Advanced Review

Climate change and marine benthos: a review of existing research and future directions in the North Atlantic

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There is growing evidence that climate change could affect marine benthic systems. This review provides information of climate change-related impacts on the marine benthos in the North Atlantic. We cover a number of related research aspects, mainly in connection to two key issues. First, is the relationship between different physical aspects of climate change and the marine benthos. This section covers: (a) the responses to changes in seawater temperature (biogeographic shifts and phenology); (b) altered Hydrodynamics; (c) ocean acidification (OA); and (d) sea-level rise-coastal squeeze. The second major issue addressed is the possible integrated impact of climate change on the benthos. This work is based on relationships between proxies for climate variability, notably the North Atlantic Oscillation (NAO) index, and the long-term marine benthos. The final section of our review provides a series of conclusions and future directions to support climate change research on marine benthic systems. © 2015 John Wiley & Sons, Ltd.

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INTRODUCTION

The North Atlantic plays a major role in climate change as it is a key node in the thermohaline circulation. The inflow of cold deep water into the northern North Atlantic and the consequent transport

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of warm surface water to the north ensure that Europe is much warmer than comparative latitudes elsewhere. This process allows the heat to be transferred to the Arctic and contributes to the melting sea ice and to the potential release of methane. The North Atlantic contains about a quarter of the anthropogenic carbon stored in the oceans as a result of an inflow of depth water and the deep mixing that occurs in this system.

Climate change is having an effect in the marine environment. As these changes are being observed, it is imperative to understand how marine systems will be affected under changing climate conditions. Our review concentrates on climate change effects observed in the benthic communities of the Atlantic region over the last hundred years.[1–9] Marine benthic communities are especially suited for long-term comparative investigations as many of the constituent species are sessile or have low mobility, are relatively long lived and so can integrate the effects of environmental change over time. The macrobenthos has an important functional role in the reworking of sediments, provides nutrients and food to higher trophic groups and allows the provision of habitats through habitat engineering species, e.g., Refs 10–14.

Given the important ecological role of benthic communities it is essential to understand and predict how they are likely to respond to climate change. Climate change is considered to be a complex problem, as conceptually summarized by the ICES Benthos Ecology Working Group (Ref 3; Figure 1). We acknowledge that the study of all of these processes is not trivial and there will be a need to undertake research with multidisciplinary teams to answer some aspects highlighted in this conceptual framework. Figure 1 is used to describe the main abiotic (e.g., storms and habitat loss) and biotic (e.g., latitudinal shifts of species, larval supply, and match/mismatch) effects that will be affecting benthic and directly interconnected (e.g., plankton) systems. It is clear that there are some wider aspects (e.g., temperature, OA, and anthropogenic interactions) will have a wider influence across all of the components in the framework. Some knowledge is already available either through directly or circumstantially evidenced effects of climate change onto the benthos, but there are still aspects that require further research. The way this review is structured is looking at the (expected) 'knowns' and consequently also the 'unknowns', for example looking at existing literature on how species are changing their distributions in response of changes in environmental conditions (e.g., temperature). Furthermore, the effects of sea level rise in intertidal areas (known as 'the coastal squeeze phenomenon') could severely affect benthic habitats with direct repercussions for the loss of benthic function and with wider effects for other ecosystem components.

Our synthesis also summarizes the current state of play with regard to OA, as evidence indicates that the oceans are becoming more acidic. Some studies report that there will be some effects for dedicated groups, whereas there are other studies that do report limited effects and consequences for benthic systems. This is an active research area, producing targeted research to understand organisms' responses to pH changes in the laboratory and field studies.

We have included a specific emphasis on knowledge gained from former benthic long-term series studies on the effects of the North Atlantic Oscillation (NAO) as a proxy for climate variability, as this information can be related to similar studies over other ecosystem components, providing useful insights on the changes observed in marine benthic communities over long-term assessments.

Finally, the conclusions section provides an overview of the current work and also a recommendation list of gaps where further research is needed.

DIRECT AND CIRCUMSTANTIAL EVIDENCE OF CLIMATE CHANGE EFFECTS

Temperature Change-Driven Effects

Distributional Shifts

Biogeographic studies have been the focus of much ecological research that has identified a link between the distribution of marine species and mean sea surface isotherms.[15,16] Oceanic changes in temperature due to global climate change are causing poleward shifts in the latitudinal distribution of species toward cooler marine environmental regions throughout the North Atlantic.[17] Such distributional shifts have already been found for several components of the marine ecosystem: fish,[18–21] phytoplankton,[22,23] zooplankton,[24–26] and also benthos.[27–29]

There is clear evidence of change in the distribution and abundance of benthic species in response to seawater temperature change, e.g., in the North Atlantic.[5,7,29–31] Most changes are initially seen to be occurring at the edge of ranges, where organisms are more likely to be physiologically stressed. Intertidal organisms, for example, have shown some of the fastest responses to climate change as they are living close to their physiological tolerance limits. Evidence of a strong climatic influence has been observed in the abundances of the co-occurring intertidal Lusitanian barnacles *Chthamalus montagui* and

