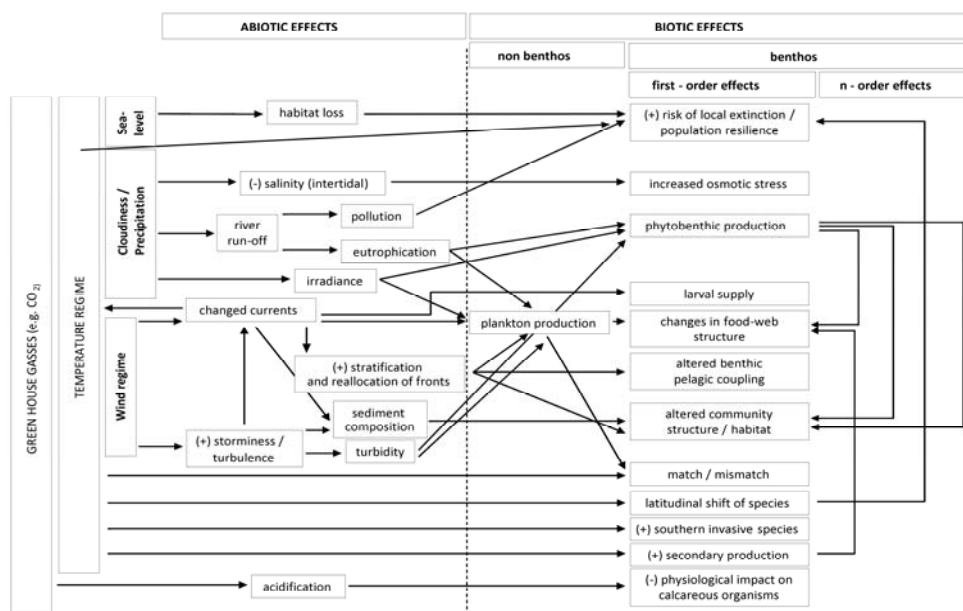


Figure 8.2. Conceptual diagram of the effects of climate change and benthic interactions (taken from ICES, 2008b), illustrating the influence of increased CO₂ and temperature (left panel) and how these factors could directly affect biotic and abiotic components (Further explanation is provided in the text.)

8.2 The impacts of climate change on the benthos

This review attempts to provide an assessment of the effects and mechanisms causing changes to the benthos (benthos, by definition, encompasses all organisms living in or on the seabed; epifauna, and infauna), which may be interlinked with climate change. It also reports on the current peer-reviewed literature and considers areas where research gaps exist.

Direct evidence of climate-change-related impacts on the marine benthos is still largely lacking, but information from other research areas, relevant in a context of climate change and variability, provides circumstantial evidence of climate-change effects. In the following sections, three main issues are addressed:

- i) **The relationship between physical aspects of climate change and the marine benthos (Section 8.3).** This investigation focuses on (i) responses to changes in seawater temperature (biogeographic shifts, phenology, parasites); (ii) altered hydrodynamics; (iii) ocean acidification; and (iv) sea-level rise–coastal squeeze (Figure 8.2).
- ii) **The possible integrated impact of climate change on the benthos, based on relationships with proxies for climate variability (Section 8.4).** Lessons learned from the relationship between the North Atlantic Oscillation (NAO) index, as a proxy for climate variability, and the marine benthos provide further insight into the possible integrated impact of climate change on the benthos.
- iii) **The interaction between climate-change- and human-activity-induced impacts on the marine benthos (Section 8.5).** As climate change may also modify human activities in the marine environment, indirect effects on the benthos are also to be expected. This section details interactions between climate change and impacts induced by human activities.

8.3 Physical aspects of climate change and marine benthos

8.3.1 Change in seawater temperature

8.3.1.1 Latitudinal distribution shifts

Biogeographic studies dating back to the 1700s have long established a link between the distribution of marine species and mean sea surface isotherms (e.g. Van den Hoek, 1982; Breeman, 1988); a change in the latitudinal distribution of species might be expected when the temperature of the oceans increases. Distribution shifts of marine species in the Northeast Atlantic – possibly linked to temperature change – have been found for several components of the ecosystem: fish (e.g. O'Brien *et al.*, 2000; Perry *et al.*, 2005; Poulard and Blanchard, 2005; Rose, 2005), phytoplankton (e.g. Beaugrand *et al.*, 2008; Leterme *et al.*, 2008), zooplankton (e.g. Lindley *et al.*, 1995; Pitois and Fox, 2006; Beaugrand, 2009), and benthos (e.g. Southward *et al.*, 2004; Eggleton *et al.*, 2007).

The relationship between temperature change and modifications to the distribution of species is, however, complicated by the effects of other environmental parameters, physical barriers to movement, and human usage of the coastal zone. Differences in life cycles, dispersal ability, and habitat connectivity may also influence the vectors of spread or retreat of coastal benthic species. All of these factors complicate the process of attributing causal mechanisms and may result in the actual distribution lying within the potential range of a species. As such, between 1986 and 2000, some evidence of change in the distribution of North Sea benthic species was detected that may be attributable to natural variation in the recruitment process of relatively short-lived species; however, there was little indication of a consistent directional trend that could be linked to temperature change (Eggleton *et al.*, 2007).

To date, clear evidence of change in the distribution and abundance of benthic species in response to temperature change has been recorded in the North Atlantic (Alcock, 2003; Southward *et al.*, 2004; Beukema *et al.*, 2009; Jones *et al.*, 2010; Wiltshire *et al.*, 2010). Most changes are initially observed at the edge of ranges, where organisms are more likely to be physiologically stressed, but there is also evidence of local and regional heterogeneity within biogeographic ranges, with infilling of gaps or loss of site occupancy away from range limits. Living close to their physiological tolerance limits, being sessile or sedentary, having typically short lifespans, and being from lower trophic levels, intertidal organisms have demonstrated some of the fastest responses to climate change.

As such, a strong climatic signal is observed in the relative abundance of the co-occurring intertidal Lusitanian barnacles *Chthamalus montagui* and *Chthamalus stellatus*, and the Boreal species *Semibalanus balanoides* over the past 50 years in the UK. Numbers of *S. balanoides*, the dominant competitor, increased during cooler periods but have declined significantly as temperatures have increased in recent years (Poloczanska *et al.*, 2008). The southern range limit of *S. balanoides* has also shifted north within the Bay of Biscay (Wethey and Woodin, 2008), whereas the northern range edges of the chthamalids have extended to Scotland (Mieszkowska *et al.*, 2006). Models based on a 50-year time-series forecast a total disappearance of *S. balanoides* from shores in southwest England by 2050 (Poloczanska *et al.*, 2008). Similarly, latitudinal shifts were observed in two intertidal and shallow subtidal barnacle species: *Solidobalanus fallax*, a West African warm-water species, not known from the European coasts until 1994 (Southward, 1998), has extended its range along the English Channel in recent decades (Southward *et al.*, 2004); *Balanus perforatus*, a

Lusitanian species, has extended its range through the eastern English Channel (Herbert *et al.*, 2003) and has now also expanded into the southern North Sea (Kerckhof, 2002; Kerckhof *et al.*, 2009). Hence, many changes in northern Europe have occurred in the breakpoint region between cooler Boreal waters to the north and warmer Lusitanian waters to the south, where many species reach their distributional limits and congeneric species from different provinces co-occur (see Alcock, 2003, for the Northeast Atlantic).

Other examples of intertidal, hard-substratum fauna distribution changes linked to changes in temperature include: the gastropods *Osilinus lineatus* (Mieszkowska *et al.*, 2006, 2007), *Gibbula umbilicalis* (Kendall, 1985; Kendall and Lewis, 1986; Mieszkowska *et al.*, 2006, 2007) and *Testudinalis* spp. (Mieszkowska *et al.*, 2006), as well as the blue mussel (*Mytilus edulis*; Europe: Berge *et al.* 2005; US Atlantic: Jones *et al.*, 2010). An example of infilling within a biogeographic range is observed for the Lusitanian intertidal, hard-substratum limpet *Patella rustica*, which has colonized a break in the distribution in northern Portugal during a period of warmer sea temperatures caused by a possible climate-driven reduction in upwelling in the southern Biscay region and a weakening of the western Iberian Shelf Current (Lima *et al.*, 2007). In fact, rates of change of up to 50 km decade⁻¹ are much greater than the average rate of range-edge shift of 6.1 km decade⁻¹ documented for terrestrial species (Parmesan and Yohe, 2003), but an order of magnitude less than those seen in plankton in the Northeast Atlantic and North Sea (Beaugrand and Reid, 2003). These different rates may arise from the difference in the degree of connectivity between pelagic, benthic, and terrestrial systems.

Though less well documented, examples of changes in geographic distribution because of temperature change also exist for subtidal, soft-substratum organisms. For example, several Lusitanian benthic species, such as the decapods *Diogenes pugilator*, *Goneplax rhomboides*, and *Liocarcinus vernalis*, have extended their range farther into the North Sea during recent decades. These southern species tend to thrive off the Belgian coast during warmer years (e.g. Laporte *et al.*, 1985; d'Udekem d'Acoz, 1991; 1997; Doeksen, 2003), but have now extended their range farther north into Dutch and German waters (e.g. Doeksen, 2003; Franke and Gutow, 2004; Van Peursen, 2008; Neumann *et al.*, 2010). Since Barnett (1972) demonstrated that the gastropod *Nassarius reticulatus* has an earlier and faster development in warmer waters, the sudden appearance of this species in the 1980s (e.g. Craeymeersch and Rietveld, 2005) can also be attributed to the temperature increase in coastal waters.

