

The Impacts of Climate Change on shallow subtidal, shelf and deep-sea habitats relevant to the coastal and marine environment around the UK and Ireland

Hill, E.¹, Grady, L.¹, Vad, J.², and Godwin, L.³

¹ Joint Nature Conservation Committee, Quay House, 2 East Station Road, Fletton Quays, Peterborough, PE2 8YY

² School of Geosciences, University of Edinburgh, Grant Institute, King's Buildings West Mains Road, EH9 3JW, Edinburgh

³ School of Environmental Sciences, University of Liverpool, Liverpool, L69 3GP, UK

KEY FACTS

What is already happening?

- North Sea infaunal (burrowing) species have shifted their distributions in response to changing sea temperature, however, most species have not been able to keep pace with shifting temperature, meaning that species are subjected to warmer conditions. Leading (expanding) edges are responding more quickly than trailing (retreating) edges, which has been observed elsewhere in the world.
- Changes in the relative abundance of several UK kelp species, linked to sea-temperature rise, is leading to alterations in the structure of kelp forest assemblages. This has implications for kelp-forest community structure and habitat resilience.
- Changes in phytoplankton and zooplankton communities attributable to climate change impacts affecting primary production directly alter the flux of Particulate Organic Carbon (POC) to the seabed, therefore reducing food supply to deep-sea organisms.
- Deep-sea sponge communities have shown resilience to changes in prevailing environmental conditions, therefore may be more adapted to climate change, however the impact of ocean acidification on calcareous and siliceous sponges is poorly understood.

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What could happen in the future?

- Modelling suggests that there will be significant shifts in range, distribution and abundance of kelp across the UK by 2050, under low (Representative Concentration Pathways of greenhouse gases,

RCP, 2.6), moderate (RCP 4.5) or high (RCP 8.5) emission scenarios in the future, altering the structure, functioning and ecosystem services provided by kelp forests.

- Modelling of climate-change impacts on benthic infauna and epifauna within the North Sea also shows altered community structures under a range of emission scenarios by end of century. Such changes are likely to have implications for food-web dynamics, fisheries, carbon cycling and ultimately human society.
- Changes in temperature and pH could lead to increased mortality of the reef forming *Desmophyllum pertusum* in situ. Lower pH also increases the dissolution of dead coral framework thereby breaking down the reef infrastructure.
- Projections to end of the century conditions have predicted a severe decline in habitat suitability for cold-water corals, for example *D. pertusum* might see the largest decline in suitable habitat with only 30 to 42% of present-day habitat persisting as climate refugia.
- Global and regional predictions demonstrate that UK deep-sea sediment habitats could be adversely affected by the impact of climate change in terms of primary production, by 2100. Under emissions scenarios RCP 4.5 and 8.5, global declines in seafloor biomass are projected to be <1% by the year 2020, declining by 3% by 2050 and 5.9% by the year 2080.

SUPPORTING EVIDENCE

Introduction

Shallow and shelf subtidal habitats and the communities of species that occupy them are an essential component of the UK's marine ecosystem. These habitats are mainly sedimentary; sediment composition varies depending on tidal regime, wave action and sediment supply. The most species-rich sediments are those that are stable over time and a community may contain over 200 species per square metre (Hiscock, 1996). Shallower depths can be dominated by hard substrata, mainly rocky habitats, characterised by rich kelp forests in the well-lit waters which give way to animal-dominated communities in deeper circalittoral zones supporting a plethora of sessile species. Deep-sea habitats are classified as being below 200 m water depth, or those beyond the continental shelf break. In UK waters, the maximum depth of deep-sea habitats is over 4000 m, located in the Southwest Canyons. A wide diversity of deep seafloor habitats and geological features occurs in UK waters, including submarine canyons, seamounts, cold-water coral reefs and gardens, sponge aggregations and soft-sediment habitats. These support diverse communities of invertebrates. Our knowledge of deep-sea habitats is still limited in relation to the extensive area of unexplored UK waters.

Shallow, shelf and deep-sea habitats and their associated communities are an integral part of a healthy ocean and provide valuable ‘ecosystem services’. In UK waters, such communities support the production of food, climate regulation, flood protection, pollution sinks and recreational and aesthetic benefits (Fletcher *et al.*, 2012). For example, sublittoral sediment communities can provide important nursery grounds for juvenile commercial species such as flatfishes and bass. Offshore, sand and gravel habitats support internationally important fish and shellfish fisheries (BRIG, 2011). Cold-water corals in the North-East Atlantic provide important habitats for fish (Costello *et al.*, 2005; Milligan *et al.*, 2016) and are important reservoirs for – and hotspots of – deep-sea biodiversity. Changes to shallow, shelf and deep-sea habitats resulting from climate-change impacts will likely alter the ecosystem services currently provided.

This report focuses on the key species and communities occurring below low water that are demonstrating ecological responses to changes in sea conditions driven by climate change. These include kelps, infaunal communities, cold-water coral reefs and gardens and deep-sea sponge communities. These communities are classified as ‘threatened and declining’ habitats under OSPAR (2023). They exclude seagrass beds, which are covered by Marsh *et al.* (2026).

Summary of the main physical conditions driving change in the shallow, shelf and deep seas

2024 was the warmest year on record in relation to global temperatures recorded since records began in 1850. 2024 had a global average temperature of 15.10°C; 0.12°C higher than the previous highest annual value in 2023 (Copernicus Climate Service C3S). For 2024, the annual average extra-polar sea surface temperature (SST) was the highest on record, at 20.87°C, 0.51°C above the 1991–2020 average, surpassing the previous records of 2023 (20.80°C) and 2016 (20.61°C). Global SST in March 2024 was the highest monthly value on record (Figure 1). Changes in SST can alter marine ecosystems in several ways.

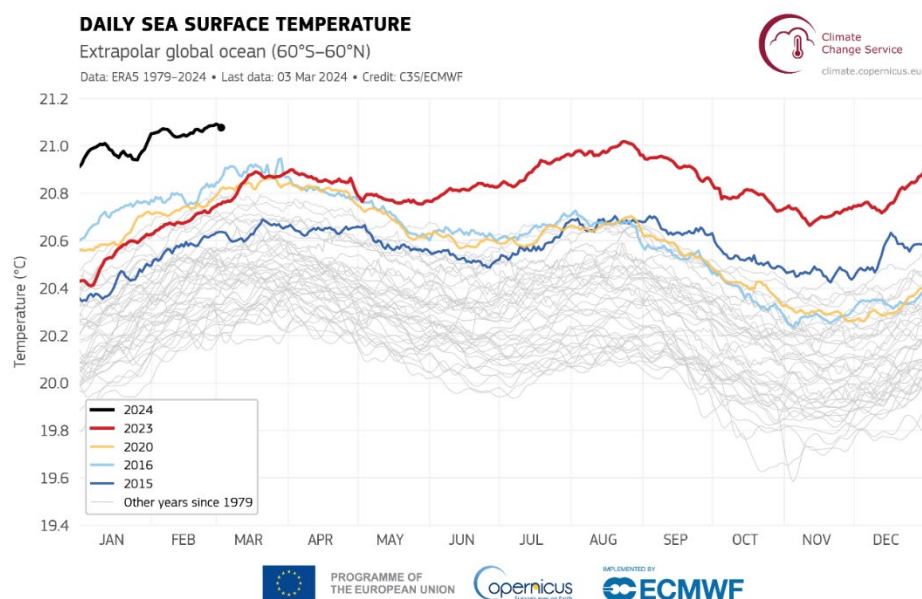


Figure 1. Daily global sea surface temperatures (SSTs) excluding the polar regions showing March 2024 as the warmest global SSTs on record.

Marine Heat Waves (MHWs) are periods of extreme high sea temperature relative to the long-term mean seasonal cycle. While negative impacts on individual species and communities cannot be ruled out, to date there has been no observed impact of altered ocean chemistry in UK shelf waters. MHWs have also recently been shown to be a key driver of species range shifts (Wernberg *et al.*, 2016; Oliver *et al.*, 2018). Biological responses to MHWs occur at the individual, population and community levels and typically intensify toward the warm trailing range edges of species distributions (Smith *et al.*, 2023).

Multiple environmental variables influence deep-sea habitats, which may be further affected by climate change in the future. Particularly relevant to deep-sea habitats in the UK are: (1) temperature, (2) oxygen, (3) pH, (4) hydrographic features and (5) primary production in the surface waters (Sweetman *et al.*, 2017). Changes in these environmental variables will likely affect viable larval recruitment, population dynamics, community structure and ecosystem functioning.

The Atlantic meridional overturning circulation (AMOC) is the system of water currents that drives warm surface water northwards and cold, deep waters back southwards within the Atlantic basin. In addition, it is the main source of oxygen for deep-water ecosystems. Decadal variability in the boundary between subpolar and subtropical waters has caused changes in the proportion of these water masses in the Iceland and Rockall basins, with a greater influence of warm subtropical waters (Spooner *et al.*, 2020). The changing subpolar ocean circulation is also having impacts on deep-sea food supply (McCarthy *et al.* 2023). Temperature in the deep sea has shown no clear trends. In deeper water of the Faroe-Shetland channel (below 1100 m) there was a declining trend in temperatures from the 1950s to the 1990s. Since the 2000s through to the early 2020s an increasing trend is evident (Cornes *et al.*, 2023). Upper ocean waters in the Rockall Trough to the west of the UK (30–800 m), display a similar decadal pattern to the Faroe-Shetland Channel to the north of the UK with a period of elevated temperatures during the mid-2000s, declining thereafter (Cornes *et al.*, 2023). The combination of increasing SST and freshwater input from melting sea ice intensifies stratification in the surface waters and is weakening the AMOC (Defrance *et al.*, 2017).

Increasing SST also impacts deep-sea ecosystems, by decreasing oxygen solubility and impacting hydrographic features. As warming increases stratification, vertical mixing lessens and oxygenated water cannot be transported, creating deoxygenation zones below 1000 m which will further impact conditions for deep sea life to survive. Decreasing ocean pH due to increased CO₂ creates problems for organisms that have hard exoskeletons of calcium carbonate such as cold-water corals and crustaceans, by dissolving their skeletons and therefore reducing their abundance.

In the North-East Atlantic, shifts in phytoplankton community composition, abundance and distribution have been revealed by the Continuous Plankton Recorder surveys (Beaugrand 2009; Hinder *et al.*, 2012; Rivero-Calle *et al.*, 2015; Martinez *et al.*, 2016). These shifts in phytoplankton have been coupled to shifts in community composition, abundance and distribution of zooplankton and higher trophic levels, for example fish, linked to increased temperatures (Beaugrand 2009; Hátún *et al.*, 2009). Changes in phytoplankton and zooplankton communities will directly affect the flux of Particulate Organic Carbon (POC) through the water column to the deep-sea floor, potentially reducing food availability for filter feeding and deposit feeding invertebrates.

WHAT IS ALREADY HAPPENING?

