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Impacts of climate change on shallow and shelf subtidal habitats

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EXECUTIVE SUMMARY

There is evidence that climatic processes influence species abundance and community composition in soft-sediment habitats in the North Sea. There is no obvious signal of warming-effects in southern and south-westerly sediments, although changes to the species dominating crustacean assemblages in the Bristol Channel and the occurrence of previously undocumented species in the western Channel (e.g. the brittle star *Amphiura incana* and the shrimp *Athanas nitescens*) suggest some degree of climate-influence.

Hard-substrate habitats in southern and south-westerly waters appear to be affected, with changes in algal distribution and abundance and the appearance and increased occurrence of a previously unrecorded warm-water barnacle all linked to increased seawater temperatures.

Climate change is likely to impact the benthos in future. The changes documented in soft-sediment communities are expected to continue, and probably escalate, in response to the cumulative effects of seawater warming and ocean acidification. Species forming cold-water coral reefs and maerl beds may experience shifts in distribution as a result of intolerance to altered seawater temperature and chemistry, with knock-on effects on community composition and function.

Future impacts on these habitats are likely to have socio-economic ramifications, as cold-water coral reefs and maerl beds are protected under European legislation and soft-sediment communities are an important food resource for commercial fish.

There are knowledge-gaps in a number of areas. We are currently unable to fully assess the scale of benthic species and community responses in relation to climate change, understand how climate interacts with other marine stressors or model future species distributions for many benthic species. An appropriate benthic monitoring programme, coupled with continued involvement in international initiatives, is essential for characterising climate impacts on UK benthos.

INTRODUCTION

This report summarises evidence of current and predicted future climate change effects on shallow and shelf subtidal habitats and ecology. It covers algae and invertebrates (with the exception of non-native species and those subject to commercial fisheries) on soft- and hard-substrates. Coastal and intertidal habitats, fish, fisheries and non-native species are considered in separate Annual Report Card (ARC) science reviews. Seagrass habitats extend in most cases to subtidal systems, but they are predominantly connected to the intertidal, so dealt with in the intertidal habitats and ecology ARC science review. The information in the report represents documented evidence available to the authors at the time of writing and relates to UK, Crown Dependency (Channel Islands and Isle of Man) and Irish waters. We have also included information from neighbouring states (e.g. German and Belgian North Sea waters) where water bodies are shared and climate-related effects may extend into UK waters.

Section 1 (What is already happening?) is structured around the UK Charting Progress Regions and, Irish and Crown Dependency waters, summarising evidence available for different habitats in each region. Where the available evidence relates to more than one region, these are grouped together. Section 2 (What could happen?) is based on indirect observational and experimental evidence largely applicable across regions and is structured by species- or habitat-type.

Climate change may influence shallow and shelf subtidal habitats and ecology through a number of mechanisms, including seawater temperature change, increased incidence and severity of storms, changing salinity and oceanographic patterns, sea-level rise, and ocean acidification. Our report focuses primarily on seawater temperature change and related physical variables such as the North Atlantic Oscillation Index, as much of the evidence currently available (mainly based on peer-reviewed literature) relates to such factors. Although ocean acidification is increasingly seen as one of the major climate-related problems, this issue has been dealt with in detail in the Ocean acidification report card (Williamson *et al*., 2013). As in the 2010 / 2011 shallow and shelf subtidal habitats and ecology ARC, here we provide a summary of the most recent advances in acidification effects on shelf subtidal ecology and readers are referred to the 2009 Special Topic Report Card for a more thorough description of the issues.

This report is an update of the 2010 / 2011 shallow and shelf subtidal habitats and ecology ARC. Sections may be similar to previous ones when no new information is available for a region or issue. No sections have been removed, as none of the issues detailed in the previous review have since proven to be unrelated to climate. No major new issues are introduced in this update, as we are not aware of any having been identified at the time of writing.

The report is limited in size, so focuses only on climate effects. It is important to note that such effects operate within the context of natural change in biological communities (stochastic change or temporal cycles) and other anthropogenic impacts such as fishing, which is a major large-scale stressor of benthic communities, pollution, minerals extraction and marine construction. These other ecosystem drivers should not be overlooked, but we often do not understand how they interact; they may add-to, multiply or negate the effects of climate change. We have included information on alternative causes of change, where it is available, but the overall picture of change is likely to be more complex than a straightforward relationship with individual climate-change parameters and the information presented here should be viewed in this context.