A change in the geographic distribution of habitat-forming or habitat-engineering species, such as various macroalgae (Vance, 2004; Mieszkowska *et al.*, 2006), by definition, means a change in habitat type, and hence assemblage and functioning (M. T. Burrows, pers. comm.). It might, as such, have important consequences for the ecosystem goods and services provided to mankind.

A shift in the distribution of species might also trigger a change in species richness in certain areas. As a consequence of the greater benthic species richness in southern waters of northwest Europe compared with those to the north, an increase in species richness is to be expected in the North Sea as the climate warms: namely, more species will probably enter the area from the south than will leave it to the north (Hawkins *et al.*, 2009; Beukema and Dekker, In press).

8.3.1.2 Phenology

Phenology is the study of periodic recurring life-cycle events of species and how they are influenced by changes in climate regime. These life-cycle events include (i) reproductive output, (ii) larval transport and settlement, and (iii) recruitment and post-recruitment development of benthic organisms. Recruitment and development play important roles in benthic community structure, diversity, and functioning. A variety of biotic and abiotic factors modulate these life-cycle processes, of which some are direct (e.g. physiological responses) and others are more indirect (e.g. changes in trophic interactions), and are likely to be influenced by climate change.

Many macrobenthic organisms have pelagic larvae and are planktonic (meroplankton) for a short time during their life cycle. Studying the timing of these recurring life-cycle events and how they are influenced by seasonal and interannual variability (phenology) may reveal sensitive indicators of the effects of climate change. Indeed, recent studies have revealed that meroplankton are more sensitive to increases in sea temperature than holoplankton. Edwards and Richardson (2004) demonstrated that the timing of the seasonal peak of meroplankton occurred 27 days earlier (echinoderm larvae 47 days) in the North Atlantic, based on a 45-year study period (Figure 8.3; see also Lindley *et al.*, 1993). The abundance of meroplankton also changed, revealing an increase in decapod and echinoderm larvae and a decrease in bivalve larvae caused by rising sea surface temperature (SST) in the North Sea from 1958 to 2005 (Kirby *et al.*, 2008). Similar changes were also found for holoplankton and fish larvae (e.g. Southward *et al.*, 1995; Lindley and Batten, 2002; Greve *et al.*, 2005).

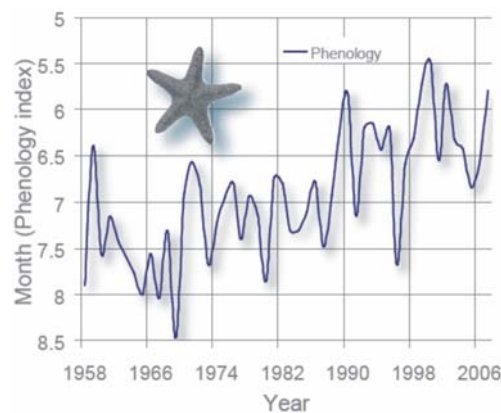


Figure 8.3. Interannual variability in the peak seasonal development of echinoderm larvae (an indicator of plankton phenology) in the North Sea. The general trend through time is towards an earlier seasonal cycle (Source: Edwards *et al.*, 2009).

Changes in temperature may directly influence mortality, reproduction, onset of spawning, and the embryonic and gonad development of benthic species, and thus may change phenological processes. For example, rising sea temperature affects the gametogenesis and spawning of *Echinocardium cordatum*, an abundant echinoderm species in the North Sea (Kirby *et al.*, 2007). In coastal waters of northern Europe, severe winters are often followed by high densities of intertidal bivalve recruits (Beukema *et al.*, 1998; Strasser *et al.*, 2003). This was partly attributed to lower metabolism during cold winters resulting in higher biomass and production of more eggs in spring (Beukema *et al.*, 1998). Indeed, rising sea temperature was found to reduce reproductive output and advance the spawning of intertidal bivalves (Honkoop and van der Meer, 1998; Philippart *et al.*, 2003), but recruit density was highly variable and only a minor part was explained by the effects of temperature on

reproductive output (Honkoop *et al.*, 1998). Several other environmental factors related to climate change and temperature rise may have influenced recruitment, such as changes in predation pressure or food availability (Hiddink *et al.*, 2002; Philippart *et al.*, 2003). These examples demonstrate the complex interactions and species-specific responses in benthic systems in relation to climate change. It is unlikely that changes in the abundance of meroplankton can be related directly to changes in adult populations because post-recruitment and juvenile dynamics are not well understood for most benthic organisms.

The shift in timing of meroplankton peaks described above seems to be a direct effect of sea temperature rise, but differences in the response between ecosystem components may also lead to indirect effects, such as altered competitive interactions or changes in foodwebs. The timing of the spring bloom remained fairly constant in the North Atlantic and the North Sea when compared with earlier cycles of meroplankton (and holoplankton; Edwards and Richardson, 2004; Wiltshire *et al.*, 2008). Other factors, independent of changes in temperature, such as photoperiod, seem to trigger the timing of the phytoplankton bloom (Eilertsen *et al.*, 1995). In contrast, phytoplankton biomass increased in several areas of the Northeast Atlantic during recent decades (Reid *et al.*, 1998; Raitsos *et al.*, 2005; McQuatters-Gollop *et al.*, 2007). However, the temporal mismatch between primary producers and consumers can have cascading effects on higher trophic levels, as already demonstrated for fish and bird populations (Conover *et al.*, 1995; Beaugrand *et al.*, 2003; Hipfner, 2008), with repercussions for foodweb structure. For benthic organisms, possible mismatch scenarios are most significant during the planktonic phase (at least for planktotrophic larvae) or during the post-recruitment phase on the sediment. Juvenile benthic organisms especially, which lack energy reserves and have a higher weight-specific metabolic demand, are supposed to depend much more on an adequate food supply than adults; therefore, they are more susceptible to starvation during times of food deprivation, possibly caused by climate-change effects (Ólafsson *et al.*, 1994).

The match–mismatch hypothesis (MMH; Cushing, 1990) provides a general and plausible framework for understanding variations in recruitment by means of species phenology, but it is difficult to test and has mainly been applied and debated in fishery science (Beaugrand *et al.*, 2003; Durant *et al.*, 2007). The mismatch between phytoplankton blooms and benthos dynamics has been little studied by either correlative approaches or experimental work. One exception is the study by Bos *et al.* (2006), who tested the MMH experimentally for the bivalve *Macoma balthica* against phytoplankton concentration. Although they found a clear effect of the timing of spawning on the growth and development of larvae, this was not related to changes in phytoplankton concentration, and the underlying mechanisms remain unclear. Also, Philippart *et al.* (2003) gained empirical evidence for the MMH and demonstrated that mortality of *M. balthica* juveniles became more density-dependent with an increase in the degree of mismatch. However, further experimental studies of the effects of temperature on the biology of benthic species and possible mismatch based on food availability are needed to clarify this situation. The response to climate change is often species-specific and may be determined by the timing (phenology) of particular processes. This suggests that a better knowledge of the life history of benthic organisms is needed for an adequate explanation of population changes and prediction of ecosystem responses (Richardson, 2008).

8.3.1.3 Parasites

Environmental change, such as higher temperature, and changing precipitation and currents, attributable to climate change, may alter parasite–host interactions (viral, bacterial, protozoan, and metazoan; Mouritsen and Poulin, 2002a) and, as such, adjust the structure and composition of natural animal communities. In intertidal communities, the most common parasites are trematodes, gastropods, and to a lesser extent bivalves, are the first intermediate host, and molluscs, crustaceans, polychaetes, or fish are the second intermediate host, with shorebirds or fish often as the definitive host. Parasitic nematodes use benthic invertebrates as the intermediate or only hosts. Cestodes and acanthocephalans use crustaceans as intermediate hosts, whereas decapods are often infected by nematomorphs, nemertean egg parasites, rhizocephalans, and parasitic isopods (Mouritsen and Poulin, 2002b). Parasites alter the survival, reproductive success, growth, and behaviour of their host (Mouritsen and Poulin, 2002b).

Parasites may also invade new areas, as illustrated by the protozoan *Perkinsus marinus*, which infects the eastern oyster (*Crassostrea virginica*). The parasite was originally found in Chesapeake Bay and the Gulf of Mexico, but in the early 1990s, an apparent range extension led to an epizootic outbreak over a 500-km range north of Chesapeake Bay (Ford, 1996; Cook *et al.*, 1998). The outbreaks coincided with increasing water temperatures during winter (Cook *et al.*, 1998; Ford and Chintala, 2006), with salinity also positively related to infection intensities (Ragone and Burrenson, 1993; Powell *et al.*, 1996; Mouritsen and Poulin, 2002a).