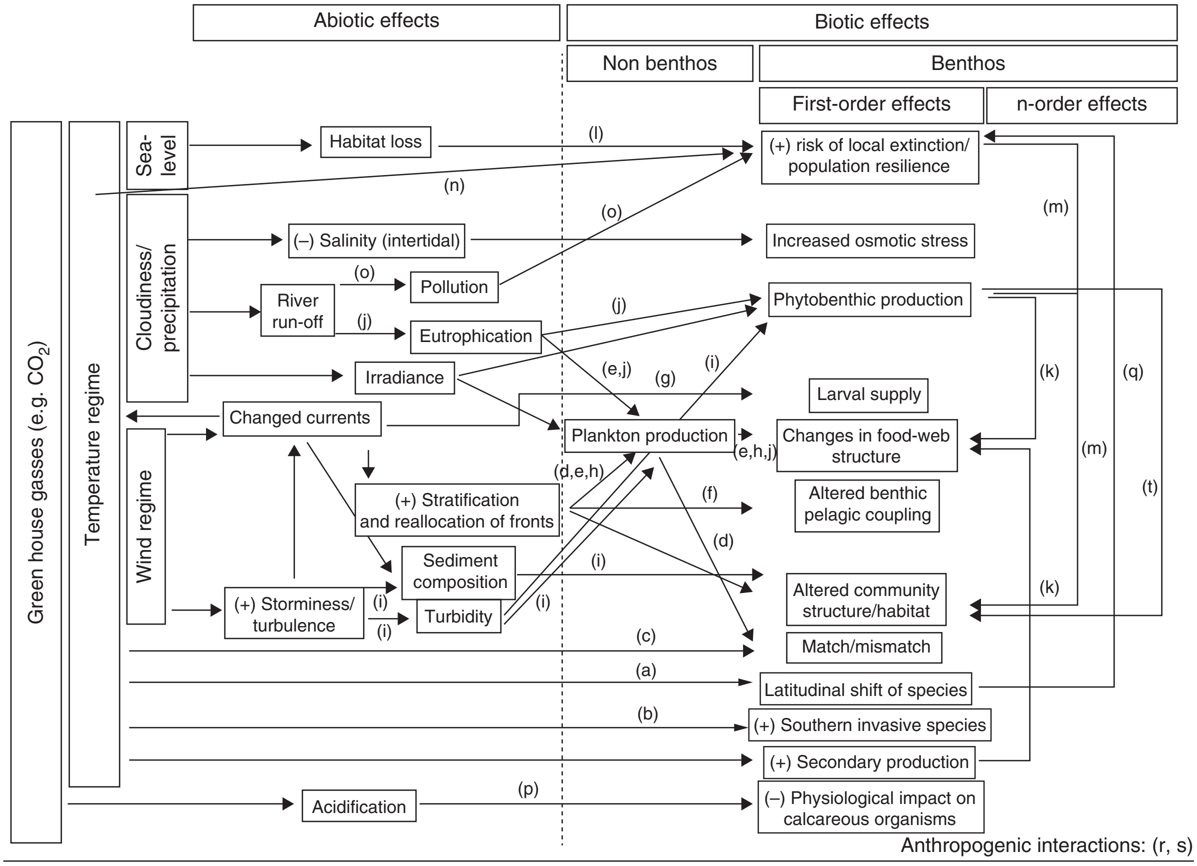


FIGURE 1 | Conceptual diagram of the effects of climate change and benthic interactions[196] illustrating the influence of increased CO_2 and temperature (left panel) and how these factors could directly affect biotic and abiotic components (Reprinted with permission from Ref 3. Copyright 2009 ICES [BEWG]).

Chthamalus stellatus and the Boreal species *Semibalanus balanoides* over the past 60 years in the UK. *S. balanoides*, considered a dominant competitor, proliferated during cooler periods but has declined significantly due to temperature-driven competitive dominance of the Chthamalids as the marine climate has warmed in recent decades.[32] These changes in abundance translate up to the biogeographic scale, with the southern range limit of *S. balanoides* retreating north within the Bay of Biscay region,[33] and the northern range limit extending in waters off Scotland in response to warming sea temperatures since the 1980s.[27] Models based on a 50-year time-series predict a total disappearance of *S. balanoides* from shores in Southwest England by 2050.[34] Similarly, latitudinal shifts were observed in two other intertidal and shallow subtidal barnacle species. *Solidobalanus fallax*, a West African warm water species not known from European coasts prior to 1994[35] has extended its range along the English Channel in recent decades.[29] *Balanus perforatus*, a Lusitanian species, has extended its range through the eastern English Channel[36] and has now also expanded into the southern North Sea.[37,38] 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.[5] Other examples of intertidal, hard substrate fauna distribution changes linked to changes in temperature comprise the gastropods *Phorcus lineatus*,[27,39] *Gibbula umbilicalis*,[27,39–41] *Testudinalis testudinalis*,[27] and the blue mussel *Mytilus edulis* (Europe[42]; US Atlantic[30]). Though less well-documented, examples of changes in geographic distribution due to temperature change have also been found for subtidal, soft substrate organisms. The decapods *Diogenes pugilator*, *Goneplax rhomboides*, and *Liocarcinus vernalis* have extended their range further into the North Sea during the past decades. These southern species tend to thrive off the Belgian coast during warmer years,[43–46] but have now extended their range further north into Dutch and German waters.[46–49] Barnett[50] further demonstrated that the gastropod *Nassarius reticulatus* has an earlier and faster development in warmer waters. The sudden appearance of the latter species in the 1980s[51] may also be attributed to the temperature increase in coastal waters. Clearly, there is potential for international scientific collaboration to unify some of these observation programs and to share data in order to identify and quantify changes in distribution of these benthic species across wider geographic areas.

Rates of change in distribution of up to 70 km per decade as observed for marine benthic species are much greater than the average rate of range edge shift of 6.1 km per decade documented for terrestrial species,[17,52] but an order of magnitude less than those seen in the plankton in the Northeast Atlantic and North Sea.[53] These different rates may arise from the difference in the degree of connectivity between pelagic, benthic, and terrestrial systems. The integration of knowledge and research on climate change-induced shifts in distribution within and between benthic ecosystems will help to elucidate where synchronicity in change occurs and hence identify and predict major changes.

In addition to these shifts in global distribution patterns, changes have also been observed as infilling of gaps in the species' distribution, continuity, or loss of site occupancy away from range limits, which adds to the local and regional heterogeneity in species distribution patterns. An example of infilling within a biogeographic range is observed for the Lusitanian intertidal, hard substrate limpet *Patella rustica*. This species has colonized a gap in its 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.[54]

In conclusion, many examples of distribution shifts exist for marine benthic species with leading range edges expanding for those of Lusitanian origin, whereas trailing range limits of Boreal species are retreating. Most examples comprise range extensions within intertidal organisms, although some evidence for range extensions in subtidal species was found.[49] Such changes were particularly clear in the break point between Lusitanian and Boreal waters around the UK and northern France. Changes in distribution may finally also comprise infilling of gaps in the species' distribution continuity or loss of site occupancy away from range limits. Because changes in distribution patterns cover wide geographic areas often spanning entire continents, research of distribution shifts would clearly benefit from increased international collaboration. Although the speed at which these shifts take place varies considerably between the terrestrial, planktonic, and benthic ecosystem, research across different ecosystems would help in identifying synchronicity in change, biological mechanisms underpinning such responses and hence (climatic) events better.

Life History Effects in Benthos

Life cycle events of species are greatly dependent on climate-related factors such as temperature, e.g., Ref 55 and may hence be influenced by climate change. These life cycle events include: (1) reproductive output, (2) recruitment and postrecruitment development, and (3) larval transport and settlement, all playing an important role in benthic community structure, diversity, and functioning. A variety of biotic and abiotic factors influence these life cycle processes, of which some are direct (e.g., physiological responses) and others are indirect (e.g., changes in trophic interactions). Studying the timing of these recurring life cycle events in benthic systems and how these are influenced by seasonal and interannual variability could help to understand the effects of climate change on benthos.