1. WHAT IS ALREADY HAPPENING?

1.1 The North Sea: Charting Progress Regions 1 (Northern North Sea) and 2 (Southern North Sea).

Trans-regional patterns: North Sea soft-sediment benthos

Current efforts to describe benthic changes in relation to climate change and its effects are widely scattered across UK waters. There is detailed time-series information available for site-specific areas. These dedicated efforts have merit in their own right, but it is also clear that these temporal data-point sources only provide assessments over small areas therefore their relevance over larger scales still remains unclear. Documented changes in the North Sea ecosystem that occurred from the late 70s may have been influenced by warming sea-surface temperature. Those changes were recorded mainly in the plankton but there are clear links to the benthic communities. Research has found changes in the benthic community structure in the western North Sea (north east coast of England), and the eastern North Sea (Skagerrak) displayed a transition in the late 70s (Edwards *et al*., 2002). Similarly, there was also a transition between the 70s and 80s in the holoplanktonic fraction of the zooplankton community from the western and eastern North Sea (Austen, 1990, Evans and Edwards, 1993). These observations are in agreement with an increase in planktonic biomass and extent of the plankton periods (mainly flagellates) in the German Bight (Radach, 1990). Furthermore, climate-focused research in pelagic ecosystems in the North Sea (Kirby *et al*., 2007, 2008, 2009) has provided clear links to the benthic systems when climate change is the common cause of these effects. 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 sea surface temperature (SST). Furthermore, the larvae of benthic echinoderms and decapod crustaceans have shown an increase since the mid 1980s that accords with the rise in SST in the North Sea, while bivalve larvae have decreased (Kirby *et al*., 2008; Alvarez-Fernandez *et al*., 2012).

Overall, it is clear that uniform benthic monitoring and assessment is needed to characterise species distributions and responses in relation to climate change in UK waters. Current UK efforts to document status and change of benthic assemblages have prompted research scientists to collaborate on a number of initiatives (e.g. MECN, MCCIP) (e.g. Spencer *et al*., 2011, 2012). As well of gathering information, the storage of data is also being facilitated by initiatives such as (MEDIN) and the UK National Biodiversity Network. In addition to these clear initiatives, it is also important to acknowledge the value of observations collected by naturalists, excellent examples of biological information collected by anglers, divers and also fishermen can help us to distinguish overall ecological changes at localised areas. The value of these opportunistic observations can help as initial evidence for future assessments in relation to species distributions and responses for climate change investigations. Internationally, the International Council for Exploration of the Sea (ICES) via the North Sea Benthos Project and Study Group on Climate Related Benthic Processes in the North Sea are providing a forum for scientists to conduct benthic communities assessments over larger spatial scales than those typically achievable by national initiatives alone and are, thus, vital for understanding responses to change in multi-nation bounded waters such as the North Sea.

Northern North Sea (Region 1): Soft-sediment benthos

The northern North Sea is known to be influenced by the influx of deep Atlantic water (Reiss and Kröncke, 2004). The area has been intensively studied for decades; examples of early pioneer work relates back to Petersen (1914, 1918), who assessed the distribution of macrobenthic soft sediment fauna. This work has enabled research scientists to continue with long-term assessments to monitor status and change in the region's macrobenthos.

Early work conducted by Buchanan, in 1963, was marked by the commencement of the 'Dove Time series', at stations M1 and P, off the north-east coast of the UK. These assessments were to help understand benthic communities in relation to environmental conditions and human activities in the area. In this area climate change has been implicated in the changes documented by rising total numbers and biomass in the benthic communities at station M1, that have been mainly attributable to a combination of effects of climatic variation, which were caused by: biological interactions, winter temperature (a combination of 'cold water' and 'warm winter state') and carbon flux to the benthos.

Warmer seawater temperatures during winter periods together with phytoplankton supply have been suggested as causal for instability of benthic communities (Buchanan and Moore, 1986a, b; Buchanan *et al*., 1986) at station P. Clear changes were observed in relation to dominant species (i.e. general rise in number and biomass of infaunal benthos) which were attributable to climatic events. Further work conducted by Frid *et al*. (2009) in the same area hasdescribed the benthic community changes in relation to fishing impacts, but also identified additional influences on the benthos to be a combination of phytoplankton supply and climatic warming effects.

Another study conducted by Rees *et al*. (2006) linked reduced density and species richness to warm winter temperatures. Benthic communities of the former sewage sludge disposal site in the area of north-east England (stations located in the proximity of the Dove Time Series station M1) showed a clear temporal correlation between benthic macrofauna and winter values of the NAO for the preceding year. This represents a pattern of response for benthic assemblages composed of many taxa with a more northern (cold water) distribution in the absence of compensatory increases in those with more southerly associations.

Southern North Sea (Region 2): soft-sediment benthos

The information compiled in this section is part of extensive work conducted by European colleagues. Currently, available research in this area is not being conducted under UK auspices.

Climatic factors most likely play a dominant role in structuring macrobenthic communities in the North Sea, principally in the winter and spring (Dippner and Kröncke, 2003). Research has also demonstrated that macrofaunal communities are severely affected by cold winters, whereas storms and hot summers have no direct impact on the benthos (Kröncke, 1998). Studies in the Southern North Sea demonstrated that macrofaunal communities were sensitive to a combination of hydrographic effects and also affected by temperature changes. These effects showed alteration in species number, abundance and biomass of the coastal macrobenthos (Kröncke *et al*., 1998). Studies targeted on the effect of severe winters in long-term variability of benthic macrobenthos from the German Bight to the Dogger Bank reflected that benthic communities are mainly influenced by winter temperatures and storm frequencies (Kröncke *et al*., 1998, 2001; Schröeder, 2003). Kröncke (2011) conducted an integrated analysis on the benthic communities of the Dogger Bank over 1920-2010. These results suggested that the communities were mainly influenced by the biological regime shift (during the 1980s and in 2001). Some of the community changes observed at the Dogger Bank were an indication of the climate driven effects in water masses, currents, storms, food availability and turbidity. The results from this study indicated that both the direct human impact resulting from the fisheries activity as well as climate change affected the Dogger Bank macrofauna in the 20th century. Construction of an offshore wind farm is planned in this area. The project is considered one of the biggest infrastructure projects for offshore wind energy (http://news.bbc.co.uk/1/hi/8448203.stm). This large scale project might result in the closure of some parts of the Dogger Bank for fisheries, providing an ecological opportunity to study the macrofauna recovery in these areas from fishing effects.