Mud snails and corophiid amphipods often co-occur in high densities in coastal areas of the temperate North Atlantic, where they act as first and second intermediate hosts for a number of trematodes. Snails often show decreased resistance to extreme abiotic conditions when infected by trematodes, and they are often castrated (Mouritsen and Poulin, 2002b). Infestation of amphipods may cause anaemia, which is the most probable cause of increased surface activity observed among infected specimens. This parasite-induced behaviour may facilitate transmission of infective stages to shorebird hosts feeding on the amphipod (Mouritsen and Jensen, 1997). In the Danish Wadden Sea, a dense field of *Corophium volutator* disappeared completely, and the density of the mud snail *Hydrobia ulvae* declined by 40% during spring 1990 as a result of an epizootic by trematodes. High spring temperature accelerated both the development rate and the release of infective larval stages of an infectious trematode from the snail. This event coincided with a high positive NAO index, high temperatures, strong winds, and increased precipitation in northern Europe (Mouritsen and Poulin, 2002a, and references therein). The transmission rates of larval parasites from snail to amphipods and the rate of parasite-induced amphipod mortality are both strong positive functions of temperature (Jensen, K., and Mouritsen, 1992; Mouritsen and Jensen, 1997; Mouritsen, 2002). Using a simulation model, Mouritsen *et al.* (2005) demonstrated that a 3.8°C increase in ambient temperature would probably result in a parasite-induced collapse of the amphipod population in the Wadden Sea. This temperature increase is within the range predicted to prevail by the year 2075. As *C. volutator* builds tubes in sediment, the collapse of its population led to drastic changes in erosion patterns, sediment characteristics, and microtopography, as well as marked changes in the abundance of other macrofaunal species in the mudflat (Poulin and Mouritsen, 2006).

Marine bivalves harbour a diversity of trematode parasites that affect the population and community dynamics of their hosts (Thieltges *et al.*, 2006). The parasites may lead to a reduction in condition, make the bivalves more vulnerable to predation or, in the

case of *Mytilus edulis*, reduce the production of byssal threads. Infection leads eventually to partial or complete castration and may induce behavioural changes that facilitate transmission of the parasite to the final host (Mouritsen and Poulin, 2002b). Thieltges and Rick (2006) demonstrated that, for the trematode *Renicola roscovita*, a major parasite in North Sea bivalves, the optimum temperature for transmission is 20°C. Similar observations were made for another trematode, *Himasthla elongata*, indicating that transmission to second intermediate bivalve hosts may peak during years with warm summers ($\geq 20^\circ\text{C}$) in the variable climate regime of the North Sea.

A clear example of the effects of temperature on bacterial- or viral-induced diseases was observed on sea fans around the southwest UK (ukbars.defra.gov.uk). During 2003–2006, Hall-Spencer *et al.* (2007) observed widespread incidence of disease outbreaks in the pink sea fan (*Eunicella verrucosa*) around Lundy and from Lyme Bay to Plymouth. Laboratory analysis of specimens revealed water temperatures of 15°C had no effects, whereas temperatures of 20°C induced disease symptoms (Figure 8.4).

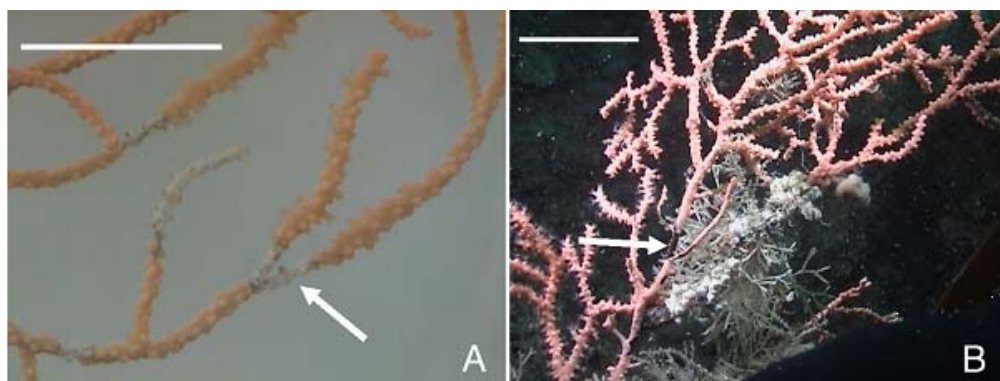


Figure 8.4. *Eunicella verrucosa* at 21m depth at Knoll Pins, Lundy, on 16 May 2003. (A) early onset of coenchyme necrosis (arrow), and (B) post-necrotic exposure of gorgonian skeleton (arrow) with fouling community of hydroids, barnacles *Solidobalanus fallax*, and bryozoans *Cellaria* sp. Scale bars = 40 mm. Source: Hall-Spencer *et al.*, 2007.)

8.3.2 Altered hydrodynamics

The hydrodynamic regime of the North Atlantic is characterized by a number of physical properties and circulation patterns that undergo substantial variability at seasonal–decadal time-scales. This variability can be affected by climate change, but it is rarely possible to separate these effects from natural variation in the system. Climate change may affect *inter alia* the mixed-layer depth, position of frontal regions, frequency and pathways of storms, and the occurrence of convection events, but these climate-change effects are not comprehensively understood (see Sections 2 and 3).

But how can changes in the physical properties of the water column affect benthic communities on the seabed? The hydrodynamic regime influences the benthos in various direct and indirect ways. Hydrodynamics can directly influence the benthos via the transport and dispersal of larvae, juveniles, and even adults, with important consequences for population dynamics (e.g. Palmer *et al.*, 1996; Todd, 1998; Levin, 2006) and can increase mortality caused by oxygen depletion (stratification) or storm events. The physical and chemical properties of the water column, especially of the upper layers, determine productivity in the ocean. Thus, among indirect effects, the influences of hydrodynamics on primary and secondary production in the water column and on the transport pathways of these food sources to the benthic system are probably most important (Rosenberg, 1995).

These effects are not restricted to shallow waters with a tight coupling of pelagic and benthic processes. Changes in surface-water hydrodynamics can also have implications for deep-sea benthic ecosystems (Davies *et al.*, 2007). Analyses of sediment cores from the Nordic seas also demonstrate a tight benthic-pelagic coupling for deep basins below 1200 m throughout the past 25 000 years (Bauch *et al.*, 2001). In the Northeast Atlantic, up to 4% of the surface production of the spring bloom reaches the seabed (Gooday, 2002), resulting in a response of the deep-sea benthic biota ranging from bacteria to megabenthos (Davies *et al.*, 2007). However, observed effects on benthic communities can rarely be related to a single hydrodynamic property, because they are often interrelated, and benthic communities are affected by a multitude of different environmental and anthropogenic drivers. Therefore, the following examples of climate-change effects on benthos via changes in hydrodynamics are somewhat uncertain and reflect the complexity in the coupling of benthic and water-column processes.

Oxygen depletion (i.e. hypoxia and anoxia) caused by high bottom-water temperature, reduced water circulation (enhanced by thermal stratification), and coastal eutrophication is considered among the most widespread deleterious influences on estuarine and marine benthic environments (Halpern *et al.*, 2007). Predicted global climate change is expected to expand hypoxic zones by (i) increased water-column stratification and warming that inhibits water exchange and (ii) changes in precipitation patterns that enhance discharges of freshwater and agricultural nutrients. At present, ca. 500 000 tonnes of benthic biomass are missing worldwide over a total area of 245 000 km² as a result of hypoxia (i.e. <2 mg l⁻¹ dissolved O₂; Diaz and Rosenberg, 2008). Levin *et al.* (2009) demonstrated that oxygen depletion causes a reduction in the diversity of the benthos through loss of less-tolerant species and increased dominance of tolerant opportunists (e.g. nematodes, foraminifera, and small soft-bodied invertebrates with short generation times and elaborate branchial structures).

The magnitude of this effect depends on the area affected and the frequency, intensity, and duration of oxygen depletion. Benthic mass mortality has been observed, for example, after long-lasting hypoxic periods (i.e. “dead” zones; Diaz and Rosenberg, 2008; Seitz *et al.*, 2009). Additionally, bottom-water oxygen deficiency also alters biogeochemical processes that control nutrient exchanges at the sediment–water interface (i.e. benthic–pelagic coupling), for example, by the release of phosphorus from bottom sediment (e.g. Jensen, H., *et al.*, 1995; Conley *et al.*, 2009). Another well-documented example of the effect of depleted oxygen conditions on biogeochemistry is the reduction in denitrification (e.g. Childs *et al.*, 2002) caused by low concentrations of bottom-water nitrate and a less-efficient reoxidation of reduced elements. However, until now, the extent to which climate change, by increasing hypoxic events, will affect the mortality of benthic species and nutrient fluxes remains unclear. Extensive oxygen-depletion zones were found (e.g. in the North Sea) during the 1980s, but less so after this period, although bottom-water temperatures were above average. The oxygen depletions during the 1980s were considered to be at least partly related to eutrophication (von Westernhagen *et al.*, 1986; Rachor, 1990), and possible temperature effects in recent years might have been masked by a reduction in riverine nutrient input to the North Sea.