Indeed, recent studies have shown that the meroplankton, to which many benthic species belong to during the early stages of their life cycle, is particularly sensitive to increases in sea temperature compared to the holoplankton. Edwards and Richardson[56] showed that the timing of the seasonal peak of meroplankton occurred 27 days earlier (echinoderm larvae 47 days) in the North Atlantic during warmer periods based on a 45-year study period (Figure 2). Figure 2 illustrates the annual peak seasonal abundance 'center of gravity index' of echinoderm larvae from 1958 to 2008 in the central North Sea (i.e., the peak in seasonal

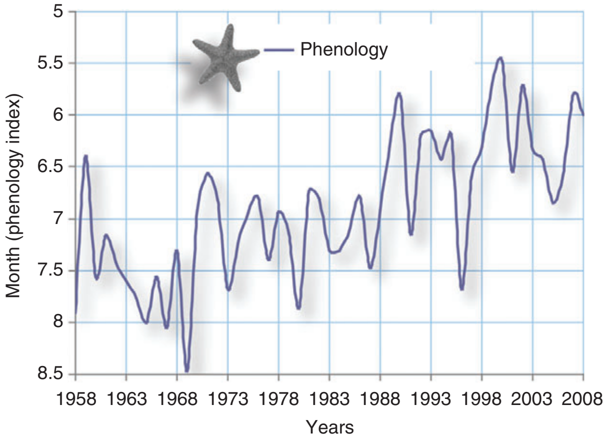


FIGURE 2 | Interannual variability in the peak seasonal development of echinoderm larvae (an indicator of plankton phenology) in the North Sea. The general trend through time is toward an earlier seasonal cycle (Reprinted with permission from Ref 197. Copyright 2009 SAHFOS).

appearance) helping to demonstrate an earlier development of echinoderm larvae.[56] Additionally, the abundance of meroplankton changed in the North Sea from 1958 to 2005, showing an increase of decapod and echinoderm larvae and a decrease of bivalve larvae due to rising sea surface temperature (SST).[57] Similar patterns were also observed for some holoplankton and fish larvae, e.g., Refs 2, 58, 59.

Changes in temperature may influence mortality, reproduction, the onset of spawning, and the embryonic and gonad development of benthic species and may, therefore, alter phenological processes. Changes in the timing of gamatogenesis and spawning of *Echinocardium cordatum*, for example, has been observed in relation to rising sea temperature in the North Sea.[60] In coastal waters of northern Europe, severe winters are often followed by high densities of intertidal bivalve recruits.[61,62] This is partly attributed to a lower metabolism during cold winters, resulting in a higher biomass and the production of more eggs in spring.[61] Rising sea temperature was found to reduce the reproductive output and results in a delay in spawning of intertidal bivalves,[63,64] although the recruit density was highly variable.[65] Other environmental factors related to climate change and temperature rise may have influenced recruitment, such as changes in predation pressure or food availability.[64,66] At present, it is however unknown to what extent changes in the abundance of meroplanktonic larvae and juveniles have repercussions for adult populations, especially as postrecruitment and juvenile dynamics of benthos still are poorly understood. The available evidence demonstrates that these interactions are complex, and it is hence not yet possible to reliably predict the—expectedly species-specific—responses to climate change.

The different responses between ecosystem components to temperature may also lead to indirect effects, resulting in altered competitive or trophic interactions. The timing of the spring phytoplankton bloom has remained rather constant in the North Atlantic and the North Sea, contrary to the earlier arrival of larval meroplanktonic (and holoplanktonic) organism.[56,67] Other factors, which are independent of changes in temperature, such as photoperiod, appear to trigger the timing of the phytoplankton bloom.[68] Phytoplankton biomass has increased in several areas of the Northeast Atlantic during recent decades.[69–71] The concept of mismatch is used to describe the different effects on timing of life history assets associated with the effects of climate change. For benthic organisms, the mismatch scenarios could be most significant during the planktonic phase (in the case of planktotrophic larvae) and postrecruitment phase on the sediment, during which larvae are most dependent on phytoplanktonic food availability.[72] Juvenile benthic organisms, especially those without energy reserves (i.e., nonlecitrophic larvae) and with a higher weight-specific metabolic demand, will be more dependent on food supply and, therefore, more susceptible to starvation during food deprivation as a result of a mismatch due to climate change effects.[72] The match/mismatch hypothesis[73] provides a general and plausible framework for understanding variations in recruitment by means of species phenology, but the hypothesis is difficult to test and has mainly been applied in fisheries science to date.[74,75] To our knowledge, no study of potential mismatches between benthic larvae arrival and planktonic food source productivity was carried out so far, emphasizing the existing lack of knowledge about benthic larvae and recruitment processes in relation to climate change.

The temporal mismatch between primary producers and consumers can have cascading effects at higher trophic levels, as already demonstrated for fish and bird populations[74,76,77] with repercussions on the whole food web structure. Being at the basis of the benthic food web, mismatch effects in the benthos may hence have cascading effects throughout the whole marine food web. The possibility of climate-induced trophic cascades was recently suggested for the coastal marine ecosystem.[78] Effects on key species in food webs, either bottom-up or top-down, have the potential to cause severe ecosystem changes, as effects can act across major ecosystem components, e.g., Ref 79.

Altered Hydrodynamics Effects

The hydrodynamic regime of the North Atlantic Ocean is characterized by a number of physical properties and circulation patterns, which show substantial variability at seasonal to decadal time scales. This variability itself can be affected by climate change, but these effects can only rarely be separated from the natural variation observed in this system.[80]

The physical properties of the water column affect seafloor communities in various direct and indirect ways. Hydrodynamics can directly influence the benthos via the transport and dispersal of larvae, juveniles, and adults, with important consequences for population dynamics[81–83] and can increase mortality due to oxygen depletion (stratification) or storm events. Among the indirect effects, the influence of hydrodynamics on primary and secondary production in the water column and the transport pathways of these food sources to the benthic system are probably the most important.[84] These effects are not restricted to shallow waters with a tight coupling of pelagic and benthic processes, as changes of surface water hydrodynamics also have implications for deep-sea benthic ecosystems.[85]