The bivalve mollusc *Abra alba* has shown significant changes in abundance related to mild (high numbers) and cold (low numbers) winters (Fromentin and Ibanez, 1994; Van Hoey *et al*., 2007), which seems to coincide with the regime shift observed in the North Sea in 1998 (Kröncke *et al*., 1998; Reid *et al*., 1998, 2001; Weijerman *et al*., 2005). The observed patterns tend to concord with the changes in the hydroclimatic state of the North Sea, caused by variability in the NAO. However, there is no indication of a trend that might be the result of long-term warming.

1.2 Southern and south-westerly waters: Charting Progress Regions 3 (Eastern English Channel) 4 (Western English Channel, Celtic Sea and South-West Approaches) and 5 (Irish Sea and North Channel)

Trans-regional patterns: Soft-sediment benthos in the Channel

The western English Channel is located at the biogeographic boundary between northern Boreal and southern Lusitanian species and has, therefore, served as an important area for monitoring the effects of climate change on marine organisms. While the consequences of a changing climate have been relatively well documented for fish, plankton and intertidal benthos of the region (see, for example, Genner *et al*., 2004; Hawkins *et al*., 2008; Beaugrand *et al*., 2009), subtidal benthos have received far less attention and there are no long-term benthic timeseries from the UK side of the Channel (there are timeseries from the French coast, but these have not been investigated with respect to climate change). In such circumstances, comparison of historical and contemporary data can provide a means to investigate whether there are any indications of climate effects on the benthos of the region.

One such comparison is that made between benthic communities from the Channel region sampled by Norman Holme during the late 1950s (Holme 1961, 1966) and communities in the same area sampled by Hinz *et al*. (2011)

in 2006. Holme was particularly interested in the distribution of Lusitanian and Boreal species and he and his colleagues' early surveys uncovered variations in penetration of 'western' species (those normally inhabiting the Celtic Sea and likely to be cold-water species) into the Channel, as well as possible temperature-related penetrations of 'Sarnian' species from the Gulf of St. Malo into the wider Channel and population fluctuations caused by mortality during severe winters (Holme 1983).

The 2006 survey re-sampled a subset of Holme's original stations, over a large area of the Channel coast. The main aims of this resurvey were to describe the current status of the communities and investigate potential changes. Benthic species distributions remained similar, in general, between the 1950s and 2006, with little or no obvious trends consistent with warming sea temperatures. The eastward movements of Lusitanean species that have been observed in some intertidal fauna were not generally reflected in the subtidal benthos, although some additional species not documented by Holme in the 1950s were observed (such as the brittle star *Amphiura incana* and and the shrimp *Athanas nitescens*). Comparisons between historical and contemporary datasets can be complicated by methodological constraints and fishing is likely to have exerted an influence on the benthic communities in the western Channel (Capasso *et al*., 2009), making it difficult to separate causal factors. Nevertheless, the area is a biogeographic boundary where (arguably) temperature-driven distribution changes are most likely to be displayed and there is ample evidence of change for other species groups, so the observation of additional benthic species in the 2006 survey suggests that further work in this area is warranted.

Trans-regional patterns: Hard substrates in the Channel and South-West Approaches

This section includes information on changes occurring across the UK Charting Progress regions. Such evidence comes from a combination of timeseries studies at individual sites, ad-hoc scientific surveys and formalised naturalist / public observations, such as the Seasearch programme (www.seasearch.org.uk).

(i) Crustacea

The warm-water barnacle *Solidobalanus fallax* has been increasing in occurrence along western European coasts in recent years, thought to be the result of rising seawater temperatures (Southward *et al*., 2004). *S. fallax* was first recorded in UK waters in 1988, on hydroids dredged from south- west Cornwall (Southward *et al*., 2004)). It does not appear to have been described in Europe prior to this, with records limited to Atlantic and north-western coasts of Africa. However, it is difficult to distinguish from related species, so may have been present but recorded as, for example, *Balanus crenatus*.

The 2004 review of distribution records indicated that *S. fallax* has increased significantly around the south and south-west of the UK (Southward *et al.* 2004). It appears to have become widespread off Devon and Cornwall and, by 2004, had been recorded from Dorset, Lundy, the Gower Peninsula and Pembrokeshire. The barnacle settles on living and inert substrates and is often found on plastic discards, suggesting that these items may provide a vector for its spread along the southern British Isles (Southward *et al*., 2004). In this context, seawater warming and increased incidence of plastic discards may have interactive effects on the spread of the barnacle, the plastics providing a transport vector and increased temperatures providing environmental conditions suitable for establishment. No new information on *S. fallax* distribution was available to the authors at the time of writing, so it is not clear if the species has continued to spread around the British Isles.