As mentioned above, changes in thermal stratification of the water column have an important impact on heat flux, which can lead to oxygen depletion. Conversely, if the climate becomes stormier, stratification will decrease because of increased mixing depth, and the risk of oxygen depletion will be reduced. For example, Rabalais *et al.*

(2007) demonstrated that the 2005 hurricanes in the Gulf of Mexico disrupted stratification and aerated bottom waters. But in turn, physical disturbance by wave stress during storm events can itself increase mortality of benthic species, at least in shallow waters (<50 m), although studies of such effects are limited (Rees *et al.*, 1977; Nehls and Thiel, 1993; Turner *et al.*, 1995; Posey *et al.*, 1996). It is still unclear whether the frequency, intensity, and pathways of storms or extra-tropical cyclones have changed or will do so in future (see Section 2). The findings are equivocal, demonstrating evidence for an increasing trend in storm activity (Alexandersson *et al.*, 2000; Ulbrich *et al.*, 2009), as well as for stable conditions (Barring and von Storch, 2004; Raible *et al.*, 2008), during the past century in the Northeast Atlantic. Nevertheless, modelling studies based on global warming scenarios indicate a weak increase in storm activity in future (WASA Group, 1998; Donat *et al.*, 2010). However, storms are not an unusual disturbance event in marine benthic systems and can be attributed to natural variability within the system. Nevertheless, local changes in the granulometry or lithology of the bottom sediment caused by changes in storminess could have a long-term effect on the benthos, although this is unclear at present.

Future changes in stratification of the water column may not only have the impacts mentioned above, but can also indirectly affect the benthos via changes in food supply. In temperate stratified waters (e.g. the North Sea), primary and secondary production is elevated along thermohaline frontal regions where summer-stratified waters are separated from permanently mixed waters. The quality and quantity of sedimenting organic matter is an important factor influencing benthic communities (Rosenberg, 1995; Dauwe *et al.*, 1998). The relatively high primary production and the prolonged sedimentation of fresh organic matter along fronts affect abundance, biomass, growth, and functional composition of benthic communities (Dauwe *et al.*, 1998; Amaro *et al.*, 2003, 2007). Climate-change projections of the spatial extent of stratified waters in the North Sea indicate a northward expansion of the stratified areas (J. Van der Molen, pers. comm.) and, thus, would lead to changes in the position of seasonally developed frontal regions and their associated benthic communities.

The hydrodynamic regime plays an important role in structuring benthic communities, as demonstrated by many correlative studies (Butman, 1987; Snelgrove and Butman, 1994; Wieking and Kröncke, 2001; Kröncke, 2006; see also Section 8.4). Marine benthic systems, which are often dominated by organisms with planktonic life stages, are especially sensitive to alteration in oceanographic patterns affecting dispersal and recruitment (Ólafsson *et al.*, 1994; Gaylord and Gaines, 2000). It is conceivable that altered patterns of mass transport could tip the balance of larval recruitment to adult mortality and lead to local population reduction or even extinction (Svensson *et al.*, 2005). Given the uncertainty of the response of hydrodynamics to climate projections, potential associated changes in the benthos are currently unpredictable.

8.3.3 Ocean acidification

Global industrialization has led to increasing levels of CO₂ in the atmosphere, reaching a rate which is 100-fold faster than any change during the past 650 000 years (Fabry *et al.*, 2008). Approximately one-third of the anthropogenic CO₂ in the atmosphere has been taken up by the oceans over the past 200 years (Sabine *et al.*, 2004). The solution of CO₂ in seawater leads to an increased partial CO₂ pressure (hypercapnia), and a reduction in pH and calcium carbonate saturation, with diverse effects on marine organisms. If the rate of growth of CO₂ production continues, the

expected pH of seawater could fall during the 21st century by up to 0.5 units below its pre-industrial level of pH 8.2 (Caldeira and Wickett, 2003; Blackford and Gilbert, 2007). A reduced calcium carbonate saturation results in lower calcification rates in marine organisms, and a diminished pH affects various physiological processes. Combined, these effects may result in changes in biodiversity, trophic interactions, and other ecosystem processes (Fabry *et al.*, 2008). At present, benthic organisms are mostly neglected when calculating global carbon-flux models. However, several benthic groups contribute substantially to the global carbon budget and their physiology is also affected by acidification. The omission of benthic processes from global carbon models leads to false estimates of fluxes at large scales and future predictions of climate-change scenarios (Lebrato *et al.*, 2010).

Until now, calcification processes of tropical reefs and planktonic coccolithophores have been the main focus of research on ocean acidification, and information on other taxa and/or processes is scarce. Reviews by Langdon and Atkinson (2005) and Kleypas and Langdon (2006) have outlined the effects of acidification on coral reefs. For deep-sea fauna, especially cold-water corals, which are normally adapted to very little variation in pH (Fabry *et al.*, 2008), calcification may be severely affected, and changes in distribution can be expected (Guinotte *et al.*, 2006; Turley *et al.*, 2007). Cold-water corals are probably one of the most vulnerable habitat-forming calcifiers in the North Atlantic, providing habitat for a variety of associated benthic species (Jensen, A., and Frederiksen, 1992; Mortensen *et al.*, 1995; Husebø *et al.*, 2002). They are found throughout the North Atlantic, usually between depths of 200 and 1000 m (Figure 8.5), but shallower records also exist from Norwegian fjords (Fosså *et al.*, 2002). In UK waters, the distribution of the cold-water coral *Lophelia pertusa* has been recorded mainly off the continental shelf. Most records are from the Sea of the Hebrides, west of Scotland. These reefs were first mapped in 2003 and are known as the Mingulay Reef Complex (Roberts *et al.*, 2005, 2009b). Roberts *et al.* (2009b) confirmed the distribution of live coral-reef areas at 120–190 m depth. Distinctive mounded bathymetry was formed by reefs of *L. pertusa*, with surficial coral debris dating to almost 4000 years BP (Figure 8.5). Guinotte *et al.* (2006) estimated that the calcification of ca. 70% of the cold-water corals worldwide will be affected by predicted ocean acidification within the next 100 years. Unfortunately, no experimental results on the effect of acidification on cold-water corals have yet been published (Turley *et al.*, 2007). However, palaeo-ecological studies have already revealed that acidification events 50 million years ago, at ranges similar to those predicted for future changes, resulted in the extinction of a substantial proportion of benthic calcifiers (Zachos *et al.*, 2005).