In many shelf sea regions, the main aspects to consider regarding hydrodynamics are stratification and hypoxia. Oxygen depletion (i.e., hypoxia and anoxia) caused by high bottom water temperature, reduced water circulation (enhanced by thermal stratification), and/or coastal eutrophication are considered among the most widespread deleterious influences on estuarine and marine benthic environments.[86] Predicted global climate change is expected to expand hypoxic zones by (1) increased water-column stratification and warming that inhibits water exchange, (2) enhanced respiration due to increased temperatures, and (3) changes of precipitation patterns that will enhance discharges of fresh water and associated agricultural nutrients. At present 'dead zones' due to hypoxia are thought to cover a total area of 245 000 km^2 (i.e., <2 mg l^{-1} dissolved O$_2$) with an estimated loss of about 500,000 metric tons of benthic biomass.[87] Levin et al.[87] showed that oxygen depletion causes a reduction in the diversity of the benthos, through the loss of less tolerant species and the increased dominance of tolerant opportunists (e.g., nematodes, foraminifers, and small-sized 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 the oxygen depletion. Benthic mass mortality has been observed, for example after long-lasting hypoxic periods.[8,88] Additionally, bottom water oxygen deficiency alters biogeochemical processes that control nutrient exchanges at the sediment–water interface (i.e., benthic–pelagic coupling), e.g., by the release of phosphorus from bottom sediment.[89,90] Furthermore, a well-documented example of the effect of depleted oxygen conditions on biogeochemistry is the reduction of denitrification.[91] Although it remains unclear to what extent climate change will affect the mortality of benthic species and alter nutrient fluxes due to changes in hypoxic events, an increase in intensity and extent of hypoxic zones can be expected especially in the coastal and shelf regions.[88] Extensive oxygen depletion zones were found, for example, 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[92,93] and possible temperature effects in recent years might have been masked by a reduction in riverine nutrient inputs into the North Sea. In the Baltic Sea, large areas of the seabed are affected by hypoxia, which increased substantially during the last 115 years. This was mainly caused by eutrophication, but further aggravated by a temperature increase during the last two decades.[94] Thus, the spread of hypoxic zones seem to be an in-combination effect of eutrophication and climate change effects, this at least in some densely populated regions. These two anthropogenically driven influences on coastal marine ecosystems need to be addressed in combination by ecosystem management if aiming at a reduction of hypoxia and anoxia in marine ecosystems.

While changes in thermal stratification of the water column have an important impact on heat flux, which can lead to oxygen depletion, a stormier climate will decrease stratification due to the increased mixing depth and the risk of oxygen depletion will reduce. For example, Rabalais et al.[95] 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 depth), although studies of such effects are limited.[96–99] While it is still unclear whether the frequency, intensity, and pathways of storms or extratropical cyclones have changed due to climate warming, or how extreme weather events could change in the future, the evidence for an increasing trend in storm activity is unclear,[100,101] but this is also the case for stable conditions[102,103] in the Northeast Atlantic, during the last century. Also modeling studies based on global warming scenarios indicate a weak increase of storm activity in the future.[104,105] However, storms are not an unusual disturbance event in marine benthic systems and their effects can be considered part of the natural variability within the system. Local changes of the granulometry of the bottom sediment caused by changes in storminess may, however, have a long-term effect on the benthos.

Future changes in stratification of the water column may not only have the impacts mentioned above, but could also indirectly affect the benthos via changes in food supply. In temperate-stratified waters, 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.[84,106] The relatively high primary production and the prolonged sedimentation of fresh organic matter along frontal regions affect the abundance, biomass, growth, and functional composition of benthic communities.[106–108] 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 so would lead to changes in the geographic 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.[109–112] Marine benthic systems, which are often dominated by organisms with meroplanktonic life stages, are especially sensitive to changes in oceanographic current patterns affecting dispersal and recruitment.[72,113] It is conceivable that altered patterns of mass transport could tip the balance between larval recruitment and adult mortality, especially in populations with prevailing low recruitment, and may lead to local population reduction or even extinction.[114]

Ocean Acidification Effects

Ocean acidification (OA) refers to the process of lowering the oceans' pH (mainly by increasing the concentration of hydrogen ions) by dissolving additional carbon dioxide in seawater from the atmosphere or by other chemical reaction caused by human introduction or by natural processes. It is acknowledged that as a consequence of human activities, atmospheric CO_2 concentration has risen from 280 to 380 ppm since preindustrial times, and ocean biogeochemistry models predict that this could reach up to 1200 ppm by the end of the century.[115] The oceans act as a major sink for atmospheric CO_2 and the majority of the CO_2 from anthropogenic emissions is being absorbed by the ocean. The increased in partial pressure of CO_2 is predicted to induce a 0.3–0.4 units in pH by 2100, leading to acidified conditions. This phenomenon is referred to as OA.

Research on OA has concentrated on assessing the calcification processes of tropical reefs and planktonic coccolothophorids. A number of reviews have outlined the effects of acidification on coral reefs.[116,117] For deep-sea fauna, which is normally adapted to very little variation in pH,[118] and especially cold water corals, calcification may be severely affected and changes in distribution can be expected.[119,120] It is believed that 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.[121–126] Distinctive mounded bathymetry was formed by reefs of *Lophelia pertusa* with surficial coral debris dating to almost 4000 years before present. Guinotte et al.[119] estimated that the calcification of about 70% of the cold water corals worldwide will be affected by predicted OA within the next 100 years.

For benthic organisms, the volume of dedicated research effort has increased over time. A substantial number of short-term laboratory experiments on benthic organisms aiming to ascertain the effects of OA (mainly PCO_2 and temperature) on single benthic species have provided some indication of effect (either based on temperature responses or to the altered pH variation). Research using 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.[127] Shell construction in echinoderms in particular was severely affected. This may, even at a global scale, have unforeseen effects as echinoderms contribute a substantial proportion of the global production of carbonate.[128] Laboratory experiments conducted under normal and reduced pH showed the effects of acidification on the brittle star *Amphiura filiformis*. This echinoderm managed to rebuild missing arms, although their skeletons suffered from this activity. The need for more energy provoked brittle stars in more acidic water to break down their muscle tissue. At the end of 40 days, their intact arms had 20% less muscle mass than did those in normal seawater.[129]Other physiological processes such as fertilization success, developmental rates, and larval size may reduce with increasing CO_2 concentrations,[115,130] eventually leading to increased mortality of the affected organisms. Most existing studies have focused on organisms that live on or above the sea floor, which were assumed to be the most susceptible. Little is known about the sensitivity of the benthic infauna.[131]

Current evidence suggests that there is significant variability in the pH sensitivity of a number of different benthic groups.[132–134] Even among organisms that depend on $CaCO_3$ structures, variability in tolerance has been observed, with echinoderms showing less tolerance to pH change than molluscs.[135] In contrast, the polychaete *Nereis virens* is able to tolerate a lower pH, e.g., pH as low as 6.5,[136,137] whereas others may compensate against a lower pH for a while, but are susceptible to long-term exposure. Benthic species have different acid–base regulation abilities leading to the prediction that some species with high metabolic rates may be more severely impacted by OA because oxygen binding in their blood is more pH sensitive.[138]

Differential sublethal 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. Internationally, there is significant effort for addressing the effects of OA on the ecology, behavior, and physiology of benthic organisms such as molluscs and echinoderms (e.g., EU:

EPOCA, BioACID, UKOA, MedSea, and in the US projects such as FOCE/FACE projects). Clearly, there is a need to assess the effects of OA on biodiversity and functioning of marine systems. There are many unanswered important questions relating to the potential community level effects resulting from OA on benthic species and habitats. Hall-Spencer et al.[139] 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 CO_2 source. Prediction of the long-term implications for the diversity of marine organisms and for ecosystem functioning at larger scales remains challenging.