Another crustacean species that may be broadening its range into UK waters is the snakelocks anemone shrimp *Percilimenes sagittifer*. The first recorded sighting of *P. sagittifer* in the UK is believed to have been made in Dorset in September 2007 (Dorset Seasearch, 2007). The species was recorded again in October 2008, although it was not present during re-surveys in the winter (Seasearch, 2008). By 2011, it had also been recorded in Devon (Seasearch, 2011). Only small numbers of individuals have been observed and these observations come from recreational dive surveys, so this information remains speculative in the absence of systematic evidence. We are not aware of any targeted monitoring programme designed to confirm if the shrimp has become established in UK waters, nor are we in possession of any documented evidence that its appearance is due to seawater warming. However, it is a southern species only recorded as far north as France and the Channel Islands until 2007, so its distribution would benefit from further attention.

(ii) Algae

Effects of increasing seawater temperature can also be seen in algal communities from southern and south-westerly waters. Boreal macroalgae are showing a continual decline in abundance in shallow subtidal zones around the south coast of England, whereas Lusitanian species are increasing in abundance and relative dominance is switching to warm-water species in the Western English Channel and Celtic Sea (unpublished analyses of the MarClim[1] project dataset 2002-2010, www.mba.ac.uk/marclim; see also Mieszkowska *et al*., 2006). The boreal species *Alaria esculenta* continues to show declines in abundance in shallow subtidal zones around the Western English Channel, close to its southern range limit (Vance 2004, MarClim data - 2002-2010). The Lusitanian kelp *Saccorhiza polyschides* has rapidly increased in abundance in this region over the last few years and is displacing cold water laminarians over large areas of the intertidal. There is currently insufficient evidence to ascertain whether *S. polyschides* is also displacing laminarians below the low-water mark, but the distinction between species' intertidal and subtidal populations is somewhat artificial and it is not unreasonable to suggest such effects are also occurring subtidally.

[1]MarClim (Marine Biodiversity and Climate Change) was a four year multi-partner project investigating the effects of climatic warming on biodiversity of marine intertidal species, co-ordinated by the Marine Biological Association of the UK.

Western Channel, Celtic Sea and South-West Approaches (Region 4): Severn Estuary / Bristol Channel crustacea

Long-term monitoring of crustacean populations in the Severn Estuary / Bristol Channel indicates that climate change is influencing hyperbenthic assemblages in the region.

Standardised monthly macro-crustacean and mesozooplankton sampling has been undertaken since the early 1980s at Hinkley Point power station, on the Somerset coast. Of the 15 macro-crustacean species captured to-date (Henderson and Bird, 2010), three of the most numerous – the common shrimp *C. crangon*, the pink shrimp *Pandalus montagui* and the Atlantic prawn *Palaemon serratus* - have been increasing approximately exponentially since the early 1990s, in concert with increased seawater temperatures. There is strong evidence of density-dependent control in the *C. crangon* populations, in addition to the positive correlation with average water temperature between January and August (Henderson *et al*., 2006). There have also been recent notable increases in the abundance of the velvet swimming crab *Necora puber* and the sardine crab *Polybius henslowii*. Coincident with this has been a decline in the abundance of the shore crab *Carcinus maenas*.

There has also been a significant increase in the inter-annual abundance of mysids in the Bristol Channel since 1996 (Plenty, 2012). All the local mysid species (*Schistomysis spiritus*, *Gastrosaccus spinifer*, *Mesodopsis slabberi* and *Neomysis integer*) are now abundant for a greater number of months compared to the early 1980s and the breeding activity / success of two species, *M. slabberi* and *S. spiritus*, has increased since 1981 (Plenty, 2012). These changes in mysid abundance, phenology and breeding activity / success have been closely related to shifts in climate, particularly an increase in air and water temperatures, during more recent years. There has also been a shift in the dominance structure of the mysid assemblages. *M. slabberi* is now the dominant mysid species of the Bristol Channel, being more abundant than *S. spiritus* in most years since 1997. This shift towards a *M. slabberi* dominated assemblage more typical of lower latitude estuaries than UK waters is, in part, explained by increases in air and water temperatures and variations in the North Atlantic Oscillation Index (NAOI)

These trends are not apparent in all of the crustacean species monitored, with the only other abundant prawn in the area (*Pasiphaea sivado*) showing no trend in abundance over the past three decades and no clear climate-related trends in the isopods, amphipods or cumaceans.