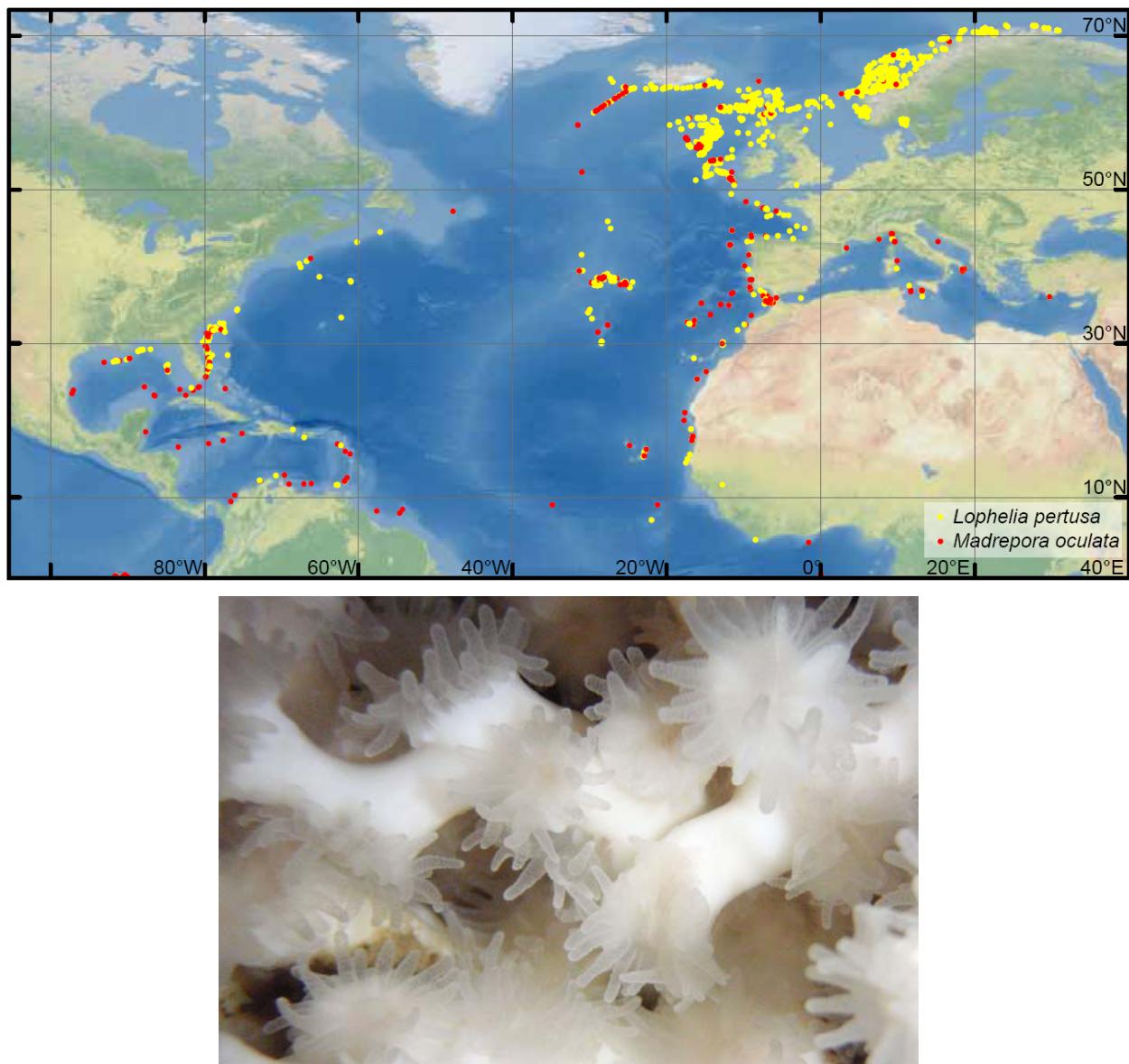


Figure 8.5. Upper panel: Distribution of *Lophelia* and *Madrepora* reefs throughout the North Atlantic (map plotted by J. Titschack; cold-water corals extracted from version 2.0 of the global points dataset compiled by UNEP World Conservation Monitoring Centre (UNEP-WCMC) from various scientific institutions, 2006). Lower panel: Polyps of the cold-water coral *Lophelia pertusa* collected at Mingulay Reef Complex. (Courtesy of Murray Roberts.)

Some studies on other calcareous organisms, such as echinoderms, bivalves, barnacles, foraminifera, and gastropods, suggest that they will also experience difficulties in the formation (calcification) of their shells and skeletons (see references in Table 8.1). Shell construction in echinoderms in particular is severely affected. This may, even on a global scale, have unforeseen effects because echinoderms contribute a substantial part of the global production of carbonate (Lebrato *et al.*, 2010). Laboratory experiments conducted under normal and reduced pH, demonstrated the effects of acidification on the brittlestar *Amphiura filiformis*. These echinoderms managed to rebuild missing arms, although their skeleton suffered from this activity. The need for more energy provoked brittlestars in more acidic water to break down their muscles. At the end of 40 days, their intact arms had 20% less muscle mass than those from normal seawater (Wood *et al.*, 2008). Other physiological processes, such as fertilization success, developmental rates, and larval size, may reduce with

increasing CO₂ concentrations (Kurihara and Shirayama, 2004), eventually leading to increased mortality of the affected organisms.

Most existing studies have focused on organisms that live on or above the seabed, which were assumed to be most susceptible; little is known about the sensitivity of the benthic infauna (Widdicombe and Spicer, 2008). Recent experiments have identified significant variability in the pH sensitivity of a number of different benthic groups. Even among organisms that depend on CaCO₃ structures, variability in tolerance has been observed, with echinoderms displaying less tolerance of pH change than molluscs (Shirayama and Thornton, 2005). Some infaunal species, however, inhabit naturally hypoxic and hypercapnic environments (e.g. Atkinson and Taylor, 1988), and they are able to tolerate a lower pH (e.g. the polychaete *Nereis virens* tolerates a pH as low as 6.5; Batten and Bamber, 1996; Widdicombe and Needham, 2007), whereas others may temporarily compensate against a lower pH, but are susceptible to long-term exposure (Table 8.1). Benthic species have different acid–base regulation abilities, leading to the prediction that some species with high metabolic rates may be more severely affected by ocean acidification because oxygen binding in their blood is more pH sensitive (Pörtner and Reipschläger, 1996).

Differential effects between species may lead to major changes in the composition of the benthic community, as some species are severely affected and other less so. A number of ongoing large research projects are currently addressing the effects of ocean acidification on the physiology of benthic organisms, such as molluscs and echinoderms (e.g. the European Project on Ocean Acidification (EPOCA), Biological Impacts of Ocean Acidification (BioACID), UK Ocean Acidification Research Programme (UKOARP), and Mediterranean Sea Acidification (MedSeA)). Although effects on biodiversity are predicted by many authors, published evidence to support this contention is scarce. Hall-Spencer *et al.* (2008) demonstrated a large biodiversity loss of 30% in the benthic community associated with a gradient of pH from 8.2 to 7.8 away from hydrothermal vents in the Mediterranean that provided a natural CO₂ source. Prediction of the long-term implications for the diversity of marine organisms and for ecosystem functioning at larger scales is challenging (Widdicombe and Spicer, 2008).

Table 8.1. Published reactions of benthic species to increased CO₂ levels and low pH. Extended from Table 1 in Fabry *et al.* (2008) and other sources listed in the table.

TAXA	SPECIES	DESCRIPTION	CO ₂ SYSTEM PARAMETERS	SENSITIVITY	REFERENCE	
Mollusca	<i>Haliotis laevigata</i>	Greenlip abalone	pH 7.78; pH 7.39	5 and 50% growth reductions	Harris <i>et al.</i> (1999)	
	<i>Haliotis rubra</i>	Blacklip abalone	pH 7.93; pH 7.37	5 and 50% growth reductions	Harris <i>et al.</i> (1999)	
	<i>Mytilus edulis</i>	Blue mussel	10 000 ppmv	pH 7.1	Shell dissolution	Lindinger <i>et al.</i> (1984)
				pCO ₂ 740 ppmv	25% decrease in calcification rate	Gazeau <i>et al.</i> (2007)
				pH 6.6	100% mortality within 30 days	Bamber (1990)
	<i>Mytilus galloprovincialis</i>	Mediterranean	pH 7.3 ~ 5000 ppmv	Reduced metabolism, growth rate	Michaelidis <i>et al.</i> (2005)	
	<i>Crassostrea gigas</i>	Pacific Oyster	pCO ₂ 740 ppmv	pH 6.0	10% decrease in calcification rate	Gazeau <i>et al.</i> (2007)
				pH 6.0	100% mortality within 30 days	Bamber (1990)
	<i>Placopecten magellanicus</i>	Giant scallop	pH <8.0	Decrease in fertilization and embryo development	Desrosiers <i>et al.</i> (1996)	
	<i>Tivela stultorum</i>	Pismo clam	pH <8.5	Decrease in fertilization rates	Alvarado-Alvarez <i>et al.</i> (1996)	
	<i>Pinctada fucada martensii</i>	Japanese pearl oyster	pH 7.7	pH 7.4	Shell dissolution, reduced growth	Reviewed in Knutzen (1981)
				Ω _{arag} =0.3	Increasing mortality	
<i>Mercenaria mercenaria</i>	Clam	Ω _{arag} =0.3	Juvenile shell dissolution, leading to increased mortality	Green <i>et al.</i> (2004)		
<i>Strombus lohuanus</i>	Gastropod	pH 7.9	Survival rate significantly lower	Shirayama and Thornton (2005)		
Arthropoda	<i>Cancer pagurus</i>	Edible crab	1% CO ₂ ~ 10 000 ppmv	Reduced thermal tolerance, aerobic scope	Metzger <i>et al.</i> (2007)	
	<i>Porcelana platycheles</i>	Porcelain crab	pH 7.4	After 40 days no effect detected	Calosi <i>et al.</i> (2009)	
	<i>Callinassa</i> sp.	Mud shrimp	pH 6.3	Tolerant	Torres <i>et al.</i> (1977)	
	<i>Necora puber</i>	Swimming crab	pH 6.16	100% mortality after 5 days		
	<i>Amphibalanus amphitrite</i>	barnacle	pH 7.4–8.2	Weakening of shell	McDonald <i>et al.</i> (2009)	
	Echinodermata	<i>Strongylocentrotus pupuratus</i>	Sea urchin	pH ~6.2–7.3	High sensitivity inferred from lacking of pH regulation and	cf. Burnett <i>et al.</i> (2002)
<i>Psammechinus miliaris</i>		Sea urchin		Passive buffering via test dissolution during emersion	Spicer (1995); Miles <i>et al.</i> (2007)	
<i>Hemicentrotus pulcherrimus</i>		Sea urchin	~500–10 000 ppmv	Decreased fertilization rates, impacts larval developments	Kurihara and Shirayama (2004)	
<i>Echinometra mathaei</i>		Sea urchin				
<i>Cystechinus</i> sp.		Deep-sea urchin	pH 7.8	80% mortality under simulated CO ₂ sequestration	Barry <i>et al.</i> (2002)	
Sipuncula	<i>Sipunculus nudus</i>	Peanut worm	1% CO ₂ 10 000 ppmv	Metabolic suppression	Pörtner and Reipschläger (1996)	
				Pronounced mortality in 7-week exposure	Langenbuch and Pörtner (2004)	
Polychaeta	<i>Nereis virens</i>		pH 6.5	Tolerant	Batten and Bamber (1996)	
Nematoda	<i>Procepalotrix simulus</i>		pH <5.0	Tolerant	Yanfang and Shichum (2005)	
Foraminifera	<i>Marginoptera kudakajimensis</i>		pH 7.7–8.3	Decline in calcification rate, possibly precluding survival	Kuroyanagi <i>et al.</i> (2009)	

8.3.4 Sea-level rise: coastal squeeze

In many European estuaries, extensive areas of intertidal habitat could disappear in future as a result of rising sea levels that squeeze tidal flats against established sea defences (Fujii and Raffaelli, 2008). Increasingly, beaches are also becoming trapped between human development on land and rising sea levels (Schlacher *et al.*, 2007). Over the past century, for example, there has been a landward encroachment of the low-water mark along 67% of the eastern coastline of the UK (Taylor *et al.*, 2004). This phenomenon is better known as “coastal squeeze” (Doody, 2004). The impact of coastal squeeze on marine benthic organisms is more complex than merely the loss of habitat. Various associated environmental changes, such as steepening of the intertidal slope, sediment coarsening, and upstream saline water intrusion in estuarine environments, might also be expected (Fujii and Raffaelli, 2008).