Sublittoral and deep-sea sediment

Pelagic primary production reveals climatic influence (Behrenfeld *et al.*, 2006; Blanchard *et al.*, 2012; Boyce *et al.*, 2010;), with some studies, at a global scale, suggesting increased SST will lead to reduced primary productivity (Behrenfeld *et al.*, 2006). At a regional scale the patterns are more complex, but for much of the British Isles, except for the west coasts of Ireland and Scotland, a negative relationship between increasing SST and primary productivity has been observed (Dunstan *et al.*, 2018). Such a reduction in primary productivity with increased SST is therefore likely to lead to food shortages for smaller bodied infauna and increased community fluctuations.

As each species responds differently to climate change pressures, this will ultimately change how overall communities are structured. Clare *et al.* (2017) analysed data from the Dove Time Series (1972–2012) to investigate the influence of changes in SST and primary productivity (a proxy for food availability) on benthic community structure. In general, large, long-lived fauna experienced changes in relative abundance concordant with changes in food availability. Increased detrital production allowed species that were food limited to increase in abundance and out compete species that had lower energy requirements leading to the observed changes (Clare *et al.*, 2017). Small, generally shorter-lived fauna experienced some changes in community structure related to changes in SST, but this effect was dampened as food availability increased (Clare *et al.*, 2017). Increased food availability nullified the effect of increased temperatures because there was sufficient food to meet the increased metabolic demands associated with increased temperatures.

Hiddink *et al.* (2015) examined geographical and bathymetric shifts of 65 benthic infaunal invertebrates in the North Sea comparing distributions in 1986 with those of 2000. They found temperatures had increased throughout the North Sea coinciding with a north-westerly shift (range-centre, leading and trailing edge) and deepening of many species' ranges. Leading edges expanded faster than trailing edges (Hiddink *et al.*, 2015), which has also been noted in global-scale analyses (Poloczanska *et al.*, 2013).

In the Western English Channel, one study compared benthic communities sampled in 1958/59 with those sampled in 2006 and found no broad-scale temporal differences related to warming, although four warm-water affinity species were detected in the later survey, but not in the earlier one (Hinz *et al.*, 2011). The authors suggest this could have been in response to climate warming (Hinz *et al.*, 2011). More recently, Navarro-Barranco *et al.* (2017) investigated changes in amphipod assemblages between 2008–2014 at station L4, which forms part of the Western Channel Observatory (www.westernchannelobservatory.org.uk) and is one of the best studied marine areas in Europe. Amphipod abundance, richness and community structure were influenced by seasonal and year-to-year variability, however,

increased Sea Bottom Temperature (SBT) resulted in a significant increase in amphipod abundance and richness with this environmental driver accounting for 57% and 23% of the variability in abundance and richness, respectively (Navarro-Barranco *et al.*, 2017).

Although not a UK deep-sea habitat, the Porcupine Abyssal Plain (PAP) Sustained Observatory in the mid-Atlantic, approximately 500 km west of Ireland, has focussed on the study of connectivity between the surface and seabed. In-situ measurements of climatically and environmentally relevant variables have been made for more than 30 years (Hartman *et al.*, 2021). Soft sediment community changes in the PAP have been attributed to variation in the quantity and quality of food supplied to the community via supply of POC, with changes in climate suggested as the contributing factor (Billett *et al.*, 2001; Hudson *et al.*, 2003). Changes in megafauna recruitment, immigration, emigration and mortality related to climate-induced variations in food supply could explain this (Ruhl and Smith, 2004; Horton *et al.*, 2020).

Changes in seafloor community structure are likely to have consequences for carbon cycling and organic matter remineralisation, for example, at the PAP during a period when megafaunal densities were high, the surface sediment was turned over in less than four months (Ginger *et al.*, 2001).

Sublittoral rock and hard substrata

Yesson *et al.* (2015) collated and analysed data on changes in large UK brown algal abundance. At the UK scale, *Chorda filum*, *Laminaria ochroleuca*, *Saccharina latissima* all reduced in abundance, however, for the warm-water species, *L. ochroleuca*, this was not related to changes in temperature. Four kelp species showed significant relationships between abundance patterns and SST with *C. filum* abundance positively correlated with winter SST whereas *L. digitata*, *L. hyperborea* and *S. latissima* abundance was negatively correlated with winter SST. Interestingly, for the cold-water species, *L. digitata* and *L. hyperborea*, abundance was positively correlated with summer SST. Abundance also varied across regions with a general pattern of relative stability or increased abundance through time in northern regions (Scotland, northern England) and a reduction in abundance in southern regions (south-west England). It should be noted that 74% of site-level studies were based on just two time points with only 3% of sites having four temporal observations for any species and therefore the data are better interpreted at a UK scale rather than regional. Results for kelp species from this study should therefore be interpreted with some caution.

The warm-water species, *L. ochroleuca*, reaches its northern range limit in the Western English Channel and Celtic Seas, while the cold-water species, *Alaria esculenta*, reaches its southern range limit in the same region with both species proposed as good indicators for climate-driven changes in abundance and distribution (Mieszkowska *et al.*, 2006; Smale *et al.*, 2014).

There has been an observed increase in the abundance of *L. ochroleuca* linked to increases in SST at sites around Plymouth, Isles of Scilly and Lundy Island, in some cases becoming the dominant species (Plymouth and Isles of Scilly) (Smale *et al.*, 2014; Teagle and Smale, 2018).

Declines in abundance were also noted for *Saccorhiza polyschides* in the Western English Channel and Celtic Seas and *C. filum* and *L. hyperborea* in the English Channel (Yesson *et al.*, 2015). While the decline in *S. polyschides* was not related to changes in SST at the UK scale, the declines in *L. hyperborea* and *C. filum* were correlated with SST (see above). While declines in the dominant intertidal/ shallow subtidal kelp *L. digitata* have not been observed in the UK, declines have been observed along the Brittany, Normandy and French English-Channel coasts which have been linked to harvesting pressures as well as climate change (Raybaud *et al.*, 2013). Given that *L. digitata* found in south-west England occupies the same temperature isotherm as French populations (King *et al.*, 2017) it is highly likely that *L. digitata* abundance will decline in the western English Channel in the near future.

Cold-water coral reefs and gardens

The cold-water coral *Desmophyllum pertusum* forms reefs which may be circular, dome-shaped or elongated, forming distinct patches or arranged in lines of 'islands' along the edges of the continental shelf, sea mounts, offshore banks and other raised seabed features, notably in Hatton Bank, Darwin Mounds and Mingulay reef in north-west Scotland and the Canyons in south-west England. In favourable environmental conditions, reefs can form long banks of coral up to 5 km in length and 1 km wide, reaching heights of 200 m covering several square kilometres. Cold-water coral reefs support a diverse range of other biota (Perry and Tyler-Walters, 2016). Coral gardens can comprise a range of coral types including hard/stony corals, soft corals, black corals, sea pens and gorgonians. Evidence of climate change impacts on coral gardens in UK waters and the North-East Atlantic more generally, is poor.

Laboratory studies have been used to investigate the impact of elevated temperature and lower pH on *D. pertusum*. They show that temperature and pH impact key physiological and metabolic processes including calcification but with the species possibly exhibiting some level of long-term acclimatisation to future conditions (Hennige *et al.*, 2015; Büscher *et al.*, 2017, 2022). Specifically, elevated temperature has been shown to increase *D. pertusum* calcification rate while acidification leads to a decrease (Hennige *et al.*, 2015; Büscher *et al.*, 2022). Effects of temperature could therefore mitigate effects of acidification, when food supply is not limited and higher coral energy demands can be met (Büscher *et al.*, 2017, 2022; Chapron *et al.*, 2021; Gomez *et al.*, 2022). Mitigation of the physiological impacts of these two stressors is also likely to occur at the expense of other metabolic processes (Büscher *et al.*, 2022). Furthermore *D. pertusum* exhibits limited capacity to enhance its feeding behaviour when food availability is temporarily high, contradictory to other coral species

(Büscher *et al.*, 2017; Chapron *et al.*, 2021; Gomez *et al.*, 2022). This would indicate that the ability of *D. pertusum* to cope with changes in temperature and pH could lead to increased mortality in situ. In addition to the ocean acidification effects reported on live *D. pertusum* fragments or colonies, lower pH also increases the dissolution of dead coral framework (Hennige *et al.*, 2015, 2020; Büscher *et al.*, 2022; Wolfram *et al.*, 2022; Krueger *et al.*, 2023) and lead to the development of coralporosis, a weakening of the coral exoskeleton (Hennige *et al.*, 2020).

While previous studies have found that low oxygen concentrations could be stressful for certain species of UK cold-water coral including for reef-forming *D. pertusum*, discoveries of thriving South-East Atlantic deep-sea coral reefs in hypoxic waters have somewhat modulated this perspective. Indeed, *D. pertusum* reefs discovered in the south-east Atlantic show that the coral species is able to thrive in hypoxic (and relatively warm) waters (Hebbeln *et al.*, 2020). Therefore, *D. pertusum* seems to present a higher than previously expected tolerance to low oxygen conditions, partly due to the constant availability of large quantities of high-quality organic matter as food intake (Hebbeln *et al.*, 2020). In addition, it is important to note that *D. pertusum* populations seem to have low adaptive capacities when exposed to a reduction in oxygen concentration (Dodds *et al.*, 2007). Therefore, deoxygenation in UK waters in combination with other stressors should still be considered when investigating the impact of climate change on cold-water corals.

Adequate food supply could be crucial to allow deep-sea corals to maintain in changing seawater conditions. *D. pertusum* reefs have been estimated to require substantial amount of food derived from surface productivity (de Clippele *et al.*, 2021; Maier *et al.*, 2019, 2020, 2023). Yet, modelling studies have found changes in the amount and quality of surface productivity, ultimately impacting what is transported to the seabed (Sweetman *et al.*, 2017). This would suggest the emergence of a ‘disbalanced energy budget’ in cold-water corals (Maier *et al.*, 2023). Consideration of the seasonal variability in food supply to cold-water coral reefs also needs to encompass the impact of seasonality on *D. pertusum* and other coral species physiology and metabolism (van der Kaaden *et al.*, 2021; Maier *et al.*, 2021, 2023; De Froe *et al.*, 2022) as well as the wider reef and coral garden composition (Kazanidis *et al.*, 2021).

Deep-sea sponge aggregations

Overall, there is limited information about the impact of environmental change on deep-sea sponges. Sponges are often presented as potential winners of climate change and broadly expected to be more resilient than other benthic groups such as corals (Bennett *et al.*, 2017; Bell *et al.*, 2018; Scanes *et al.*, 2018; Beazley *et al.*, 2018, 2021). However, differences between species are significant with shallow-water species expected to be more robust to temperature fluctuations than deeper specimens (Guzman and Conaco, 2016; Carballo and Bell, 2017). Broadly temperature along with salinity and silica concentration has been found to drive sponge distribution the North-east Atlantic (Davison *et al.*, 2019; Kazanidis *et al.*,

2019; Burgos *et al.*, 2020; Graves *et al.*, 2023), hinting that deep-sea sponges are associated with specific water masses (Kazanidis *et al.*, 2019; Puerta *et al.*, 2020; Roberts *et al.*, 2021). At small timescales, some deep-sea sponge grounds are known to experience large variation in temperature. In the Faroe-Shetland Channel for example, sponge grounds sit at a depth where temperature can change by up to 7°C within one hour (Bett, 2001; Kazanidis *et al.*, 2019). Nevertheless, sponge mass-mortality events have been observed in Norway, potentially triggered by unusually warm temperatures (Guihen *et al.*, 2012). Experimental work, however, suggests that deep-sea sponges can be resilient to temperature increase alone, showing signs of cellular and metabolic stress but not mortality and good recovery abilities (Strand *et al.*, 2017).