For example, recent evidence on OA effects and metal toxicity has indicated a clear metal toxicity and DNA damage to crustaceans under high CO_2 experimental conditions.[140] Meta-analysis has demonstrated that some of the effects of OA will certainly vary between groups; some results showed that significant negative effect on survival, calcification, growth, development, and abundance (Figure 3). Overall, survival and calcification are the responses most affected by acidification, with 27% reductions in both responses, whereas growth and development are reduced by approximately 11–19%, respectively, for conditions roughly representing future scenarios.[141–143]

In this review we have included some examples of OA research relevant to marine benthos, but it is not the intention to list all of the available peer-reviewed literature. There is a comprehensive body of evidence developed under the EU Epoca program available (http://www.epoca-project.eu/) and within published meta-analysis in the available peer-reviewed literature, which shows that OA effects vary across different organisms.[133,144,145]

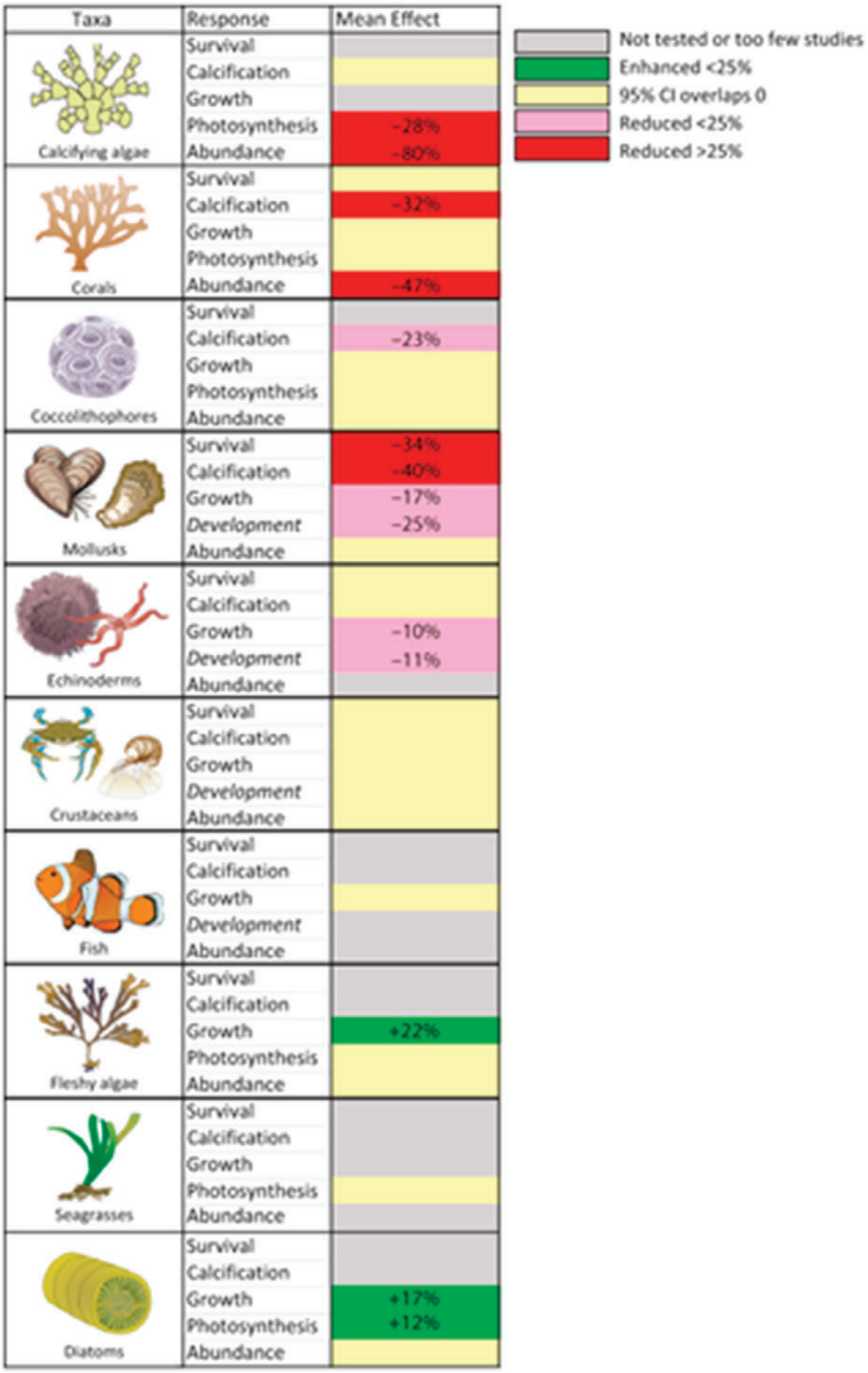
Research on OA is advancing rapidly and the information being generated will help us to understand the wider implication for marine systems of lower levels of pH and in relation to other stressors (e.g., temperature, metals, invasive species, and diseases). The current evidence has shown that some individual benthic species will be more prone to OA effects, whereas other species will be more resilient and more able to overcome these effects. The physiological responses, behavior, and phenotypic plasticity (defined as the ability of an organism to change its phenotype to adapt) for coping with environmental variation includes all aspects of environmentally induced changes (e.g., morphological, physiological, behavioral, and phenological) that may or may not remain fixed throughout an individual's lifespan.[146] For example, research conducted on the gastropod *Littorina littorea* demonstrated that negative effects due to low pH and elevated temperature on shell morphology may occur through metabolic disruption.[146]

When assessing the effect of OA in marine systems it is important to consider that the majority of experiments will only be able to mimic the OA effects over a limited period (e.g., over small spatial and short temporal scales), on a single pool of species and over periodic events. It is important to consider the information generated from these multifactorial experiments and the need to scale-up these effects to understand benthic function as well as placing OA with other environmental changes (co-stressors). Clearly there are still gaps which will need to be addressed to fully understand the effects of OA and the wider implications on biodiversity and function of marine ecosystems.