Hosting a rich benthic fauna, fulfilling various ecological functions (McLachlan and Brown, 2006), and providing various goods and services to mankind (Beaumont *et al.*, 2007; Rönnbäck *et al.*, 2007), intertidal systems may be impoverished by coastal squeeze. In the Humber Estuary, UK (Fujii and Raffaelli, 2008), for example, model simulations demonstrated that a sea-level rise of 0.3 m could result in a 23% loss of macrobenthic biomass. Some nuances are, however, needed here: in the Wadden Sea, sea-level rise is expected to result in increased amounts of intertidal zoobenthos in areas with predominantly high tidal flats, whereas declines are expected in lower-lying areas (Beukema, 2002). However, such changes will occur only if sea-level rise proceeds too rapidly to be compensated by extra sedimentation. Sea-level rise is further expected to not only cause a shift in the position of the intertidal zones but also to narrow or broaden them and, in this way, to affect total biomass and productivity of the benthos. In some cases (e.g. on the Basque coast), human pressures during the 20th century overwhelmed the effects of sea-level rise on benthic habitats because they were much more dominant in intensity and extension (Chust *et al.*, 2009).

Human interventions (e.g. shoreline armouring, beach nourishment) to combat changes in beach environments, such as erosion and shoreline retreat, may add to the ecological impact of sea-level rise (Schlacher *et al.*, 2007). As demonstrated by various monitoring programmes, the *in situ* ecological consequences of such engineering activities on beaches can be substantial at local scales and include loss of biodiversity, productivity, and critical habitats, as well as modifications of the subtidal zone, which is an important recruitment zone for many sandy-beach animals (e.g. Speybroeck *et al.*, 2006). In addition, *ex situ* effects on the benthos can be observed. In the case of beach nourishment, fill-sands are usually collected offshore, causing various impacts on the offshore benthos, such as shifts towards lower size classes of nematodes (Vanaverbeke *et al.*, 2003), with a consequent recovery of 4.5 to more than 10 years (Foden *et al.*, 2009). In cases of shoreline armouring, the high demand for clay as soil material for dikes has been shown to cause local destruction of saltmarsh ecosystems at clay excavation sites, with the first signs of terrestrial recovery evident from 8 years onward (Vöge *et al.*, 2008).

8.4 Climate-variability proxies (North Atlantic Oscillation)

Climate-change effects on benthos can rarely be studied at the long time-scales of climate. In this context, cores from marine sediments act as a natural archive, reflecting pelagic and benthic processes from past millennia (Hald, 2001). Changes in calcareous nanoplankton communities in the eastern North Atlantic during the past

130 000 years, preserved in sediment cores, record the major climate-change events of the past (Stolz and Baumann, 2010). Comparisons between planktonic and benthic foraminiferan communities in the cores show that changes in plankton were also evident in the benthic environment, indicating a strong benthic–pelagic coupling (Bauch *et al.*, 2001). Thus, palaeoecological studies demonstrate that past climate-change events have substantially affected pelagic and benthic species and communities.

In order to reveal links between present-day benthic species or communities and climate on shorter time-scales, comparisons are made with proxies for climate variability. One of these proxies, important for the North Atlantic region, is the NAO. The NAO is a pattern of atmospheric variability in the North Atlantic region, and the derived NAO index is a measure of the strength of the sea-level air-pressure gradient between Iceland and the Azores (see Sections 2 and 10). The NAO index represents an integration of several climatic variables (e.g. water temperature, prevailing wind direction and speed, precipitation). Changes in biomass, abundance, community structure, and function of benthic systems, directly or indirectly related to variability in the winter NAO index (Figure 8.6), have been described from a number of different areas in recent decades (Frid *et al.*, 1996; Kröncke *et al.*, 1998, 2001; Frid *et al.*, 1999, 2009b; Wieking and Kröncke, 2001; Dippner and Kröncke, 2003; Franke and Gutow, 2004; Schröder, 2005; Rees *et al.*, 2006; Van Hoey *et al.*, 2007; Neumann *et al.*, 2008).

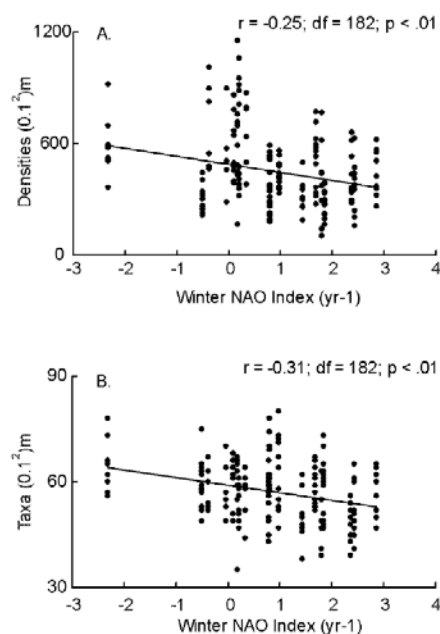


Figure 8.6. Example of the relationship between (A) average density and (B) numbers of taxa across the annually sampled stations off the Tyne (UK) and the North Atlantic Oscillation (NAO) index for the preceding year. (Source: Rees *et al.*, 2006.) Note that opposite relationships with the NAO index were also found (see text).

In the North Sea, severe winters, which are associated with a low NAO index, as occurred in 1962/1963, 1978/1979, and 1995/1996, led to a marked reduction in the number of benthic species and a shift in community structure, not only in the intertidal and shallow subtidal but also in deeper offshore areas (Ziegelmeier, 1964; Beukema, 1979; Kröncke *et al.*, 1998; Armonies *et al.*, 2001; Reiss *et al.*, 2006; Neumann *et al.*, 2009). The link to cold winters is probably related to increased mortality of sensitive benthic species. Changes in the frequency of occurrence of extremely cold

winters may alter the structure of benthic communities in the long term, depending on the resilience of the community. In the German Bight, the benthos changed on a decadal scale between the 1970s, 1980s, and 1990s, again with a substantial decline in diversity and abundance after severe winters (Schröder, 2005; Rehm and Rachor, 2007). On the other hand, mild meteorological conditions connected with a positive NAO index resulted in an increase in the abundance, species number, and biomass of the macrofauna (Beukema, 1990; Kröncke *et al.*, 2001).

Kröncke *et al.* (1998, 2001) described changes in a nearshore macrofauna community in the southern North Sea and found that total abundance, species numbers, and total biomass in spring correlated significantly with the NAO index, with SST being the mediator between climate and fauna. Furthermore, Dippner and Kröncke (2003) demonstrated in a modelling study that atmospheric winter circulation over the North Atlantic area is an optimal predictor in forecasting the structure of macrofaunal communities the following spring (Figure 8.7), although since 2000, this correlation and hence the predictability of the structure of the macrofauna community disappeared (Dippner *et al.*, 2011). Significant correlations with the NAO index were found for species diversity in the western Baltic and an Arctic fjord in Svalbard (Beuchel *et al.*, 2006; Gröger and Rumohr, 2006) and for abundance and biomass in the Skagerrak and Kattegat (Tunberg and Nelson, 1998).

All of these examples from correlative research approaches demonstrated that climate variability may have an important influence on benthic community structure, abundance, and species diversity, but the factors causing these changes are not well understood. For example, mortality can be affected by winter temperatures and disturbance of the entire community by storms (see above); both climatic parameters are correlated with the NAO index. Also, major changes in dominant wind direction are related to changes in the NAO. Thus, changes in benthic communities may occur through a variety of single mechanisms or combinations of mechanisms, which may also act synergistically or antagonistically. For example, Wieking and Kröncke (2001) described the effects of the NAO index on North Sea ecosystem processes via a temperature increase or decrease and via changes in hydrodynamics affecting primary production, larval supply, sediment composition, and food availability. Indirect effects of climate change may also occur through changes in food supply to the benthic system.