The effect of ocean acidification on deep-sea sponges is poorly studied, with the assumption that (1) calcareous sponges will experience similar impacts to other calcifying organisms under acidified conditions and (2) most other species would be mostly resilient to decrease in pH due to their silica skeletons (Bell *et al.*, 2018). This is confirmed on shallow-water species experimentally (Duckworth *et al.*, 2012) and by studies that have examined organisms in the vicinity of natural CO₂ seeps (Morrow *et al.*, 2015). However, decreased feeding rate has been identified in some deep-sea sponges exposed to lower pH (Robertson *et al.*, 2017). Ocean acidification can impact silica flux from surface to deep waters (Petrou *et al.*, 2019), leading to unclear effects on sponges, which rely on silica to build their skeletons (Maldonado *et al.*, 2019, 2021).

Hindcast modelling studies have shown that deep-sea sponge grounds have persisted despite large variability in organic carbon flux to the sea floor (Samuelsen *et al.*, 2022). This highlights a potential resilience of deep-sea sponge grounds to changes in food supply, possibly through the sponge loop, where sponges recycle organic matter into particulate detritus which acts as a food source (Bart *et al.*, 2021). Sponge density across a shorter 18-year time-series study was shown to fluctuate with food supply at the seabed, highlighting that while assumed slow-growing, sponge populations are dynamic and respond to inter-annual changes (Kahn *et al.*, 2012).

WHAT COULD HAPPEN IN THE FUTURE?

Sublittoral and deep-sea sediments

An Ecological Niche Model (ENM) based on IPCC SRES scenario A1B climate model (Nakicenovic and Swart, 2000; mean 2.8°C; range 1.7–4.4°C) was then used to predict the 2099 distribution of the 75 chosen species. The model predicted bottom temperature increases of 0.15–5.4°C across the North Sea with an increase in salinity of 1.7 in the northern North Sea and off the Dutch coast. For 18 (50%) of 36 epifaunal species the ENM predicted a northward range shift with the brittle star, *Ophiothrix fragilis*, predicted to shift up to 109 km and 65% of all epifaunal species investigated were predicted to shift their range between 10 and 50 km. A further 18 (50%) epifaunal species were predicted to shift southwards with 16 of the 18 species shifting in a south-easterly direction. The hermit crab, *Pagurus prideaux* and its associated cloak anemone, *Adamsia carciniopados* were predicted to shift southwards by 105 km, with 50% of all species predicted to shift 10–50 km. A greater number of infaunal species are expected to shift their distribution in a more-expected northward direction (77%). Shifts of 60 km or more were predicted for the bivalves *Nucula nitidosa* (60 km) and *Ennucula tenuis* (76 km), the brittle star *Acrocnida brachiata* (60 km), the amphipod *Harpinia antennaria* (75 km) and the mollusc *Chaetoderma nitidulum* (88 km). Overall, 60% of species were predicted to shift ranges by 10–50 km towards the north. Only 9% of infaunal species were predicted to shift range towards the south (Weinert *et al.*, 2016). The potentially unexpected southward shifts particularly for epifauna, may be a consequence of regional conditions and other interacting affects (Junker *et al.*, 2012; VanDerWal *et al.*, 2012) as well as a key habitat barrier in the North Sea being the 50 m contour separating the shallow southern North Sea with the deeper northern North Sea. That may act as a barrier to northward extension of some species (Weinert *et al.*, 2016).

In terms of changes in habitat space, 58% of epifauna and 72% of infauna were predicted to see a reduction in the availability of suitable habitat, while 38% of epifauna and 2% of infauna were expected to experience range expansion. Changes in community structure could alter ecosystem functioning and trophodynamics of North Sea benthic habitats. In turn this may impact important ecosystem services, for example biogeochemical processes, nutrient cycling, water quality and fisheries. The northward movement and therefore predicted loss of ecosystem engineers such as the burrowing shrimp *Callianassa subterranea* and the sea urchin *Brissopsis lyrifera* could alter community structure and ecosystem functioning (Weinert *et al.*, 2016). At the same time, changes in the distribution and abundance of benthic communities may alter trophodynamics and competition (Kirby *et al.*, 2007). However, such ecosystem-level responses will depend on the species involved, with some studies suggesting ecosystem functioning and service provision remaining stable over long periods of time (Frid and Caswell, 2015; Clare *et al.*, 2015).

Projected changes in climate drivers will affect deep-seafloor sediment communities in ways that lead to range shifts (Brito-Morales *et al.*, 2020), loss of suitable habitat (Morato *et al.*, 2020), decreases in food availability and biomass (Jones *et al.*, 2014) and ultimately biodiversity decrease (Levin *et al.*, 2020).

Although predictions of the strength of decline in POC flux both through the water column and at the seafloor vary, the consensus is that POC flux to benthic habitats will decline under future climate simulations as increased stratification and slowed mixing reduces the nutrient supply for primary production at the ocean's surface and the reduction in POC flux will be the largest in the Atlantic Ocean, at depths relevant to UK deep-sea environments (Sweetman *et al.*, 2017). Ultimately this will result in a reduction of food and chemical energy supply for deep-seafloor habitats (Jones *et al.*, 2014; Yool *et al.*, 2017). Reductions in POC flux to deep-sea habitats are likely to be exacerbated by the combined impacts of climate change which lead to increased freshwater input from melting sea ice and weakening circulatory systems (Kwiatkowski *et al.*, 2019).

Declines in global seafloor biomass are predicted for the near future (2050) and end of century. Under Representative Concentration Pathways (RCP) emissions scenarios 4.5 and 8.5 (IPCC, 2014), global declines in seafloor biomass were projected to decline 4% by 2050 and 5.9% by the year 2080. In the North-East Atlantic, these projections are higher: a 19.5% decline in benthic biomass by 2090 is predicted under RCP 4.5 and by 38.5% under the RCP 8.5 (see Figure 2) (Jones *et al.*, 2014). These global and regional predictions demonstrate that UK deep-sea habitats are likely to be adversely affected by the climate change impacts in terms of primary production, by 2100.

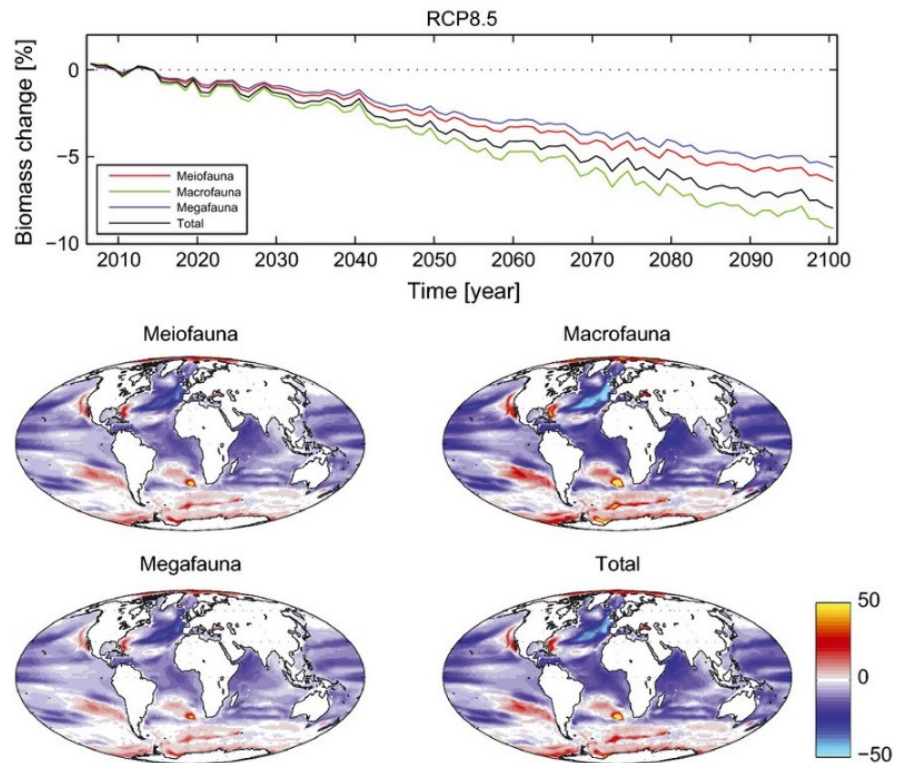


Figure 2. Changes in benthic biomass between 2006–2015 and 2091–2100 under scenario RCP8.5. The graph shows projected changes in biomass of metazoan size-categories of benthos across the modelled time series (as annual means). The maps below show percentage changes in multi-model mean benthic biomass on seafloor (mg C m^{-2}). Benthic biomasses are presented as totals (metazoans only) and split into three size classes. (Source: Jones *et al.*, 2014.)

Sublittoral rock and hard substrata

ENMs provide predictions of changes in the abundance and distribution of European kelp species to future warming. Depending on the magnitude of warming their models suggest that there will be a reduction in the abundance of *L. digitata* across much of southern and central England and Wales (English Channel, Western English Channel, Celtic Seas and Irish Sea) with 50 to 100% of their model runs predicting loss of this species in parts of these regions by 2050 under RCP 2.6, 4.5 and 8.5 scenarios. By 2050 it is likely that Scottish populations will also have experienced a reduction in abundance, however, this species is likely to persist in Scotland beyond the end of the century (Raybaud *et al.*, 2013). Another study using ENMs based on two climate models (AOGCM and MIROC5) and two climate change scenarios (RCP2.6 and 8.5) predicted by 2090–2100 that the warm-water kelp *L. ochroleuca*, currently limited to south-west England, would remain stable in its current range, but expand through south-west England and Wales under RCP 2.6 and throughout the entire UK where suitable habitat exists (i.e. southern and south-west England, Wales, Northern Ireland and western and northern Scotland, including the Orkney and Shetland Islands) under RCP8.5 (Assis *et al.*, 2018). In contrast, *L. hyperborea* and *A. esculenta* would be lost from southern England and Wales under RCP8.5 but persist in these regions under RCP2.6 (Assis *et al.*, 2018). Under RCP 8.5, losses of *S. latissima* and *L. digitata* are predicted in

south-west England by 2090–2100, but these species remain stable throughout the rest of the UK (Assis *et al.*, 2018). The predicted range contraction for *L. digitata* is slightly more conservative than that reported by Raybaud *et al.* (2013) and is likely a result of different methodologies, climatic predictors and climate models used. Assis *et al.* (2018) also suggested that *S. polychides* populations would remain stable in the UK.