Sea Level Rise and Coastal Squeeze Effects

Extensive areas of intertidal habitat could disappear in many European estuaries in the future due to rising sea levels that squeeze tidal flats against established sea defenses during the 21st century.[147] Beaches are also increasingly becoming trapped between human development and coastal defenses on land and rising sea levels.[148] Over the past century, for example, 67% of the eastern coastline of the UK has exhibited landward retreat of the low water mark.[149] This phenomenon is better known as coastal squeeze.[150] 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 be expected as well.[147]

Hosting a rich benthic fauna, fulfilling various ecological functions[151] and providing various goods and services to mankind,[152,153] intertidal ecosystems may be impoverished by coastal squeeze. In the Humber Estuary, UK,[147] for example, model simulations showed that a sea level rise of 0.3 m might result in a 23% loss of macrobenthic biomass. There are, however, some variations: 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 areas.[154] However, such changes will occur only if sea level rise proceeds too rapidly to be compensated for by extra sedimentation. Sea level rise is further expected not only to cause a shift in the position of the intertidal zones, but also to narrow or broaden them and, in this way, to affect the total biomass and productivity of the benthos.



Taxa	Response	Mean Effect
Calcifying algae	Survival	⬜
	Calcification	🟨
	Growth	⬜
	Photosynthesis	🟥 -28%
	Abundance	🟥 -80%
Corals	Survival	🟨
	Calcification	🟥 -32%
	Growth	🟨
	Photosynthesis	🟨
	Abundance	🟥 -47%
Coccolithophores	Survival	⬜
	Calcification	🟪 -23%
	Growth	🟨
	Photosynthesis	🟨
	Abundance	🟨
Mollusks	Survival	🟥 -34%
	Calcification	🟥 -40%
	Growth	🟪 -17%
	Development	🟪 -25%
	Abundance	🟨
Echinoderms	Survival	🟨
	Calcification	🟨
	Growth	🟪 -10%
	Development	🟪 -11%
	Abundance	⬜
Crustaceans	Survival	🟨
	Calcification	🟨
	Growth	🟨
	Development	🟨
	Abundance	🟨
Fish	Survival	⬜
	Calcification	⬜
	Growth	🟨
	Development	⬜
	Abundance	⬜
Fleshy algae	Survival	⬜
	Calcification	⬜
	Growth	🟩 +22%
	Photosynthesis	🟨
	Abundance	🟨
Seagrasses	Survival	⬜
	Calcification	⬜
	Growth	⬜
	Photosynthesis	🟨
	Abundance	⬜
Diatoms	Survival	⬜
	Calcification	⬜
	Growth	🟩 +17%
	Photosynthesis	🟩 +12%
	Abundance	🟨

⬜ Not tested or too few studies
🟩 Enhanced <25%
🟨 95% CI overlaps 0
🟪 Reduced <25%
🟥 Reduced >25%

FIGURE 3 | Summary of effects of acidification among key taxonomic groups. Effects are represented as either mean percent (+) increase or percent (–) decrease in a given response. Percent change estimates were back transformed from the mean *LnRR*, and represent geometric means, that are conservative of the arithmetic means (Reprinted with permission from Ref 142. Copyright 2013 Wiley).

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.[155]

Human interventions (e.g., shoreline armouring, beach nourishment) to combat changes in beach environments, such as erosion and shoreline retreat, might also add to the ecological impact of sea level rise[148]. As demonstrated by various monitoring programs, 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 in the intertidal as well as modifications in the subtidal zone, which is an important recruitment zone for many sandy beach animals, e.g., Ref 156. Furthermore, *ex situ* effects on the benthos can also be observed. In the case of beach nourishment, sands to be placed on beaches are usually collected offshore, causing various impacts on the offshore benthos, e.g., shifts toward lower size classes of nematodes[157] and requiring a consequent benthic recovery time of 4.5 to more than 10 years.[158] In case of shoreline armoring, the high demand of clay as a soil material for dikes has been shown to cause local destruction of salt marsh ecosystems at clay excavation sites, with the first signs of terrestrial recovery only eight years after excavation.[159]

In summary, although coastal squeeze is generally associated with a faunal impoverishment because of the loss of intertidal benthic habitat, examples of local enrichment may also be detected. Coastal defense actions aimed at combating coastal erosion, may add to the loss of biodiversity in the intertidal but also in offshore benthic and saltmarsh habitats.

The North Atlantic Oscillation: A Proxy for Climate Variability

Climate change effects on benthos can rarely be studied at the time scales of climate change, as most long-term series of benthos cover, at most, the last 3 to 4 decades. In this context, cores from marine sediments act as a natural archive, reflecting pelagic and benthic processes from past millennia.[160] Changes in calcareous nanoplankton communities in the eastern North Atlantic during the last 130,000 years, preserved in sediment cores, record the major climate change events of the past.[161] Comparisons between planktonic and benthic foraminiferan communities in the cores show that the changes in the plankton were also evident in the benthic environment, indicating a strong benthic–pelagic coupling.[162] Thus, palaeoecological studies demonstrate that past climate change events have substantially affected pelagic and benthic species and communities.

The study of benthic species or communities and climate on shorter timescales, has often used comparisons with proxies for climate variability. One of these proxies, for the North Atlantic region, is the North Atlantic Oscillation (NAO). The NAO is an atmospheric teleconnection pattern affecting the climatic conditions in the North Atlantic region and the derived index (NAOI) is a measure of the strength of the sea level air pressure gradient between Iceland and the Azores. Other patterns relevant to the NE Atlantic are the Arctic Oscillation (AO) and the East Atlantic Pattern (EAP),[163] but most of the benthos studies referred to the NAOI as a proxy for climate variability. The NAOI represents an integration of several climatic variables (e.g., water temperature, prevailing wind direction and speed, and precipitation). Changes in biomass, abundance, community structure, and functioning of benthic systems directly or indirectly related to variability in the winter NAO index (Figure 4) have been analyzed in different areas in recent decades.[48,111,164–173] A number of these changes seen in benthic communities are comparable to those found in the plankton[60,71,174–176] and in fish stocks.[177–180] Reid and Edwards[181] and Beaugrand[174] concluded that a regime shift occurred at the end of the 1980s, which was directly related to a significant increase in the NAO index.