1.3 Western and northern waters: Charting Progress Regions 6 (West Scotland including the Minch), 7 (Scottish Continental Shelf) and 8 (Atlantic North-West Approaches, Rockall Trough and Faroe/Shetland Channel)

At present, we are not aware of any current evidence of climate-related effects on shallow and shelf habitats and species in these regions. However, we are aware of ongoing work which could help to understand the effects of warming and ocean acidification on cold-water corals (*Lophelia pertusa*) (Davies *et al*., 2008, 2009; Roberts *et al*., 2009). The UK Ocean Acidification (UKOA) research programme (funded by NERC/Defra/ DECC) (http://www.nerc.ac.uk/press/releases/2012/07-corals.asp) has tackled these issues by carrying out a series of experiments examining the effects of warming and acidification on cold-water corals. These laboratory studies indicate that, at least in the short term, the corals show some capacity to adapt to ocean acidification, but less ability to deal with the combined impacts of acidification and temperature increase. But understanding the implications of these experiments is virtually impossible without understanding more about the natural variability and functional ecology of these ecosystems. These issues were investigated by the 'Changing Oceans Expedition' during RRS *James Cook* cruise 073 (May-June 2012, see http://www.changingoceans2012.blogspot.co.uk/). This expedition combined further experimental work on board with detailed remotely operated vehicle survey and experimentation within coral reefs at the Mingulay Reef Complex (~130 m) and the Logachev Mound Province (600-800 m). The expedition completed a number of firsts including direct measurement of carbonate chemistry conditions above the reefs and assessment of their oxygen demand (www.changingoceans2012.blogspot.co.uk, www.lophelia.org)

There is also ongoing research on maerl beds (*Lithothamnion corallioides* and *L. glaciale*) under UKOA auspices. The available evidence also suggests algae will survive under acidified conditions, possibly by utilisation of increase pCO_2, however, stress caused by OA is likely to increase their intracellular antioxidant (DMSP) concentrations and lead to some epithelial damage. Photosynthetic yield increased under OA. There is mixed evidence on the impact of OA on biomineralisation processes some studies suggesting no impact others suggesting structural stress.

1.1.4 Associated regions: Irish waters and Crown Dependencies (the Isle of Man and Channel Islands)

We are not aware of any current evidence of climate-related effects on shallow and shelf habitats and species in these regions. As the sea does not respect national borders, some of the changes documented in southern and south-westerly waters (section 1.1.2) may reasonably be expected to extend into Irish, Isle of Man and, in the case of southern regions, Channel waters. However, climate impacts are complex and related to local conditions and we can not confidently state that changes documented in specific areas can be applied to neighbouring regions. Seawater temperature and, possibly, stratification change have been linked to shell growth in the ocean quahog *Arctica islandica* from Isle of Man waters (Butler *et al*., 2010). However, fishing pressure and minerals extraction are also known to affect this species (see OSPAR Commission, 2009) and we are not aware of documented long-term changes in *A. islandica* abundance in these waters.

2. WHAT COULD HAPPEN?

Changes may be expected in a range of seabed systems, particularly those tightly linked to phyto- and zooplankton communities impacted by future climate change. A clear example can bee seen at the Dogger Bank area, where the combination of fishing and climate since the beginning of the 20th century has influenced the macrobenthic communities (Kroencke, 2011). However, there is a severe lack of empirically-based prediction for UK subtidal species and habitats. Shallow and shelf habitats and species are most likely to be affected by changes in SST, near-bottom temperature and stratification patterns, as well as changes to ocean chemistry from increased uptake of CO_2. Acidification effects are summarised here in relation to potential associations with temperature-driven climate impacts. A detailed review of the effects of ocean acidification is presented in the 2012 MCCIP report on ocean acidification (Williamson *et al.*, 2013). Predictions of future change are based on the UKCP09 climate projections medium emissions scenario (Lowe *et al.*, 2009).

2.1 UK soft-sediment benthos

Benthic responses to climatic change may be observed to differ when assessed across spatial scales and, even locally, some effects could be influenced by a series of other factors (e.g. fishing). Specific parameters (i.e. NAO index, SST) might provide rapid signal of change on benthic communities inhabiting shallow waters, when compared with their counterparts in deeper waters (Rees *et al.*, 2007). SST for regions 1 and 2, are predicted to rise by up to approximately 3.0 °C and 3.5 °C for summer conditions by 2070-2098, respectively (relative to the 1961-1990 average). In contrast, during a winter scenario, SST only shows an increase of approximately 2.8°C in area 2. Benthic communities are likely to be responsive to changes in temperature and stratification. Schöne *et al.* (2003) showed that temperature influenced the annual shell growth of live collected *Artica islandica* in the North Sea. Effects of warmer winters on stratification and bottom water currents seem to be stronger, thus preventing downward- mixing of nutrients as well of settlement of food particles on the sea bed. In contrast, during cold winters, the stratification weakens and phytoplankton produced in the cold surface layers reaches the sea floor. Growth of the shell of *A. islandica*, seems to be directly connected to fluctuations in the NAO, so future warmer winters may continue to produce similar effects in their shell growth. Beukema *et al.* (2009) postulated that understanding the overall effects of temperature on benthic communities will be a difficult task when they are studied in relation to recruitment, mortality and individual weight (with repercussions for abundance and distribution of species). A warming climate may be directly observed in chronic effects and physiological stress and/or indirectly in alterations to specific benthic functions (e.g. predation, competition, etc). Thus, future effects are difficult to predict for the complex biological communities inhabiting soft-sediment systems.