Changes in the relative abundance or distribution of different kelp species may, therefore, have knock-on effects for the wider community. While superficially similar, recent research has demonstrated that stipes of the cold-water species dominant, *L. hyperborea* support 12 times as many sessile taxa (flora and fauna) and over 3600 times as much epibiota biomass as the warm water species, *L. ochroleuca* (Teagle and Smale, 2018). Teagle and Smale (2018) also showed that holdfast communities differed between these species, though to a lesser extent than the stipes, supporting previous research which compared *L. ochroleuca* holdfast communities with the colder-water species *L. digitata* (Blight and Thompson, 2008). Collectively these results suggest that climate mediated changes in kelp identity may result in wide-scale ecological change that has implications for higher order consumers such as crustaceans and finfish and therefore fisheries and society.

Maerl beds are made up of living and dead calcareous red algae and support high levels of diversity and are particularly susceptible to changes in ocean carbonate chemistry. Increases in SST/SBT are also likely to impact maerl beds as the development of reproductive conceptacles and growth optimally occur at lower temperatures than those predicted for UK waters into the future (Martin and Hall-Spencer, 2017).

Cold-water coral reefs and gardens

Ocean acidification could threaten scleractinian corals, due to their aragonitic skeletons and gorgonians that secrete magnesium carbonate (Kenchington *et al.*, 2012, Büscher *et al.*, 2022). However, experiments suggest that scleractinian corals demonstrate high resilience to ocean acidification alone and in combination with ocean warming, due to their capacity to increase pH within their internal calcifying fluid inducing carbonate precipitation (FAO, 2019).

Continued decrease in pH will also increase the dissolution of dead framework (Hennige *et al.*, 2015, 2020; Büscher *et al.*, 2022; Wolfram *et al.*, 2022; Krueger *et al.*, 2023), which can form about 70% of the *D. pertusum* coral colonies (Vad *et al.*, 2017). Dissolution of dead coral material through the development of coralporosis (Hennige *et al.*, 2020) is expected to lead to potential collapse of the reef framework and loss of complexity in these habitats, with potentially large consequences on the associated fauna (Hennige *et al.*, 2020; Barnhill *et al.*, 2022). Ocean acidification might be advantageous to boring sponges (Duckworth and Peterson, 2013; Wisshak *et al.* 2014), which could accelerate the collapse of reef frameworks but the bioerosion process in the deep sea is currently

poorly understood (Büscher *et al.*, 2019). Dissolution will become a threat of particular importance for deeper scleractinian coral habitats where the aragonite saturation horizon could shoal above current cold-water coral reefs (Hennige *et al.*, 2023). Shallower cold-water coral reefs in UK waters such as the Mingulay reef complex are not expected to be exposed to aragonite undersaturated waters and might therefore constitute a refugia for *D. pertusum* (Findlay *et al.*, 2013, 2014).

Caryophyllidae species have also been shown to tolerate decreases in pH (Gori *et al.*, 2016, in Last *et al.*, 2019). However, these studies do not consider the impact of acidification in combination with reduction of POC flux. If food supply reduces, this could result in a shift in energy allocation away from calcification and growth (FAO, 2019; Sweetman *et al.*, 2017). Research on other corals is limited, but gorgonians have been suggested to be more vulnerable than stony corals to ocean acidification (FAO, 2019). Increasing ocean temperature is more likely to impact coral gardens than acidification, with warming reducing calcification of some scleractinians, such as Caryophyllidae (Gori *et al.*, 2016). However, warming is more likely to impact corals living close to their upper physiological thermal limit such as in the Mediterranean and Gulf of Mexico (Puerta *et al.*, 2016). Knowledge of temperature increases on other coral species is poorly understood. Evidence on impacts of oxygen reductions on coral gardens is limited. However, some research suggests that this can lead to decreased abundance of octocorals, which in turn will impact habitat availability and complexity and reduce associated benthic biodiversity (Sweetman *et al.*, 2017).

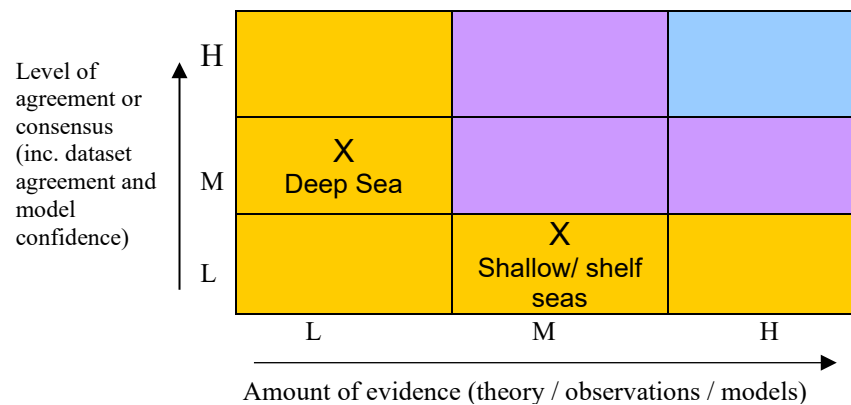
Overall, projections to end of the century conditions have predicted a severe decline in habitat suitability for cold-water corals including *D. pertusum* across the North Atlantic Ocean (Morato *et al.*, 2020). *D. pertusum* might see the largest decline in suitable habitat with only 30 to 42% of present-day habitat persisting as climate refugia, including potential loss of octocoral species (Morato *et al.*, 2020) and changes in particulate organic fluxes, temperature and aragonite saturation horizon drive predicted shift in habitat suitability (Morato *et al.*, 2020; Tong *et al.*, 2023).

Deep-sea sponge aggregations

As deep-sea sponge ground distribution is tightly related to water mass properties and circulation, any changes in ocean circulation due to climate change will lead to change in deep-sea sponge distribution (Puerta *et al.*, 2020; Roberts *et al.*, 2021). Nevertheless, studies considering the long-term temporal variability of water masses over the last 100s to 1000s of years have shown that deep-sea sponge grounds can persist in the face of large past environmental variability (Murillo *et al.*, 2016; Beazley *et al.*, 2018; Samuelsen *et al.*, 2022). The capacity of deep-sea sponge grounds to withstand future climate change is therefore unknown.

CONFIDENCE ASSESSMENT

What is already happening?

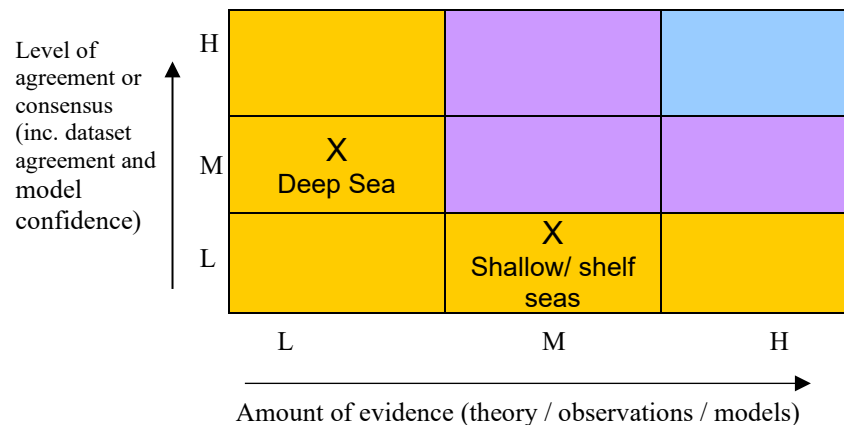


There have been a few studies investigating the impacts of climate change in the UK's shallow and shelf seas since the last relevant MCCIP Report Card in 2020, we would suggest that this is for a limited number of species and either over a very limited spatial scale or a global scale. For example, there is strong evidence that some species of kelp are responding to changes in temperature, but we know little about how this is affecting the large number of species reliant on kelp forests for habitat and food. We are also increasingly confident of the drivers of change in infaunal communities associated with a single long-term monitoring site in the North Sea but have much less knowledge regarding the other regions of the UK. For this reason, we assess that the observational evidence is medium, but the level of consensus remains low.

There is a high level of agreement and medium level of evidence concerning how the environment (food supply, physical oceanography) structures and shapes deep-sea communities and ecosystems. However, there is a medium level of agreement and low amount of evidence concerning how deep-sea habitats are currently being affected by climate change.

There is currently no comparable dataset for the variety of deep-sea habitats that exist within the UK. Even globally, few in-situ observations exist that can confirm the projected consequences of change in deep sea oceanographic conditions to species and productivity redistributions, habitat compression, biodiversity loss and changes in body size (Levin, 2021).

What could happen in the future?



MHWs are predicted to increase in frequency, spatial extent and duration into the future (Frölicher *et al.*, 2018). While there is currently no published evidence of the impacts of MHWs in shallow and shelf seas in UK waters, this is likely to change into the future. ENMs are becoming increasingly sophisticated and estimate current species distributions with some confidence, but again these are limited to a small number of taxa. In addition, such models do not take into account interacting stressors or changes in biotic interactions that may occur in response to climate change. We suggest that the evidence from models is still ‘medium’ since the last review, but the level of consensus is still low due to the limited number of taxa investigated and the range of interacting factors that are not included in ENMs.

There is a medium level of agreement on the possible effects of climate change on UK deep-sea habitats. The models used to predict the effects of climate change on deep-sea habitats are in agreement and there is good consensus on the direction of the effects of climate change. However, the models do not provide a consensus on the magnitude of the effect of climate change on deep-sea habitats and our understanding of species resilience is incomplete. The amount of evidence is low because most of the models provide global or ocean basin level predictions, with few studies providing regional predictions, for example the UK deep sea or even the North Atlantic.

To increase the level of confidence in predictions of the future effects of climate change on UK deep-sea habitats, further modelling studies are required at a local scale, for example specifically within UK waters.

KEY CHALLENGES AND EMERGING ISSUES

- There is clear evidence on the impact of marine heat waves on intertidal and shallow sea communities, however the impact is less well known in the shelf and deep-sea environments. Field-based observational research would be improved with better monitoring of a range of ecological response variables across wider geographical scales, with a focus on regions that are poorly studied but likely affected by MHWs. The usefulness of controlled experiments would benefit from more-sophisticated manipulations involving multiple stressors, simulations of MHWs with different properties and a greater diversity and number of experimental organisms.
- Given the complexity and uniqueness of the region, targeted research is needed to understand the future biogeochemical, ecological and societal consequences, or potential opportunities, of MHWs in UK waters (Jacobs *et al.*, 2024).
- There are few direct observation monitoring programmes in UK waters, therefore it is difficult to observe what impacts climate change is having on them. Deep-sea habitats in UK waters are generally poorly sampled in time and space except for Station M in the Rockall Trough, Darwin Mounds and the Mingulay reef complex, although both sites lack systematic repeat sampling. More investment is required to fully understand what changes in communities are happening in UK waters.
- Regional, rather than ocean-scale, predictions are required to understand how UK habitats will respond to future climate change. Models must consider impacts of multiple stressors on both benthic and pelagic habitats, for example the interaction between ocean acidification and changes in POC.