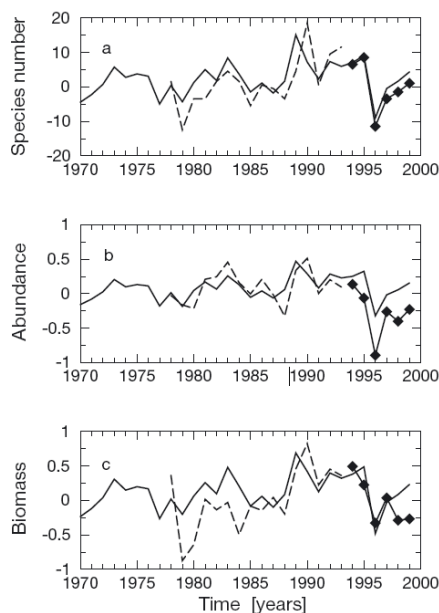


Figure 8.7. Time-series anomalies of macrofauna in the southern North Sea. Anomalies of (a) species number m^{-2} , (b) log abundance m^{-2} , and (c) log biomass m^{-2} predicted from the NAO winter index (solid line). Dashed line = observations in the fitting period 1978–1993; solid line with \diamond = observations in the forecast period 1994–1999. (Source: Dippner and Kröncke, 2003.)

The relationship between the NAO and benthic communities also seems to depend on local environmental conditions and species composition. Species diversity, for example, was found to be positively as well as negatively correlated with the NAO index (Dippner and Kröncke, 2003; Beuchel *et al.*, 2006; Rees *et al.*, 2006). Furthermore, some benthic communities respond more slowly to climate variability than others (e.g. Hinz *et al.*, 2011). This indicates that the autecology and biogeography of the local species pool plays a significant role in the response of benthic communities to climate variability, which is logical because climate stressors act on individual organisms and not on entire communities.

A number of patterns and changes seen in benthic communities are comparable with those found in plankton (e.g. Beaugrand, 2004; Bonnet and Frid, 2004; Wiltshire and Manly, 2004; Kirby *et al.*, 2007; McQuatters-Gollop *et al.*, 2007) and in fish stocks (Ehrich and Stransky, 2001; Reid *et al.*, 2001b; Kirby *et al.*, 2006; Ehrich *et al.*, 2007). Reid and Edwards (2001) and Beaugrand (2004) concluded that a regime shift occurred at the end of the 1980s, which was directly related to a significant increase in the NAO index (see Section 10).

8.5 The effects of human disturbances and climate change

Climate influences in marine systems can be distinguished as change and variability (Perry *et al.*, 2010) that together alter species and ecosystems. Climate change is considered to affect large-scale processes over the long term, whereas climate variability refers to temporal scales ranging from years to decades. The level of variability depends on the inherent characteristics of marine ecosystems (Perry *et al.*, 2010). This variability is largely the result of climate forcing, a combination of internal dynamics (e.g. interactions between species) and human activities, such as fishing, sand extraction, dredging, and construction (Perry *et al.*, 2010). The magnitude and effect of human activities on benthic systems has been studied in detail (Rachor, 1990; Frid *et al.*, 1999; Boyd *et al.*, 2005; Birchenough *et al.*, 2006; Rees *et al.*, 2006;

Birchenough *et al.*, 2010), but there is still limited understanding of interactions between these disturbances and climate variability and change.

The benthic communities of the North Sea have been studied for many decades. These studies have concentrated on describing the structure of communities and changes caused by human disturbance. There are clear gaps in understanding the multiple effects from human disturbance (e.g. fishing, aggregate extraction) in combination with those caused by climate change. Some of the examples outlined below have begun to explore these relationships and highlight the need for integrated approaches in order to determine relative responses to climate and human disturbance.

The benthic community structure in the western North Sea (northeast coast of England) and the eastern North Sea (Skagerrak) exhibited a transition during the late 1970s. This transition coincided with observed changes between the 1970s and 1980s in the zooplankton community in the western and eastern North Sea (Austen *et al.*, 1991; Evans and Edwards, 1993). It has been shown that changes in pelagic and benthic ecosystems are linked when climate change is the common cause (Kirby *et al.*, 2007, 2008, 2009). Long-term analysis of the North Sea pelagic system has identified yearly variations in larval abundance of the benthic phyla Echinodermata, Arthropoda, and Mollusca in relation to SST. Furthermore, larvae of benthic echinoderms and decapod crustaceans increased after the mid-1980s, coincident with a rise in North Sea SST, whereas bivalve larvae underwent a reduction (Kirby *et al.*, 2008). If climate change is affecting planktonic communities, inevitably there will be repercussions for benthic systems.

Off the northeast coast of England, Buchanan (1963) initiated the “Dove Time-series” (Buchanan *et al.*, 1986) during the 1960s at two stations (M1 and P). These long-term series have been used to assess natural fluctuations in benthic communities alongside fishing impacts (Figure 8.8; Frid *et al.*, 2009a). Research has also highlighted additional influences on the benthos resulting from a combination of phytoplankton supply and climatic effects (Frid *et al.*, 2009b).

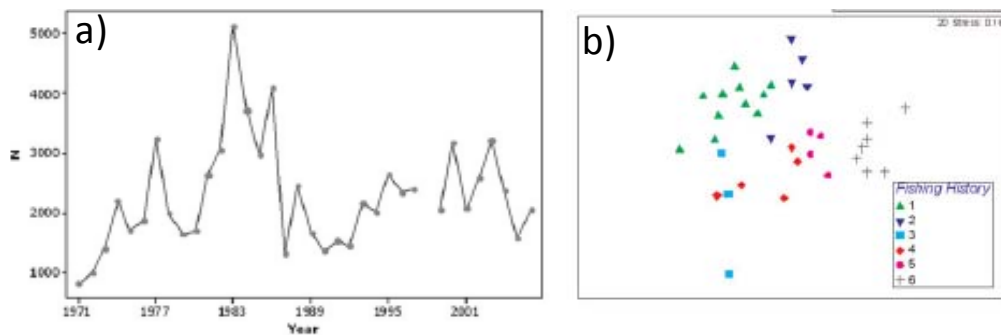


Figure 8.8. (a) Time-series plot for macrofaunal abundance (individuals m^{-2}) at the Dove Time-series Station P (west-central North Sea), based on at least five replicates, and (b) non-metric multidimensional scaling ordination of Bray-Curtis similarities in genera comparison of the macrobenthos at Station P for 1971–2006, showing variation by fishing history (fishing intensity increased in periods 1 and 2, peaked in period 3, and has subsequently declined through periods 4, 5, and 6; Source: Frid *et al.*, 2009a.)

Callaway *et al.* (2007) compared the North Sea epibenthos between periods at the start and end of the 20th century (1902–1912, 1982–1985, and 2000) and described a biogeographic shift in many epibenthic species. Most of these changes were observed in the epibenthos before the 1980s; since then, the communities have become more

resilient to long-term impacts (trawling gear removes large-bodied epifauna, such as *Modiolus modiolus* and *Aequipecten opercularis*, Figure 8.9). The reasons for the changes in the distribution of the epibenthos were considered to be a combination of high trawling effort, climate change, and eutrophication.

Recent evidence indicates that climate change is adding complexity to climate variability, and that overfishing is a global problem for marine systems. It has been suggested that marine species have developed the capacity to cope with climatic variability over long periods of time (Planque *et al.*, 2010). New approaches, based on the structure and properties of fish communities, have been proposed by Jennings and Brander (2010). These approaches have concentrated on understating underlying processes that determine size-structure of fish communities (e.g. metabolic scaling, predator–prey interactions, and energy transfer via foodwebs). This information is used to determine the size structure and productivity of the community for different climate scenarios. These tools potentially allow predictions of the effect of climate change on fish communities and thus on fisheries. This level of information is important to understand the dependence of fish communities on benthic systems. In the event that climate change could alter benthic systems, these effects could have repercussions for higher trophic levels (e.g. fish consumption).

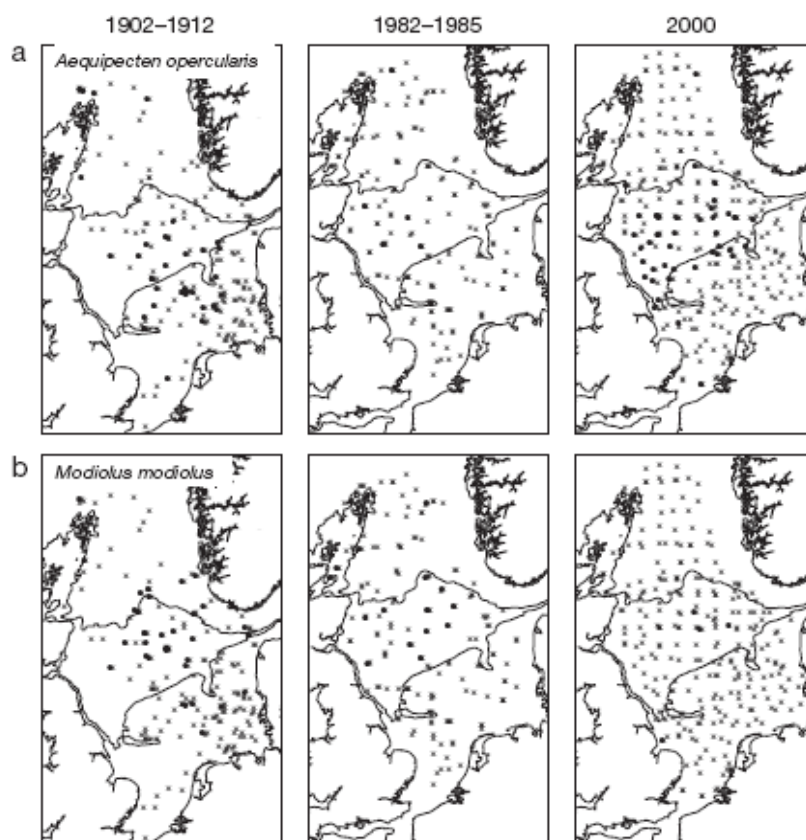


Figure 8.9. Trends in the spatial occurrence of (a) *Aequipecten opercularis*, and (b) *Modiolus modiolus*. Species with a reduced presence in 1982–1985 and 2000 compared with 1902–1912; • = species present, x = sampled station. (Source: Callaway *et al.*, 2007.)