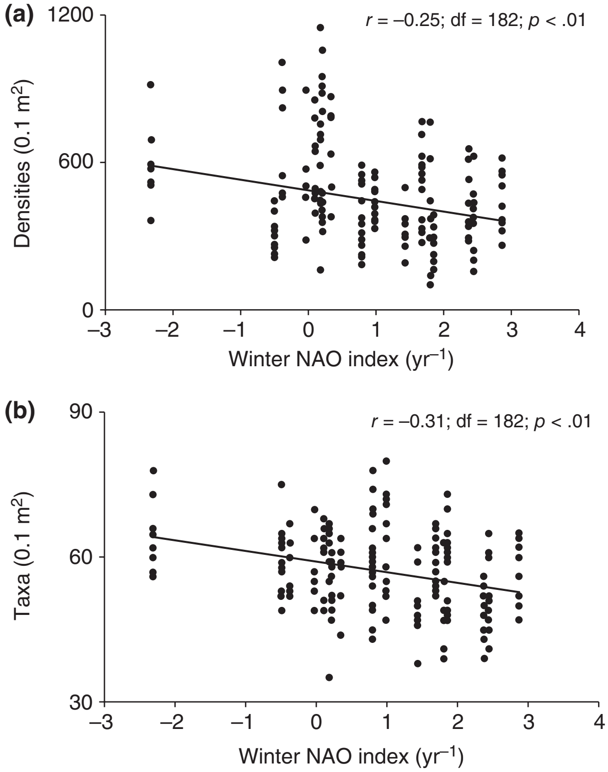


FIGURE 4 | Example of the relationship between (a) average density and (b) numbers of taxa across the annually sampled stations off the Tyne (UK) and the North Atlantic Oscillation (NAO) Index for the preceding year (Reprinted with permission from Ref 170. Copyright 2006 Cambridge University Press).

Changes in total abundance, species numbers, and total biomass of a nearshore macrofaunal community in the southern North Sea were found to be positively correlated to the NAOI, with SST being the mediator between climate and fauna.[165,167] Dippner

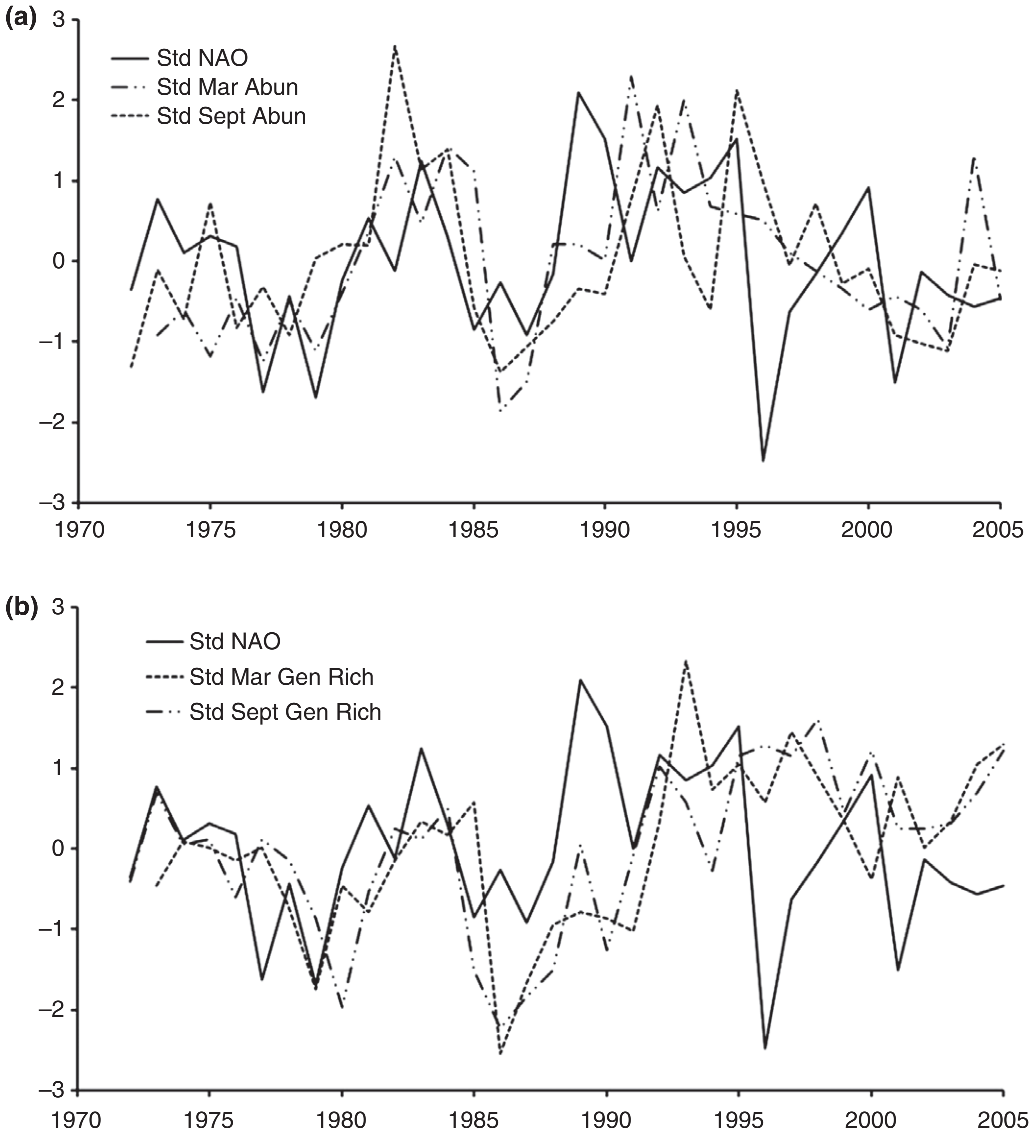


FIGURE 5 | Time-series anomalies of macrofauna in the central western North Sea. Anomalies of (a) standardized winter North Atlantic Oscillation (NAO) with March and September total abundance 0.1 m^2, (b) standardized winter NAO with March and September genera richness 0.1 m^2. Observations for the period 1972–2005 (Reprinted with permission from Ref 173. Copyright 2009 Elsevier).