REFERENCES

- Assis, J., Araujo, M.B. and Serrao, E.A. (2018) Projected climate changes threaten ancient refugia of kelp forests in the North Atlantic. *Global Change Biology*, **24**, E55–E66.
- Barnhill, K. A., Roberts, J. M., Myers-Smith, I., Williams, M., Dexter, K. G., Ryan, C., Wolfram, U. and Hennige, S. J. (2022). Incorporating dead material in ecosystem assessments and projections. *Nature Climate Change*, **13**(2), 113–115. [doi: 10.1038/s41558-022-01565-5](https://doi.org/10.1038/s41558-022-01565-5)
- Bart, M. C., Hudspith, M., Rapp, H. T., Verdonshot, P. F. M. and de Goeij, J. M. (2021) A Deep-Sea Sponge Loop? Sponges Transfer Dissolved and Particulate Organic Carbon and Nitrogen to Associated Fauna. *Frontiers in Marine Science*, **8**, 229. [doi: 10.3389/fmars.2021.604879](https://doi.org/10.3389/fmars.2021.604879)
- Beaugrand, G. (2009) Decadal changes in climate and ecosystems in the North Atlantic Ocean and adjacent seas. *Deep-Sea Research II*, **56**, 656–673. [doi: 10.1016/j.dsr2.2008.12.022](https://doi.org/10.1016/j.dsr2.2008.12.022)
- Beazley, L., Wang, Z., Kenchington, E., Yashayaev, I., Rapp, H. T., Xavier, J. R., Murillo, F. J., Fenton, D. and Fuller, S. (2018) Predicted distribution of the glass sponge *Vazella pourtalesii* on the Scotian Shelf and its persistence in the face of climatic variability. *PLoS ONE*, **13**(10). [doi: 10.1371/journal.pone.0205505](https://doi.org/10.1371/journal.pone.0205505)
- Beazley, L., Kenchington, E., Murillo, F. J., Brickman, D., Wang, Z., Davies, A. J., Roberts, E. M. and Rapp, H. T. (2021) Climate change winner in the deep sea? predicting the impacts of climate change on the distribution of the glass sponge *Vazella pourtalesii*. *Marine Ecology Progress Series*, **657**, 1–23. [doi: 10.3354/meps13566](https://doi.org/10.3354/meps13566)
- Behrenfeld, M.J., O'Malley, R.T., Siegel, D.A., McClain, C.R., Sarmiento, J.L., Feldman, G.C. *et al.* (2006) Climate-driven trends in contemporary ocean productivity. *Nature*, **444**, 752.
- Bell, J. J., Bennett, H. M., Rovellini, A. and Webster, N. S. (2018) Sponges to be winners under near-future climate scenarios. *BioScience*, **68**(12), 955–968. [doi: 10.1093/BIOSCI/BIY142](https://doi.org/10.1093/BIOSCI/BIY142)
- Bennett, H. M., Altenrath, C., Woods, L., Davy, S. K., Webster, N. S. and Bell, J. J. (2017) Interactive effects of temperature and pCO₂ on sponges: from the cradle to the grave. *Global Change Biology*, **23**(5), 2031–2046. [doi: 10.1111/GCB.13474](https://doi.org/10.1111/GCB.13474)
- Bett, B. J. (2001) UK atlantic margin environmental survey: Introduction and overview of bathyal benthic ecology. In *Continental Shelf Research*, **21** (8–10). [doi: 10.1016/S0278-4343\(00\)00119-9](https://doi.org/10.1016/S0278-4343(00)00119-9)
- Biber, M.F., Duineveld, G.C.A., Lavaleye, M.S.S., Davies, A.J., Bergman, M.J.N. and van den Beld, I.M.J. (2014) Investigating the association of fish abundance and biomass with cold-water corals in the deep Northeast Atlantic Ocean using a generalised linear modelling approach. *Deep Sea Research Part II. Topical Studies in Oceanography*, **99**, 134–145.
- Billett, D.S.M., Bett, B.J., Rice, A.L., Thurston, M.H., Galéron, J., Sibuet, M. and Wolff, G.A. (2001) Long-term change in the megabenthos of the Porcupine Abyssal Plain (NE Atlantic). *Progress in Oceanography*, **50** (1-4), 325-348. [doi: 10.1016/S0079-6611\(01\)00060-X](https://doi.org/10.1016/S0079-6611(01)00060-X)

- Birchenough, S.N., Bremner, J., Henderson, P., Hinz, H., Jenkins, S., Mieszkowska, N. *et al.* (2013) Impacts of Climate Change on Shallow and Shelf Subtidal Habitats. *MCCIP Science Review 2013*, 193-203.
- Blanchard, J.L., Jennings, S., Holmes, R., Harle, J., Merino, G., Allen, J.I. *et al.* (2012) Potential consequences of climate change for primary production and fish production in large marine ecosystems. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, **367**, 2979–2989.
- Blight, A.J. and Thompson, R.C. (2008) Epibiont species richness varies between holdfasts of northern and southerly distributed kelp. *Journal of the Marine Biological Association of the United Kingdom*, **88**, 457–469.
- Boyce, D.G., Lewis, M.R. and Worm, B. (2010) Global phytoplankton decline over the past century. *Nature*, **466**, 591.
- BRIG (2011) *UK Biodiversity Action Plan: Priority Habitat Descriptions*. JNCC, Peterborough, 100 pp.
- Brito-Morales, I., Schoeman, D.S., Molinos, J.G., Burrows, M.T., Klein, C.J., Arafeh-Dalmau, N., Kaschner, K., Garilao, C., Kesner-Reyes, K. and Richardson, A.J. (2020) Climate velocity reveals increasing exposure of deep-ocean biodiversity to future warming. *Nature Climate Change*, **10** (6), 576-581. [doi: 10.1038/s41558-020-0773-5](https://doi.org/10.1038/s41558-020-0773-5)
- Burgos, J. M., Buhl-Mortensen, L., Buhl-Mortensen, P., Ólafsdóttir, S. H., Steingrund, P., Ragnarsson, S. and Skagseth, Ø. (2020) Predicting the distribution of indicator taxa of vulnerable marine ecosystems in the Arctic and Sub-arctic waters of the Nordic Seas. *Frontiers in Marine Science*, **7**, 131. [doi: 10.3389/fmars.2020.00131](https://doi.org/10.3389/fmars.2020.00131)
- Büscher, J.V., Form, A.U. and Riebesell, U. (2017) Interactive effects of ocean acidification and warming on growth, fitness and survival of the cold-water coral *Lophelia pertusa* under different food availabilities. *Frontiers in Marine Science*, **4** (April), 249595. [doi: 10.3389/FMARS.2017.00101/BIBTEX](https://doi.org/10.3389/FMARS.2017.00101/BIBTEX)
- Büscher J.V., Wisshak M., Form, A.U., Titschack, J., Nachtigall, K. and Riebesell, U. (2019) In situ growth and bioerosion rates of *Lophelia pertusa* in a Norwegian fjord and open shelf cold-water coral habitat. *PeerJ* **7**, e7586. [doi: 10.7717/peerj.7586](https://doi.org/10.7717/peerj.7586)
- Büscher, J.V., Form, A.U., Wisshak, M., Kiko, R. and Riebesell, U. (2022) Cold-water coral ecosystems under future ocean change: Live coral performance vs. framework dissolution and bioerosion. *Limnology and Oceanography*, **67**(11), 2497–2515. [doi: 10.1002/lno.12217](https://doi.org/10.1002/lno.12217)
- Carballo, J. L. and Bell, J. J. (2017) Climate change and sponges: An introduction. *Climate Change, Ocean Acidification and Sponges: Impacts Across Multiple Levels of Organization*, 1–11. [doi: 10.1007/978-3-319-59008-0_1](https://doi.org/10.1007/978-3-319-59008-0_1)
- Chapron, L., Galand, P. E., Pruski, A. M., Peru, E., Vétion, G., Robin, S. and Lartaud, F. (2021) Resilience of cold-water coral holobionts to thermal stress. *Proceedings of the Royal Society B: Biological Sciences*, **288**(1965). [doi: 10.1098/RSPB.2021.2117](https://doi.org/10.1098/RSPB.2021.2117)
- Clare, D.S., Robinson, L.A. and Frid, C.L.J. (2015) Community variability and ecological functioning: 40 years of change in the North Sea benthos. *Marine Environmental Research*, **107**, 24–34.

- Clare, D.S., Spencer, M., Robinson, L.A. and Frid, C.L.J. (2017) Explaining ecological shifts: the roles of temperature and primary production in the long-term dynamics of benthic faunal composition. *OIKOS*, **126**, 1123–1133.
- Cornes, R.C., Tinker, J., Hermanson, L., Oltmanns, M., Hunter, W.R., LloydHartley, H., Kent, E.C., Rabe, B. and Renshaw, R. (2023) Climate change impacts on temperature around the UK and Ireland. *MCCIP Science Review 2023*, 18pp.
- Costello, M.J., McCrea, M., Freiwald, A., Lundälv, T., Jonsson, L., Bett, B.J., van Weering, T.C., de Haas, H., Roberts, J.M. and Allen, D. (2005) Role of cold-water *Lophelia pertusa* coral reefs as fish habitat in the NE Atlantic. In *Cold-Water Corals and Ecosystems*, Springer, Berlin, Heidelberg, pp. 771–805.
- Davison, J.J., van Haren, H., Hosegood, P., Piechaud, N. and Howell, K.L. (2019) The distribution of deep-sea sponge aggregations (Porifera) in relation to oceanographic processes in the Faroe-Shetland Channel. *Deep-Sea Research Part I: Oceanographic Research Papers*, **146**, 55–61. doi: [10.1016/j.dsr.2019.03.005](https://doi.org/10.1016/j.dsr.2019.03.005)
- de Clippele, L. H., Rovelli, L., Ramiro-Sánchez, B., Kazanidis, G., Vad, J., Turner, S., Glud, R.N. and Roberts, J.M. (2021) Mapping cold-water coral biomass: an approach to derive ecosystem functions. *Coral Reefs*, **40**(1), 215–231. doi: [10.1007/S00338-020-02030-5/FIGURES/9](https://doi.org/10.1007/S00338-020-02030-5/FIGURES/9)
- Defrance, D., Ramstein, G., Charbit, S., Vrac, M., Famien, A.M., Sultan, B. *et al.* (2017) Consequences of rapid ice sheet melting on the Sahelian population vulnerability. *Proceedings of the National Academy of Sciences of the United States of America*, **114**(25), 6533–6538. doi: [10.1073/pnas.1619358114](https://doi.org/10.1073/pnas.1619358114)
- de Froe, E., Maier, S.R., Horn, H.G., Wolff, G.A., Blackbird, S., Mohn, C. *et al.* (2022) Hydrography and food distribution during a tidal cycle above a cold-water coral mound. *Deep Sea Research Part I: Oceanographic Research Papers*, **189**, 103854. doi: [10.1016/J.DSR.2022.103854](https://doi.org/10.1016/J.DSR.2022.103854)
- Dodds, L.A., Roberts, J.M., Taylor, A.C. and Marubini, F. (2007) Metabolic tolerance of the cold-water coral *Lophelia pertusa* (Scleractinia) to temperature and dissolved oxygen change. *Journal of Experimental Marine Biology and Ecology*, **349**(2), 205–214. doi: [10.1016/j.jembe.2007.05.013](https://doi.org/10.1016/j.jembe.2007.05.013)
- Duckworth, A.R., and Peterson, B.J. (2013) Effects of seawater temperature and pH on the boring rates of the sponge *Cliona celata* in scallop shells. *Marine Biology*, **160**(1), 27–35. doi: [10.1007/S00227-012-2053-Z](https://doi.org/10.1007/S00227-012-2053-Z)
- Duckworth, A.R., West, L., Vansach, T., Stubler, A. and Hardt, M. (2012) Effects of water temperature and pH on growth and metabolite biosynthesis of coral reef sponges. *Marine Ecology Progress Series*, **462**, 67–77. doi: [10.3354/MEPS09853](https://doi.org/10.3354/MEPS09853)
- Dulvy, N.K., Rogers, S.I., Jennings, S., Stelzenmuller, V., Dye, S.R. and Skjoldal, H.R. (2008) Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. *Journal of Applied Ecology*, **45**, 1029–1039.