In the west-central North Sea, Rees *et al.* (2006) monitored benthic communities at a former sewage-sludge disposal site off the northeast coast of England (stations located in the proximity of the Dove Time-series station P). Sewage-sludge disposal at sea was phased out in 1998 in UK waters. Long-term datasets at the former sites

are useful because they provide information on benthic distributions in the recovery phase after the disposal of sewage ceased (Figure 8.10). Analysis of these datasets demonstrated a temporal correlation between faunal measures and winter values of the NAO for the preceding year (Figure 8.6). The densities and varieties of species tended to be lower in warmer winters characterized by westerly airflows, as occurred in the 1990s. This represents a pattern of response where taxa with a more northerly (cold-water) distribution are not compensated by an increase in species with a southerly association. Overall, macrobenthic responses following the cessation of sewage-sludge disposal in this area were predictable in relation to mild organic enrichment. A decline in species number to references levels was observed after three years.

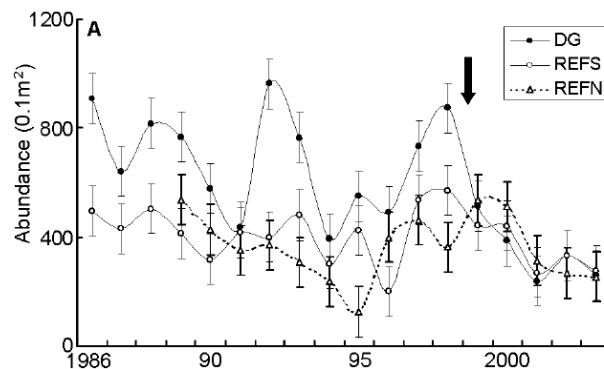


Figure 8.10. Annual trends in the abundance of the macrobenthos at the former Tyne sewage-sludge disposal site. The arrows indicate the date when the disposal at sea stopped. DG = disposal ground; REFS = south reference; REFN = north reference. (Source: Rees *et al.*, 2006.)

Additional examples of research conducted on climate and human activities in both coastal (Garmendia *et al.*, 2008) and estuarine areas (Pérez, L., *et al.*, 2009) in the Basque Country (northern Spain) has demonstrated that benthic variability is mainly explained by climate factors in coastal areas, whereas for estuarine assemblages inhabiting the same region, the observed changes were driven primarily by anthropogenic activities (e.g. wastewater discharges, habitat alteration). This indicates that human activities can mask the effects of climate change on benthic systems in estuaries, but have less effect offshore.

8.6 Conclusions

A series of mechanisms have been identified in this review by which benthic communities may be influenced by climate change, although a direct link between these effects can only be demonstrated for a limited number of cases. However, strong evidence for direct links between environmental factors and benthic organisms are evident for more cases. As climate change will affect many of these factors, it will also alter the benthos.

A number of examples of latitudinal shifts in the distribution of benthic species, largely resulting from increases in sea temperature, have been described for the Northeast Atlantic, with most examples from fauna on intertidal hard substrata. In intertidal and subtidal soft sediment, the rate of shift in distribution may be up to 50 km decade⁻¹. Under climatic influences, some key organisms, such as habitat-forming or parasitic species, will shift north of their normal distribution, and substantial impacts are to be expected. It has been suggested that, in some cases, marine benthic species have developed the capacity to cope with “stressors” (e.g. climatic variability or other pressures) over long periods of time.

A variety of biotic and abiotic factors interact with life-history features of benthic species, which may be directly or indirectly influenced by climate change. As a consequence, benthic ecosystems show complex interactions and species-specific responses in relation to climate change. A temporal mismatch between primary producers and consumers, for example, can have cascading effects on the entire foodweb, with potential effects on both larval and juvenile benthic organisms. Altered hydrodynamics on the other hand may (i) affect the distribution of benthic species, owing to changes in the dispersion of (post-) larval and/or juvenile benthic organisms (altered ocean currents), (ii) contribute to a spatial and temporal extension of anoxic and hypoxic zones (stratification), and/or (iii) affect benthic communities, especially in intertidal and shallow areas (coastal squeeze, increased storminess).

The effects of ocean acidification on coral reefs are well known, but as this process intensifies, it might also affect all benthic and other calcareous organisms. Next to calcification problems, other physiological processes (e.g. fertilization success) may be hampered, and mortality may increase as a result of ocean acidification.

Most of the impacts mentioned above are, however, deductive and, therefore, do not demonstrate a proven link between climate change and benthic ecosystems. In this perspective, lessons can be drawn from the study of the ecosystem impacts of the NAO, a descriptor of present-day climate variability. Statistically significant correlations have been found between the NAO and benthic community structure, species abundance, biomass, and species diversity, but many broke down when using the latest data, indicating that the processes behind these correlations are still unknown. Improved information on the synchronicity of benthic change in relation to other ecosystem components and their responses to human activities is needed in order to understand and confidently describe patterns of benthic responses to climate change. Finally, it is important to highlight that changes in benthic structure will have repercussions on the whole marine ecosystem, with consequences for ecosystem functioning and services, including climate regulation.

8.6.1 Knowledge gaps

Most of the impacts on the benthos from climate change are deductive and/or speculative. In order to improve this situation, the following gaps in knowledge have been identified.

- A causal relationship between a temporal mismatch between benthic species, their food resource, and climate change is difficult to prove, given the relatively poor knowledge of the life cycle of many benthic species.
- The mechanisms behind the cause–effect relationship between benthic ecosystems and the NAO remain largely unknown and need clarification. Other teleconnection patterns (i.e. Eastern Atlantic) could be influential to benthic communities in mid-latitudes (e.g. Bay of Biscay), in which the signature of the NAO is much lower.
- Although causal links between the benthos and hydrodynamics have been described, knowledge of the relationship between climate change, hydrodynamics, and benthos is still based on circumstantial evidence.
- The effects of climate change are largely the outcomes of processes acting on individuals, but are generally observed at population, community, and ecosystem levels. Therefore, it is necessary to concentrate efforts on the description of changes to species and complement these observed responses to other levels of the ecosystem.

- Almost all studies on the effect of ocean acidification and the benthos focus on specific taxa over very limited areas and time. At present, integrated, large-scale studies focusing on climate change, ocean acidification, and human activities are lacking.

8.6.2 Research needs

Evidence provided in this review has highlighted scientific gaps in this rapidly developing climate-change research. There is a need for a “three-track” approach to future studies of how climate change impacts benthic ecosystems. These key stages are (i) integrated monitoring, (ii) experiments, and (iii) modelling.

Our conceptual framework (Figure 8.2) highlights the importance of a well-designed assessment procedure that will reliably detect changes in the benthic ecosystem in order to meet the high-level objectives associated with international policies (e.g. MSFD). There is, therefore, a need for long-term, large-scale, integrated inventories and monitoring in order to provide the background information necessary to test and modify current hypotheses that are based on short-term and localized data. Standardized national monitoring strategies need to be coordinated in order to permit a regional assessment of the effects of climate change on the benthos (see also Birchenough and Bremner, 2010; Dauvin, 2010). These studies should not only focus on the classic structural descriptors of benthic communities, such as abundance and species richness, but should also address population genetics. In this way, the connectivity between populations, or species–species and species–environment interactions, may be explored in order to increase general knowledge of life cycles and the functioning of benthic ecosystems. Empirical programmes should be complemented with experimental studies (e.g. mesocosm experiments), which will lead from general observation to a wider understanding of specific responses. Furthermore, this will contribute to our understanding of the life history of benthic organisms, which is needed to explain population dynamics and to predict benthic ecosystem responses. This approach will improve our understanding of change and will allow the formulation of predictions against future scenarios.

The ability to make predictions about the responses of subtidal communities to future climate change is poor. Current capabilities to generate such information through predictive modelling techniques are mainly targeted at fish populations. These methods need to be expanded to benthic systems.

8.7 Acknowledgements

Work on this section was initiated and facilitated by the ICES Benthos Ecology Working Group (BEWG). The authors thank the colleagues of the BEWG and ICES Study Group on Climate-related Benthic Processes in the North Sea (SGCBNS) for providing valuable information during the compilation of this section, for stimulating discussions during meetings, and for fine-tuning earlier versions of this chapter. We are indebted to André Freiwald (Senckenberg Institute) for providing the distribution map of cold-water corals and to Jason Hall-Spencer (Plymouth Marine Laboratory) and Murray Roberts (Heriot Watt University) for providing images of *Eunicella verrucosa* and *Lophelia pertusa*.