Any changes resulting from seawater warming are likely to operate within the context of a chemically-stressed environment, as seawater uptake of CO_2 leads to increasing ocean acidification. The potential effects of ocean acidification on benthic fauna are covered in detail in some of the available reviews (see Turley *et al.*, 2009; Gattuso and Hansson, 2011; Wicks and Roberts, 2012). Studies of benthic species from UK waters have shown that short-term exposure to low-pH environments seems to have relatively little effect on the polychaete *Nereis virens*, the crab *Necora puber*, or the echinoderm *Amphiura filiformis* (Spicer *et al.*, 2007; Widdicombe and Needham, 2007; Wood *et al.*, 2008). However, long-term fitness may be compromised by short-term acclimation responses (Wood *et al.*, 2008) and there is evidence that reduced pH may impact on biologically-mediated benthic nutrient cycling (Widdicombe and Needham, 2007; Widdicombe *et al.*, 2009). In addition, evidence from comparable benthic communities in other northern European waters suggests that acidification may impact on the overall diversity of benthic communities, affecting both species composition and abundance (Widdicombe *et al.*, 2009). Such changes are likely to be habitat-specific, with sandy communities appearing more sensitive than those in muds (Widdicombe *et al.*, 2009). Although acidification effects in soft sediments are likely to interact with those of changing temperature and stratification patterns, the cumulative effects of multiple climate-driven co-stressors, the full life cycle and physiology of individuals, ecological interactions and potential adaptations are, as yet, unknown.

2.2 *Lophelia pertusa* reefs in northern and north-western waters

While shallow southern and south-eastern UK waters are predicted to show the greatest increases in SST and near-bottom temperatures under the UKCP09 projections, deep-water habitats to the north and north-east of the UK may also be impacted by seawater warming. The scleractinian cold-water coral *Lophelia pertusa* forms biodiverse and functionally-important deep-water reef habitats (Davies *et al.*, 2009). The majority of the world's *Lophelia* reefs are concentrated in the North Atlantic (Guinotte *et al.* 2006) and they are represented in UK waters in northern and western Scottish waters (Charting Progress regions 1, 6, 7 and 8). These habitats are in decline in OSPAR regions I-III and V, caused primarily by the damaging effects of bottom fishing (Hall-Spencer and Stehfest, 2008). However, they are also likely to be vulnerable to climate change. Modelling work has linked their distribution to temperature (Davies *et al.*, 2008) and *Lophelia* from the Mingulay reef complex, off the Scottish west coast, has shown sensitivity to changes in water temperature of as little as 2°C (Dodds *et al.*, 2007). Experimental studies on the coral's physiology suggest that they are highly vulnerable to temperature increase and modelled predictions showed that much of the Atlantic Ocean may become corrosive to aragonitic shells and skeletons within the next century, with cold-water corals may be amongst the most vulnerable to ocean acidification and warming.

Near-bottom temperatures in regions 1, 6 and 7 are predicted to rise by approximately 2-2.5°C in 2070-2098 (relative to the 1961-1990 average). Reefs in region 6 may experience summer temperatures in the region of 15-16°C, some 2-3 degrees warmer than their upper required temperature of 13°C (Hall-Spencer and Stehfest, 2008). Bottom temperatures in region 8 may increase by up to 1°C from 2070-2098, so reefs in this area - which include the majority of UK records

- are less likely to be impacted than those in regions 1, 6 and 7. The effects of increased temperature may be compounded by further impacts related to seawater acidification. *Lophelia* reefs are thought to be limited, in part, by seawater aragonite saturation (Guinotte *et al*., 2006) and projected decreases in saturation due to increased CO_2 uptake may lead to impacts on growth and increased vulnerability to dissolution (Davies *et al*., 2007). These changes will also occur in the context of changing oceanographic conditions, which could affect pelagic productivity and food supply to deep sea habitats such as the *Lophelia* reefs (Hall-Spencer and Stehfest, 2008).

2.3 Maerl beds in southern, western and north-western waters

Maerl, species of detached coralline red algae, may be vulnerable to future climate impacts. Of the three major European maerl-forming species, two appear to be limited by temperature in UK waters, with *Lithothamnion corallioides* confined to Scotland and Northern Ireland and Lithothamnion corallioides reaching only as far north as the southwest of the British Isles (Birkett *et al*., 1998). *L. corallioides* from the west coast of Ireland has been shown to respond positively to a 4°C increase in temperature (Blake and Maggs, 2003), suggesting the species may benefit from warming waters. Maerl beds are rare in England and Wales, but there are isolated occurrences in Dorset, Cornwall, Pembrokeshire, the Lleyn Peninsula, the Isle of Man and around Lundy (Hall-Spencer *et al*., 2008). *L. corallioides* in these areas may benefit from the near-bottom temperature increases of up to approximately 2.5-3.5°C forecast for Charting Progress regions 3, 4 and 5 in 2070-2098. Such increases could facilitate the spread of *L. corallioides* to further locations along the south and south-west coasts of England and Wales, although expansion would also be limited by the suitability of other factors such as water movement and salinity (Wilson *et al*., 2004).