- Dunstan, P.K., Foster, S.D., King, E., Risbey, J., O’Kane, T.J., Monselesan, D. *et al.* (2018) Global patterns of change and variation in sea surface temperature and chlorophyll a. *Scientific Reports*, **8**, 14624.
- Fagerström, V., Broström, G. and Larsson, A.I. (2022) Turbulence affects larval vertical swimming in the cold-water coral *Lophelia pertusa*. *Frontiers in Marine Science*, **9**, 1062884. doi: [10.3389/FMARS.2022.1062884](https://doi.org/10.3389/FMARS.2022.1062884)
- FAO (2019) *Deep-ocean Climate Change Impacts on Habitat, Fish and Fisheries*. FAO Fisheries and Aquaculture Technical Paper No. 638. FAO, Rome, 186 pp. Licence: CC BY-NC-SA 3.0 IGO. Available at: openknowledge.fao.org/handle/20.500.14283/ca2528en
- Findlay, H.S., Artioli, Y., Moreno Navas, J., Hennige, S.J., Wicks, L.C., Huvenne, V.A.I., Woodward, E.M.S. and Roberts, J.M. (2013) Tidal downwelling and implications for the carbon biogeochemistry of cold-water corals in relation to future ocean acidification and warming. *Global Change Biology*, **19**(9), 2708–2719. doi: [10.1111/GCB.12256](https://doi.org/10.1111/GCB.12256)
- Findlay, H.S., Hennige, S.J., Wicks, L.C., Navas, J.M., Woodward, E.M.S. and Roberts, J.M. (2014) Fine-scale nutrient and carbonate system dynamics around cold-water coral reefs in the northeast Atlantic. *Scientific Reports*, **4**, 3671. doi: [10.1038/srep03671](https://doi.org/10.1038/srep03671)
- Fletcher, S., Saunders, J., Herbert, R., Roberts, C. and Dawson, K. (2012) *Description of the Ecosystem Services Provided by Broad-Scale Habitats and Features of Conservation Importance that are Likely to be Protected by Marine Protected Areas In The Marine Conservation Zone Project Area*. Natural England Commissioned Reports, Number 088.
- Frid, C.L.J. and Caswell, B.A. (2015) Is long-term ecological functioning stable: The case of the marine benthos? *Journal of Sea Research*, **98**, 15–23.
- Frölicher, T.L., Fischer, E.M. and Gruber, N. (2018) Marine heatwaves under global warming. *Nature*, **560**, 360–364.
- Gibson, R.N., Atkinson, J.A.R., Gordon, J.D.M., Smith, I.P. and Hughes, D.J. (eds) (2011) Impact of ocean warming and ocean acidification on marine invertebrate life history stages: Vulnerabilities and potential for persistence in a changing ocean. *Oceanography and Marine Biology: An Annual Review*, **49**, 1–42.
- Ginger, M., Billett, D.S.M., Mackenzie, K.L., Kiriakoulakis, K., Neto, R.R., Boardman, D.K., Santos, V.L.C.S., Horsfall, I.M. and Wolff, G.A. (2001) Organic matter assimilation and selective feeding by holothurians in the deep sea: some observations and comments. *Progress in Oceanography*, **50**, 407–421. doi: [10.1016/S0079-6611\(01\)00063-5](https://doi.org/10.1016/S0079-6611(01)00063-5)
- Gómez, C.E., Gori, A., Weinnig, A.M., Hallaj, A., Chung, H.J. and Cordes, E.E. (2022) Natural variability in seawater temperature compromises the metabolic performance of a reef-forming cold-water coral with implications for vulnerability to ongoing global change. *Coral Reefs*, **41**(4), 1225–1237. doi: [10.1007/S00338-022-02267-2](https://doi.org/10.1007/S00338-022-02267-2)
- Gori, A., Ferrier-Pagès, C., Hennige, S.J., Murray, F., Rottier, C., Wicks, L.C. and Roberts, J.M. (2016) Physiological response of the cold-

- water coral *Desmophyllum dianthus* to thermal stress and ocean acidification. *PeerJ*, **4**, e1606. [doi: 10.7717/peerj.1606](https://doi.org/10.7717/peerj.1606)
- Graves, K.P., Bridges, A.E.H., Dabrowski, T., Furey, T., Lyons, K. and Howell, K.L. (2023) Oceanographic variability drives the distribution but not the density of the aggregation forming deep-sea sponge *Phoronema carpenteri*. *Deep Sea Research Part I: Oceanographic Research Papers*, **191**, 103917. [doi: 10.1016/J.DSR.2022.103917](https://doi.org/10.1016/J.DSR.2022.103917)
- Guihen, D., White, M. and Lundälv, T. (2012) Temperature shocks and ecological implications at a cold-water coral reef. *Marine Biodiversity Records*, **5**(3). [doi: 10.1017/S1755267212000413](https://doi.org/10.1017/S1755267212000413)
- Guzman, C. and Conaco, C. (2016) Gene Expression Dynamics Accompanying the Sponge Thermal Stress Response. *PLOS ONE*, **11**(10), e0165368. [doi: 10.1371/journal.pone.0165368](https://doi.org/10.1371/journal.pone.0165368)
- Hartman, S.E., Bett, B.J., Durden, J.M., Henson, S.A., Iveren, M., Jeffreys, R.M., Horton, T., Lampitt, R., and Gates, A.R.. 2021. Enduring science: Three decades of observing the Northeast Atlantic from the Porcupine Abyssal Plain Sustained Observatory (PAP-SO). *Progress in Oceanography* **191**, 201508. [doi: 10.1016/j.pocean.2020.102508](https://doi.org/10.1016/j.pocean.2020.102508)
- Hátún, H., Payne, M.R., Beaugrand, G., Reid, P.C., Sandø, A.B., Drange, H., Hansen, B., Jacobsen, J.A. and Bloch, D. (2009) Large biogeographical shifts in the north-eastern Atlantic Ocean: From the subpolar gyre, via plankton, to blue whiting and pilot whales. *Progress in Oceanography*, **80**, 149–162. [doi: 10.1016/j.pocean.2009.03.001](https://doi.org/10.1016/j.pocean.2009.03.001)
- Hebbeln, D., Wienberg, C., Dullo, W.-C., Freiwald, A., Mienis, F., Orejas, C. and Titschack, J. (2020) Cold-water coral reefs thriving under hypoxia. *Coral Reefs*, **39**, 853–859. [doi: 10.1007/s00338-020-01934-6](https://doi.org/10.1007/s00338-020-01934-6)
- Henderson, P.A. and Bird, D.J. (2010) Fish and macro-crustacean communities and their dynamics in the Severn Estuary. *Marine Pollution Bulletin*, **61**, 100–114.
- Henderson, P.A., Seaby, R.M. and Somes, J.R. (2006) A 25-year study of climatic and density-dependent population regulation of common shrimp *Crangon crangon* (Crustacea : Caridea) in the Bristol Channel. *Journal of the Marine Biological Association of the United Kingdom*, **86**, 287–298.
- Henderson, P.A., Seaby, R.M.H. and Somes, J.R. (2011) Community level response to climate change: The long-term study of the fish and crustacean community of the Bristol Channel. *Journal of Experimental Marine Biology and Ecology*, **400**, 78–89.
- Hennige, S.J., Wicks, L.C., Kamenos, N.A., Perna, G., Findlay, H.S. and Roberts, J.M. (2015) Hidden impacts of ocean acidification to live and dead coral framework. *Proceedings of the Royal Society B: Biological Sciences*, **282**(1813), 1–10. [doi: 10.1098/rspb.2015.0990](https://doi.org/10.1098/rspb.2015.0990)
- Hennige, S.J., Wolfram, U., Wickes, L., Murray, F., Roberts, J.M., Kamenos, N.A., Schofield, S., Groetsch, A., Spiesz, E.M., Aubin-Tam, M.-E. and Etnoyer, P.J. (2020) Crumbling reefs and cold-water coral habitat loss in a future ocean: evidence of “coralporosis” as an indicator of habitat integrity. *Frontiers in Marine Science*, **7**, 559310. [doi: 10.3389/fmars.2020.00668](https://doi.org/10.3389/fmars.2020.00668)

- Hennige, S.J., Mienis, F., Wheeler, A. and Huvenne, V.A.I. (2023) Waters of Ireland and the UK. In *Cold-Water Coral Reefs of the World*, pp. 145–169. doi: [10.1007/978-3-031-40897-7_6](https://doi.org/10.1007/978-3-031-40897-7_6)
- Hiddink, J.G., Burrows, M.T. and Molinos, J.G. (2015) Temperature tracking by North Sea benthic invertebrates in response to climate change. *Global Change Biology*, **21**, 117–129.
- Hinder, S.L., Hays, G.C., Edwards, M., Roberts, E.C., Walne, A.W. and Gravenor, M.B. (2012) Changes in marine dinoflagellate and diatom abundance under climate change. *Nature Climate Change*, **2**. doi: [10.1038/NCLIMATE1388](https://doi.org/10.1038/NCLIMATE1388)
- Hinz, H., Capasso, E., Lilley, M., Frost, M. and Jenkins, S. (2011) Temporal differences across a bio-geographical boundary reveal slow response of sub-littoral benthos to climate change. *Marine Ecology Progress Series*, **423**, 69–82.
- Hiscock, K. (ed) (1996) *Marine Nature Conservation Review: Rationale and Methods*, JNCC, Peterborough, ISBN 1 86107 410 7.
- Horton, T., Thurston, M.H., Vlierboom, R., Gutteridge, Z., Pebody, C.A., Gates, A.R., *et al.* (2020) Are abyssal scavenging amphipod assemblages linked to climate cycles? *Progress in Oceanography*, **184**, 102318. doi: [10.1016/j.pocean.2020.102318](https://doi.org/10.1016/j.pocean.2020.102318)
- Hudson, I.R., Wigham, B.D., Billett, D.S.M. and Tyler, P.A. (2003) Seasonality and selectivity in the feeding ecology and reproductive biology of deep-sea bathyal holothurians. *Progress in Oceanography*, **59** (4), 381–407. doi: [10.1016/j.pocean.2003.11.002](https://doi.org/10.1016/j.pocean.2003.11.002)
- IPCC (2014) *Climate Change 2014: Synthesis Report*. Contribution of working groups I, II and III to the fifth assessment report of the intergovernmental panel on climate change [eds Pachauri, R.K. and Meyer, L.A.]. IPCC, Geneva, Switzerland, 151 pp.
- Jacobs, Z.L., Jebri, F., Wakelin, S., Strong, J., Popova, E., Srokosz, M. and Loveridge, A. (2024) Marine heatwaves and cold spells in the Northeast Atlantic: what should the UK be prepared for? *Frontiers in Marine Science*, **11**, 1434365. doi: [10.3389/fmars.2024.1434365](https://doi.org/10.3389/fmars.2024.1434365)
- Jackson, E.L., Davies, A.J., Howell, K.L., Kershaw, P.J. and Hall-Spencer, J.M. (2014) Future-proofing marine protected area networks for cold water coral reefs. *ICES Journal of Marine Science*, **71**, 2621–2629.
- Jones, D.O., Yool, A., Wei, C.-L., Henson, S.A., Ruhl, H.A., Watson, R.A. and Gehlen, M. (2014) Global reductions in seafloor biomass in response to climate change. *Global Change Biology*, **20**, 1861–1872. doi: [10.1111/gcb.12480](https://doi.org/10.1111/gcb.12480)
- Junker, K., Sovilj, D., Kröncke, I. and Dippner, J.W. (2012) Climate induced changes in benthic macrofauna—A non-linear model approach. *Journal of Marine Systems*, **96–97**, 90–94.
- Kahn, A.S., Ruhl, H.A. and Smith, K.L. (2012) Temporal changes in deep-sea sponge populations are correlated to changes in surface climate and food supply. *Deep Sea Research Part I: Oceanographic Research Papers*, **70**, 36–41. doi: [10.1016/j.dsr.2012.08.001](https://doi.org/10.1016/j.dsr.2012.08.001)
- Kazanidis, G., Vad, J., Henry, L.-A., Neat, F., Berx, B., Georgoulas, K. and Roberts, J.M. (2019) Distribution of deep-sea sponge aggregations in an area of multisectoral activities and changing oceanic conditions. *Frontiers in Marine Science*, **6**. doi: [10.3389/fmars.2019.00163](https://doi.org/10.3389/fmars.2019.00163)