and Kröncke[168] also showed in a modeling study that the atmospheric winter circulation over the North Atlantic area is an optimal predictor to forecast the structure of the macrofaunal communities in the following spring, although since 2000 this correlation, and, hence, the predictability of the structure of the macrofauna community, disappeared.[182] Also in the Skagerrak and Kattegat region abundance and biomass was positively correlated to stream flow, a parameter directly affected by the NAO.[183] Nevertheless, the relationship between climate proxies such as the NAOI and benthic communities is not consistent across regions and may be influenced by the local environmental conditions (e.g., currents, storms, food availability, and turbidity) and the local species composition. Species diversity, for example, was found to be positively as well as negatively correlated to the NAOI[168,170,184] (Figure 5) or even not at all linked to climate variability.[173] In some regions, such as the North Sea, severe winters were associated with a low NAOI (e.g., 1962–1963, 1978–1979 and 1995–1996), evidenced a marked reduction in the number of thermally sensitive benthic species and a shift in community structure in the intertidal, shallow subtidal zones, and even in deeper offshore areas.[165,185–189] In contrast, mild meteorological conditions connected with a positive NAOI resulted in an increase in the abundance, species number, and biomass of the macrofauna in the same region.[167,190]

Thus, although several studies demonstrated that there is a link between benthic community attributes and proxies for climate variability in the North Atlantic, the specific response of benthic systems seems to depend on the local conditions. Evidence suggests that some benthic communities might respond more slowly to climate variability than others, e.g., Ref 191. This demonstrates 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 as climate stressors act on individual organisms and not on entire communities.

These few examples from correlative research approaches showed that climate variability may have an important influence on benthic community structure, abundance, and species diversity, although the divergent findings concerning the relationships between NAO and benthos emphasize the need to reveal the direct causal relationships linking between the benthic dynamics with climate variability, which is ambitious as the NAOI integrates several potential causal parameters. For example, extreme winter temperatures and disturbance of the benthic communities by storms can affect the mortality of benthos in a similar way; both of these climatic parameters are correlated with the NAO index. Major changes in dominant wind direction are also related to changes in the NAO. Thus, changes of benthic communities may occur through a variety of single mechanisms or combinations of mechanisms, which may additionally act synergistically or antagonistically. For example, Wieking and Kröncke[111] described the effects of changes in the NAO index on North Sea ecosystem processes via an increase or decrease in temperature and consequent changes in hydrodynamics affecting primary production, larval supply, sediment composition, and food availability. The causal factors linking climate variability and changes in the benthos will be difficult to disentangle, but several studies have indicated that temperature is an important factor.

Despite the integrative nature of the NAOI, it might be a particularly useful proxy to be used for predicting the cumulative response of the benthos to climate change, at least in regions where a link between NAOI and benthic parameters was observed. The forecast of the NAOI until 2100 revealed only little evidence of variability on a preferred timescale or a distinct long-term trend.[192] Thus, drastic changes can occur on an annual or decadal scale,[192,193] which might limit the use of the NAOI to forecast long-term changes of the benthos and understanding the linkages with the causal parameters for climate-driven changes in the benthic system is essential.

CONCLUSION

This review has outlined how climate change effects may influence benthic communities via a multitude of direct and indirect impacts, and how such changes will have repercussions for other ecosystem components. The majority of climate change-induced impacts on the benthos are, however, deductive and/or speculative. It is important to highlight that as more climate change evidence becomes available, there is also a need to assess the natural and anthropogenic factors (including climate change) that may be also influencing benthic assemblages.

To date, most of the research has been focused on specific benthic components (e.g., single species or life stages) or at assemblage levels, but such assessments in isolation will have limited validity when making predictions for responses of entire ecosystems to climate change. Climate-induced effects on key species in food webs may have cascading effects propagating through the entire food web, including pelagic components. The majority of studies of marine systems (e.g., benthic and pelagic) have been done in separate stages. This is problematic when the empirical information is used to input into an ecosystem model (e.g., ERSEM), specially when aspects of the model (pelagic vs benthic) have different level of developments, which presents problems for an accurate representation of the two systems (Blackford *pers. comm.*).

To take the next step toward a comprehensive understanding of climate change effects onto the benthos, we have identified areas where gaps in knowledge exist. The development of targeted research to understand the effects of climate change on benthic ecosystems (see our conceptual framework in Figure 1) should be combined in a three-way approach. These key stages, which should be tightly linked, are:

1. Integrated monitoring, to test, modify, and complete current hypotheses that are, as yet, mainly based on shorter-term and small-scale data. Standardized national monitoring strategies need to be coordinated internationally so as to enable a regional assessment of the effects of climate change on the benthos (see also Refs 194, 195). These studies should focus on the classic structural descriptors of benthic communities (e.g., abundance and species composition

or richness) and also address the connectivity between populations, and species–species and species–environment interactions.

2. Fit for purpose experiments, should be complemented with monitoring and vice versa as this information will help dedicated observations into a wider understanding of specific mechanisms and/or responses. Experimental information should be place into context with field information, to support understanding of variability (e.g., seasonal variability, timing of recruitment, and long-term observatories).
3. Statistical and dynamic models will be useful tools to identify 'hot spots' of climate change effects and can be used to study changes on, e.g., community, food web, and ecosystem level.

While we recommend these three key stages, we also recognized that these are not new approaches, but the need to integrate and provide complementary information is needed while studying marine climate on benthic systems.

We would like to highlight clear gaps to expand on the current knowledge in the study of climate change and marine benthos. These are:

- A causal relationship between a temporal mismatch and benthic species, their food resource and climate change is difficult to test, given the limited knowledge of the life cycle of many benthic species. Some targeted experiments looking at the synergistic effects (e.g., temperature, food, and different CO_2 levels) could help to undertand some of these responses. This work could then be scaled-up to place the results into wider perspective. This information will help to provide the necessary scientific evidence to assess susceptible areas, species, and limiting factors for targeting the study of climate change.
- The mechanisms behind the cause–effect relationship between benthic ecosystems and the NAO remain largely unknown and additional research is required. 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. There is opportunity to undertake integrative studies, which could assess the synchronicity of observed changes over different latitudes.
- 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. Habitat suitability models coupled with hydrodynamic models could help to inform species distributions better and some of the expected environmental changes over different climate scenarios.
- The effects of climate change are largely the outcomes of processes acting on individuals, but are generally observed at the population, community, and ecosystem level. Therefore, it is necessary to concentrate efforts in describing individual species changes and complementing these observed responses to other levels of the ecosystem. Experiments could help to target specific responses and then input these outcomes to test and validate models.
- Almost all studies on the impact of OA and the benthos focus on specific taxa over very limited areas and time. At present, integrated, large-scale studies focusing on climate change, OA, and human activities are lacking. It is clear that some of the observed changes are not be occurring in isolation. There is clearly a need to understand these combined effects under laboratory or mesocosm conditions.

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