The temperature-response of *L. glaciale* is not currently known. However, its southern limit is thought to be western Scotland and the coasts of Ireland, the near-bottom temperature is projected to increase by approximately 2-3°C for regions 5, 6 and 7 in 2070-2098. Within this projected temperature increase, growth rates of *L. glaciale* might be expected to increase but there is no evidence on how long those growth rates could be maintained over time. Maerl is most commonly found in the northern parts of the UK, including the west coast of Scotland, the Western Isles, Orkney and Shetland (Charting Progress regions 6 and 7, Hall-Spencer *et al*., 2008), so temperature-related changes in these regions would affect a large proportion of the UK's maerl beds. The third major European species, *Phymatolithon calcareum*, is found from southern Norway to the Mediterranean and does not appear to be susceptible to short-term increases of temperature in UK and Irish waters, although longer-term effects may only be evident after periods of acclimation (Blake and Maggs, 2003; Wilson *et al*., 2004).

Given the different temperature preferences of the individual maerl species, climate-related effects could be manifest as either overall changes to the biomass of maerl in UK waters or alterations in the relative proportions of the three major species. Such effects may have secondary implications for diversity of the biological communities inhabiting the habitat, as maerl beds host a diverse assortment of flora and fauna including rare species and some that may be endemic to the locale (Hall-Spencer *et al*., 2008). Maerl are calcifying organisms, so predictions of changes in response to temperature must be viewed in the context of the interacting and, potentially, confounding effects of ocean acidification. Acidification effects have been noted in other coralline algae and benthic calcifiers (Kleypas *et al*., 2006; Hall-Spencer *et al*., 2008). Changing ocean chemistry may threaten the growth and integrity of maerl matrices, with knock-on effects on associated biological communities. Maerl contribute to calcareous sediment production and seawater pH balance (Hall-Spencer *et al*., 2008), so dissolution of their carbonate skeletons would likely have implications for ecosystem function.

3. KNOWLEDGE GAPS

Compilation of this review has identified some clear gaps in our knowledge of climate change impacts on shallow and shelf subtidal habitats and ecology. Generating insight in these areas will allow scientists to provide better advice to policy makers, supporting the implementation of climate-related policy. Priority gaps a.) and c.) remain as in the previous ARC science review. We have altered our second priority from understanding ecosystem-level consequences of climate change through increasing knowledge of bentho-pelagic coupling and food web links, to understanding the individual and in-combination effects of multiple stressors in addition to climate change. While it clearly remains extremely important to understand ecosystem ramifications, we must first be able to adequately demonstrate that biological changes are due to climate influence and not other co-variables and understand how climate acts in concert with other stressors.

a. There is a paucity of large scale benthic biological data for UK, Crown Dependency and Irish waters, which hinders our ability to detect changes in species distribution over large areas of the sea bed. Such information, when combined with long-term monitoring and experimental studies of the effects of climate change, will allow us to identify change when it occurs and more confidently describe patterns of benthic response. The contributions of informal observers (e.g. recreational divers) are important here, as providing fully-funded monitoring programmes to cover the entire sea bed is not possible. Naturalists' observations of possible range extensions and reductions, as well as the occurrence of mass events (such as disease, die-off or mass-recruitments) can provide indications that changes are taking place and trigger formalised monitoring programmes in affected areas.

b. As more evidence of climate change effects emerges, what has become clear is that we are not paying enough attention to other natural and anthropogenic factors that also shape benthic assemblages - many studies to date have focused on climate parameters and have not explicitly considered the effects of other variables (see, for example, climate and fishing effects on benthos, Kröncke, 2011). It is imperative that we address potentially confounding factors in order to show causality for climate parameters and to understand how other factors may strenghten, weaken or confound climate effects.

c. There is a real gap in our ability to make predictions about the responses of subtidal species and communities to future climate change. We have the capability to generate such information through statistical modelling techniques, which are receiving increasing attention, yet, with the exception of fish and commercially important invertebrate species, they have not been applied in earnest to UK benthic assemblages. We need to further our capacity to model species' distributional responses to changing conditions and develop a knowledge-base that will allow us to understand the underlying mechanisms and ecosystem-level implications of such changes.

4. SOCIO-ECONOMIC IMPACTS

Little information is available on the current or future socio-economic effects of climate change on shallow and shelf subtidal habitats and ecology. However, some general areas of concern can be identified based on the evidence presented in the review.

Marine protected areas and conservation zones

Marine policy has advanced since the last ARC science review and, in UK waters, the advent of Marine Conservation Zones (MCZ; see http://www.defra.gov.uk/environment/marine/protect/mpa/mcz/) has added a new level of protection to many coastal areas. Although there is currently little direct evidence of warming-related subtidal species distribution shifts, any such shifts occurring in future will have socio-economic ramifications if they push species of conservation concern outside the boundaries of areas designed for their protection, especially if they are pushed into unsuitable habitat.