- Kazanidis, G., Henry, L.-A., Vad, J., Johnson, C., de Clippele, L.H. and Roberts, J.M. (2021). Sensitivity of a cold-water coral reef to interannual variability in regional oceanography. *Diversity and Distributions*, **27**, 1719–1731. doi: [10.1111/ddi.13363](https://doi.org/10.1111/ddi.13363)
- Kenchington, E., Siferd, T. and Lirette, C. (2012) *Arctic Marine Biodiversity: Indicators for Monitoring Coral and Sponge Megafauna in the Eastern Arctic*. National Capital Region Research Document 2012/003, Canadian Science Advisory Secretariat, p. 43.
- King, N.G., Wilcockson, D.C., Webster, R., Smale, D.A., Hoelters, L.S. and Moore, P.J. (2017) Cumulative stress restricts niche filling potential of habitat-forming kelps in a future climate. *Functional Ecology*, **32**, 288–299.
- Kirby, R., Beaugrand, G., Lindley, J., Richardson, A., Edwards, M. and Reid, P. (2007) Climate effects and benthic–pelagic coupling in the North Sea. *Marine Ecology Progress Series*, **330**, 31–38.
- Krueger, E.T., Büscher, J.V, Hoey, D.A., Taylor, D., O’Reilly, P. J. and Crowley, Q. G. (2023) Wanted Dead or Alive: Skeletal Structure Alteration of Cold-Water Coral *Desmophyllum pertusum* (*Lophelia pertusa*) from Anthropogenic Stressors. *Oceans*, **4**, 68–79. doi: [10.3390/oceans4010006](https://doi.org/10.3390/oceans4010006)
- Kwiatkowski, L., Naar, J., Bopp, L., Aumont, O., Defrance, D., Couespel, D. (2019) Decline in Atlantic Primary Production Accelerated by Greenland Ice Sheet Melt. *Geophysical Research Letters*, **46**, 11347–11357. doi: [10.1029/2019GL085267](https://doi.org/10.1029/2019GL085267)
- Last, E.K., Ferguson, M. and Robson, L.M. (2019) Mixed coral assemblage on Atlantic mid bathyal *Lophelia pertusa* reef framework (biogenic structure). In *Marine Life Information Network: Biology and Sensitivity Key Information Reviews* (ed Tyler-Walters H.) Marine Biological Association of the United Kingdom, Plymouth. Available at: www.marlin.ac.uk/habitat/detail/1198
- Levin, L.A. (2021) IPCC and the Deep Sea: A case for deeper knowledge. *Frontiers in Climate*, **3**, 720755. doi: [doi: 10.3389/fclim.2021.720755](https://doi.org/10.3389/fclim.2021.720755)
- Levin, L.A., Wei, C.-L., Dunn, D.C., Amon, D.J., Ashford, O.S., Cheung, W.W.L. *et al.* (2020) Climate change considerations are fundamental to management of deep-sea resource extraction. *Global Change Biology*, **26**(9), 4664–4678. doi: [10.1111/gcb.15223](https://doi.org/10.1111/gcb.15223)
- Maier, S.R., Kutti, T., Bannister, R.J., van Breugel, P., van Rijswijk, P. and van Oevelen, D. (2019) Survival under conditions of variable food availability: Resource utilization and storage in the cold-water coral *Lophelia pertusa*. *Limnology and Oceanography*, **64**(4), 1651–1671. doi: [10.1002/LNO.11142](https://doi.org/10.1002/LNO.11142)
- Maier, S.R., Bannister, R.J., van Oevelen, D. and Kutti, T. (2020) Seasonal controls on the diet, metabolic activity, tissue reserves and growth of the cold-water coral *Lophelia pertusa*. *Coral Reefs*, **39**(1), 173–187. doi: [10.1007/S00338-019-01886-6/METRICS](https://doi.org/10.1007/S00338-019-01886-6/METRICS)
- Maier, S.R., Brooke, S., de Clippele, L.H., de Froe, E., van der Kaaden, A.-S., Kutti, T., Mienis, F. and van Oevelen, D. (2023) On the paradox of thriving cold-water coral reefs in the food-limited deep sea. *Biological Reviews*, **98**, 1768–1795. doi: [10.1111/brv.12976](https://doi.org/10.1111/brv.12976)

- Maldonado, M., López-Acosta, M., Sitjà, C., García-Puig, M., Galobart, C., Ercilla, G., and Leynaert, A. (2019) Sponge skeletons as an important sink of silicon in the global oceans. *Nature Geoscience* 2019, **12**(10), 815–822. [doi: 10.1038/s41561-019-0430-7](https://doi.org/10.1038/s41561-019-0430-7)
- Maldonado, M., Beazley, L., López-Acosta, M., Kenchington, E., Casault, B., Hanz, U. and Mienis, F. (2021) Massive silicon utilization facilitated by a benthic-pelagic coupled feedback sustains deep-sea sponge aggregations. *Limnology and Oceanography*, **66**(2), 366–391. [doi: 10.1002/LNO.11610](https://doi.org/10.1002/LNO.11610)
- Marsh, M.K., Pugh, M., Burden, A., Garbutt, A., Harley, J., Jones, L., Angus, S., Amoudry, L.O. and Mieszkowska, N. (2026) Impacts of climate change on coastal and intertidal habitats in the UK. *MCCIP Review 2026*.
- Martin, S. and Hall-Spencer, J.M. (2017) Effects of ocean warming and acidification on rhodolith/maërl Beds. In *Rhodolith/Maërl Beds: A Global Perspective* [eds Riosmena-Rodríguez, R., Nelson, W. and Aguirre, J.]. Springer International Publishing, Cham, pp. 55–85.
- Martinez, E., Raitos, D.E. and Antoine, D. (2016) Warmer, deeper and greener mixed layers in the North Atlantic subpolar gyre over the last 50 years. *Global Change Biology*, **22**, 604–612. [doi: 10.1111/gcb.13100](https://doi.org/10.1111/gcb.13100)
- McCarthy, G.D., Burmeister, K., Cunningham, S.A., Düsterhus, A., FrajkaWilliams, E., Graham, J.A. *et al.* (2023) Climate change impacts on ocean circulation relevant to the UK and Ireland. *MCCIP Science Review 2023*, 29pp. [doi: 10.14465/2023.reu05.cir](https://doi.org/10.14465/2023.reu05.cir)
- Mieszkowska, N., Kendall, M.A., Hawkins, S.J., Leaper, R., Williamson, P., Hardman-Mountford, N.J. *et al.* (2006) Changes in the range of some common rocky shore species in Britain – a response to climate change? *Hydrobiologia*, **555**, 241–251.
- Milligan, R.J., Spence, G., Roberts, J.M. and Bailey, D.M. (2016) Fish communities associated with cold-water corals vary with depth and substratum type. *Deep Sea Research I*, **114**, 43–54. [doi: 10.1016/j.dsr.2016.04.011](https://doi.org/10.1016/j.dsr.2016.04.011)
- Morato, T., González-Irusta, J.-M., Dominguez-Carrió, C., Wei, C.-L., Davies, A., Sweetman, A.K. *et al.* (2020) Climate-induced changes in the suitable habitat of cold-water corals and commercially important deep-sea fishes in the North Atlantic. *Global Change Biology*, **26**(4), 2181–2202. [doi: 10.1111/gcb.14996](https://doi.org/10.1111/gcb.14996)
- Morrow, K.M., Bourne, D.G., Humphrey, C., Botté, E.S., Laffy, P., Zaneveld, J., Uthicke, S., Fabricius, K. E. and Webster, N. S. (2015) Natural volcanic CO₂ seeps reveal future trajectories for host–microbial associations in corals and sponges. *The ISME Journal*, **9**(4), 894–908. [doi: 10.1038/ISMEJ.2014.188](https://doi.org/10.1038/ISMEJ.2014.188)
- Murillo, F.J., Kenchington, E., Lawson, J. M., Li, G. and Piper, D.J.W. (2016) Ancient deep-sea sponge grounds on the Flemish Cap and Grand Bank, northwest Atlantic. *Marine Biology*, **163**(3), 1–11. [doi: 10.1007/S00227-016-2839-5](https://doi.org/10.1007/S00227-016-2839-5)
- Nakicenovic, N. and Swart, R. (eds.) (2000) *Special Report on Emissions Scenarios: A Special Report of Working Group Iii of The*

- Intergovernmental Panel on Climate Change*, Cambridge University Press, Cambridge, UK, 599 pp.
- Navarro-Barranco, C., McNeill, C.L., Widdicombe, C.E., Guerra-Garcia, J.M. and Widdicombe, S. (2017) Long-term dynamics in a soft-bottom amphipod community and the influence of the pelagic environment. *Marine Environmental Research*, **129**, 133–146.
- Oliver, E.C.J., Donat, M.G., Burrows, M.T., Moore, P.J., Smale, D.A., Alexander, L. V. *et al.* (2018) Longer and more frequent marine heatwaves over the past century. *Nature Communications*, **9**, 1–12.
- OSPAR, 2023. Benthic Habitats Thematic Assessment. In: *OSPAR, 2023: Quality Status Report 2023*. OSPAR Commission, London. Available at: <https://oap.ospar.org/en/ospar-assessments/quality-status-reports/qs2023/thematic-assessments/benthic-habitats/>
- Perry, A.L., Low, P.J., Ellis, J.R. and Reynolds, J.D. (2005) Climate change and distribution shifts in marine fishes. *Science*, **308**, 1912–1915.
- Perry, F. and Tyler-Walters, H. (2016) [Lophelia] reefs. In *Marine Life Information Network: Biology and Sensitivity Key Information Reviews* (eds Tyler-Walters H. and Hiscock K.). Marine Biological Association of the United Kingdom, Plymouth.
https://www.marlin.ac.uk/habitats/detail/294/lophelia_reefs
- Petrou, K., Baker, K. G., Nielsen, D. A., Hancock, A. M., Schulz, K. G. and Davidson, A. T. (2019) Acidification diminishes diatom silica production in the Southern Ocean. *Nature Climate Change*, **9**(10), 781–786. doi: [10.1038/s41558-019-0557-y](https://doi.org/10.1038/s41558-019-0557-y)
- Plenty, S.J. (2012) Long-term changes in the zooplankton community of the Bristol Channel. PhD., University of the West of England.
- Poloczanska, E.S., Brown, C.J., Sydeman, W.J., Kiessling, W., Schoeman, D.S., Moore, P.J. *et al.* (2013) Global imprint of climate change on marine life. *Nature Climate Change*, **3**, 919–925.
- Puerta, P., Johnson, C., Carreiro-Silva, M., Henry, L.A., Kenchington, E., Morato, T. *et al.* (2020) Influence of water masses on the biodiversity and biogeography of deep-sea benthic ecosystems in the North Atlantic. In *Frontiers in Marine Science*, **7**, 239. doi: [10.3389/fmars.2020.00239](https://doi.org/10.3389/fmars.2020.00239)
- Raybaud, V., Beaugrand, G., Goberville, E., Delebecq, G., Destombe, C., Valero, M. *et al.* (2013) Decline in Kelp in West Europe and Climate. *PLoS One*, **8**(6), e66044.
- Rees, H.L., Pendle, M.A., Limpenny, D.S., Mason, C.E., Boyd, S.E., Birchenough, S. *et al.* (2006) Benthic responses to organic enrichment and climatic events in the western North Sea. *Journal of the Marine Biological Association of the United Kingdom*, **86**, 1–18.
- Ribes, M., Calvo, E., Movilla, J., Logares, R., Coma, R., and Pelejero, C. (2016) Restructuring of the sponge microbiome favors tolerance to ocean acidification. *Environmental Microbiology Reports*, **8**(4), 536–544. doi: [10.1111/1758-2229.12430](https://doi.org/10.1111/1758-2229.12430)
- Rivero-Calle, S., Gnanadesikan, A., Del Castillo, C.E., Balch, W.M. and Guikema, S.D. (2015) Atlantic coccolithophores and the potential role of rising CO₂. *Science*, **350**, 1533–1537. doi: [10.1126/science.aaa8026](https://doi.org/10.1126/science.aaa8026)

- Roberts, E.M., Bowers, D.G., Meyer, H.K., Samuelsen, A., Rapp, H.T. and Cárdenas, P. (2021) Water masses constrain the distribution of deep-sea sponges in the North Atlantic Ocean and Nordic Seas. *Marine Ecology Progress Series*, **659**, 75–96. [doi: 10.3354/MEPS13570](https://doi.org/10.3354/MEPS13570)
- Robertson, L.M., Hamel, J.F. and Mercier, A. (2017) Feeding in deep-sea demosponges: Influence of abiotic and biotic factors. *Deep-Sea Research Part I: Oceanographic Research Papers*, **127** (July), 49–56. [doi: 10.1016/j.dsr.2017.07.006](https://doi.org/10.1016/j.dsr.2017.07.006)
- Ross, R.E., Alex, W., Nimmo-Smith, M. and Howell, K.L. (2017) Towards “ecological coherence”: Assessing larval dispersal within a network of existing Marine Protected Areas. *Deep-Sea Research Part 1*, **126**, 128–138. [doi: 10.1016/j.dsr.2017.06.004](https://doi.org/10.1016/j.dsr.2017.06.004)
- Ruhl, H.A. and Smith Jr., K.L. (2004) Shifts in deep-sea community structure linked to climate and food supply. *Science*, **305**(5683), 513–515. [doi: 10.1126/science.1099759](https://doi.org/10.1126/science.1099759)
- Samuelsen, A., Schrum, C., Yumruktepe, V.Ç., Daewel, U. and Roberts, E.M. (2022) Environmental change at deep-sea sponge habitats over the last half century: a model hindcast study for the age of anthropogenic climate change. *Frontiers in Marine Science*, **9**, 737164. [doi: 10.3389/FMARS.2022.737164](https://doi.org/10.3389/FMARS.2022.737164)
- Scanes, E., Kutti, T., Fang, J.K.H., Johnston, E.L., Ross, P.M. and Bannister, R.J. (2018) Mine waste and acute warming induce energetic stress in the deep-sea sponge *Geodia atlantica* and coral *Primnoa resedeaformis*; results from a mesocosm study. *Frontiers in Marine Science*, **5** (April). [doi: 10.3389/fmars.2018.00129](https://doi.org/10.3389/fmars.2018.00129)
- Smale, D.A. and Vance, T. (2015) Climate-driven shifts in species’ distributions may exacerbate the impacts of storm disturbances on North-east Atlantic kelp forests. *Marine and Freshwater Research*, **67**, 65–74.
- Smale, D.A., Wernberg, T., Yunnice, A.L.E. and Vance, T. (2014) The rise of *Laminaria ochroleuca* in the Western English Channel (UK) and comparisons with its competitor and assemblage dominant *Laminaria hyperborea*. *Marine Ecology*, **36**(4), 1033–1044.
- Smith K.E., Burrows M.T., Hobday A.J., King N.G., Moore P.J. Sen Gupta, A., Thomsen, M.S., Wernberg, T. and Smale, D.A. (2023) Biological impacts of marine heatwaves. *Annual Review of Marine Science*, **15**, 119–45
- Spooner, P.T., Thornalley, D.J., Oppo, D.W., Fox, A.D., Radionovskaya, S., Rose, N.L., Mallett, R., Cooper, E. and Roberts, J.M., 2020. Exceptional 20th century ocean circulation in the Northeast Atlantic. *Geophysical Research Letters*, **47**(10), p.e2020GL087577.
- Strand, R., Whalan, S., Webster, N.S., Kutti, T., Fang, J.K.H., Luter, H.M. and Bannister, R.J. (2017) The response of a boreal deep-sea sponge holobiont to acute thermal stress. *Scientific Reports*, **7**(1), 1–12. [doi: 10.1038/s41598-017-01091-x](https://doi.org/10.1038/s41598-017-01091-x)
- Strömberg, S. M., and Larsson, A. I. (2017). Larval behavior and longevity in the cold-water coral *Lophelia pertusa* indicate potential for long distance dispersal. *Frontiers in Marine Science*, **4** (December), 319976. [doi: 10.3389/FMARS.2017.00411](https://doi.org/10.3389/FMARS.2017.00411)

- Sweetman, A.K., Thurber, A.R., Smith, C.R., Levin, L.A., Mora, C., Wei, C.-L. *et al.* (2017) Major impacts of climate change on deep-sea benthic ecosystems. *Science of the Anthropocene*, **5**, 4. doi: [10.1525/elementa.203](https://doi.org/10.1525/elementa.203)
- Teagle, H. and Smale, D.A. (2018) Climate-driven substitution of habitat-forming species leads to reduced biodiversity within a temperate marine community. *Diversity and Distributions*, **24**(10), 1367–1380.
- Tong, R., Davies, A.J., Yesson, C., Yu, J., Luo, Y., Zhang, L. and Burgos, J.M. (2023) Environmental drivers and the distribution of cold-water corals in the global ocean. *Frontiers in Marine Science*, **10**, 1217851. doi: [10.3389/FMARS.2023.1217851/BIBTEX](https://doi.org/10.3389/FMARS.2023.1217851/BIBTEX)
- Vad, J., Orejas, C., Moreno-Navas, J., Findlay, H.S. and Roberts, J.M. (2017) Assessing the living and dead proportions of cold-water coral colonies: implications for deep-water Marine Protected Area monitoring in a changing ocean. *PeerJ*, **5**(10), e3705. doi: [10.7717/peerj.3705](https://doi.org/10.7717/peerj.3705)
- van der Kaaden, A.S., Mohn, C., Gerkema, T., Maier, S.R., de Froe, E., van de Koppel, J., Rietkerk, M., Soetaert, K. and van Oevelen, D. (2021) Feedbacks between hydrodynamics and cold-water coral mound development. *Deep Sea Research Part I: Oceanographic Research Papers*, **178**, 103641. doi: [10.1016/J.DSR.2021.103641](https://doi.org/10.1016/J.DSR.2021.103641)
- Van Der Wal, J., Murphy, H.T., Kutt, A.S., Perkins, G.C., Bateman, B.L., Perry, J.J. *et al.* (2012) Focus on poleward shifts in species distribution underestimates the fingerprint of climate change. *Nature Climate Change*, **3**, 239.
- Weinert, M., Mathis, M., Kroencke, I., Neumann, H., Pohlmann, T. and Reiss, H. (2016) Modelling climate change effects on benthos: Distributional shifts in the North Sea from 2001 to 2099. *Estuarine, Coastal and Shelf Science*, **175**, 157–168.
- Wernberg, T., Bennett, S., Babcock, R.C., De Bettignies, T., Cure, K., Depczynski, M. *et al.* (2016) Climate-driven regime shift of a temperate marine ecosystem. *Science*, **353**, 169–172.
- Wisshak, M., Schönberg, C.H.L., Form, A. *et al.* (2014) Sponge bioerosion accelerated by ocean acidification across species and latitudes?. *Helgol Marine Research*, **68**, 253–262. doi: [10.1007/s10152-014-0385-4](https://doi.org/10.1007/s10152-014-0385-4)
- Wolfram, U., Peña Fernández, M., Mcphee, S., Smith, E., Beck, R. J., Shephard, J. D., Ozel, A., Erskine, C. S., Büscher, J., Titschack, J., Roberts, J. M. and Hennige, S. J. (2022) Multiscale mechanical consequences of ocean acidification for cold-water corals. *Scientific Reports*, **12**(8052), 8052. doi: [10.1038/s41598-022-11266-w](https://doi.org/10.1038/s41598-022-11266-w)
- Yesson, C., Bush, L.E., Davies, A.J., Maggs, C.A. and Brodie, J. (2015) Large brown seaweeds of the British Isles: Evidence of changes in abundance over four decades. *Estuarine, Coastal and Shelf Science*, **155**, 167–175.
- Yool, A., Martin, A.P., Anderson, T.R., Bett, B.J., Jones, D.O.B. and Ruhl, H.A. (2017) Big in the benthos: Future change of seafloor community biomass in a global, body size-resolved model. *Global Change Biology*, **23** (9), 3554–3566. doi: [10.1111/gcb.13680](https://doi.org/10.1111/gcb.13680)