For example, maerl and *Lophelia pertusa* have restricted distributions around the UK and Ireland and are protected under Annex I of the EU Habitats Directive - maerl habitats are qualifying features of the UK Sound of Arisaig, Loch nam Madadh, Strangford Lough and Fal and Helford marine Special Areas of Conservation (SAC) and Ramsey Bay and Ballacash Channel proposed Manx Marine Nature Reserve, while *Lophelia pertusa* reefs are primary features or features of the Darwin Mounds and North West Rockall Bank candidate offshore SAC and East Rockall Bank, Mingulay SAC, Hatton Bank and Anton Dohrn Seamount possible offshore SAC (www.jncc.gov.uk) and Porcupine Seabight, Hovland Mound and Belgica Mound Irish SAC. Others, such as the horse mussel *Modiolus modiolus*, the honeycomb worm *Sabellaria alveolata* and the pink seafan *Eunicella verrucosa*, also have restricted distributions and conservation importance at national or international levels. Temperature-driven range contractions in these species may necessitate boundary-alterations in marine protected areas and conservation zones, which are likely to be socially, politically and financially demanding. Even if temperature-driven changes do not result in such extreme scenarios, alterations in the abundance or spatial distribution of conservation species may affect the type and extent of commercial and recreational activity permitted within these zones in future.

Range-expansions are likely to be less problematic, unless they introduce new species of conservation concern into UK waters. Range expansions may benefit recreation and tourism, if they introduce charismatic species into reserves, or lead to economic benefits if they either increase commercial fisheries stocks, or allow the development of novel fisheries. However, expansions of warm water species into UK waters may be detrimental to the economy if they cause a reduction in local fisheries stocks through competition or predation.

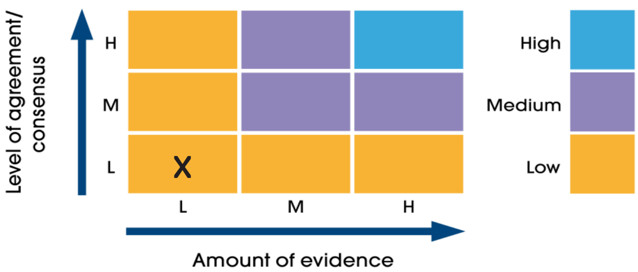
Indirect effects on fish and fisheries

Many fish species feed on benthic organisms and climate-driven impacts on benthic communities have the potential to influence population dynamics of fish predators. If changing distributions or abundance of prey species have significant effects on numbers of commercially-important predators, which themselves may be climate-stressed (see the Fish and Fisheries ARC science review), this is likely to have economic repercussions for the fishing industry. Little information is available on the socio-economic value of benthic prey and it is not clear how to value them. Moreover, we do not know whether fish predators and their benthic prey will respond in concert to changing seawater temperatures or ocean acidification, or how impacts on one trophic level will filter through others, making the situation very complex.

5. CONFIDENCE ASSESSMENTS

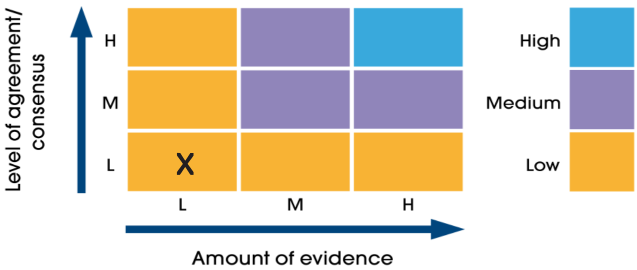
What is already happening?

Site-specific research provides strong evidence on the potential effects of climate change on benthic habitats and species in the Northern and Southern North Sea. Whilst this information is appropriate on a localised scale and for individual ecosystem components (e.g. plankton, fish, etc.), there is a need to understand how these components are linked and responding over larger spatial scales. There are indisputable gaps in coverage of some Charting Progress regions, where we have limited information on benthic status and potential responses to climate change. Additionally, in the areas where we currently have a comprehensive understanding of benthic species and communities, there is still a need to explore interactive effects of multiple human pressures (e.g. fishing, aggregate extraction, dredging and construction) as this information is essential for assessing the impacts of climate change in UK waters. Based on the reviewed information on current benthic state and gaps in knowledge, our confidence level is low.



What could happen?

We have indirect evidence of warming effects on maerl and *Lophelia* habitats, based on laboratory observations of temperature sensitivity in the individual species. However, there are current programmes (e.g. nationally via the benthic UKOA) which will help to advance our understanding of how changes in the reefs and maerl matrices will affect the communities they support. The science relating to acidification effects on particular benthic species is sound, but further evidence is required on a wider range of species and whole-community, over different functional effects, in relation to other stressors and ecological interactions. Information on ocean acidification predictions, including changes in carbonate chemistry: mainly pH, total alkalinity (TA) and dissolved inorganic carbon (DIC) is included in Williamson *et al*., 2012/13 ocean acidification report card. We currently lack the capability to make quantitative predictions about the nature and extent of any future temperature-driven shifts in benthic species distributions. Hiscock *et al.* (2004) have developed a conceptual framework for identifying species potentially affected by future temperature increases and quantitative models for predicting future distributions have been developed for marine fish. However, we are, as yet, unaware of such models being developed for predicting future species distributions or community-level effects in marine benthos. The lack of such predictive capability for both warming- and acidification-effects makes it difficult to translate evidence on links between climate and benthos into forecasts for future conditions. Additionally, we have little understanding about the interactive effects of ocean warming, stratification and acidification. Based on this information, we place a low level of confidence in our predictions of what could happen in future.



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