

Impacts of climate change on deep-sea habitats, relevant to the coastal and marine environment around the UK

R.M. Jeffreys ¹, L.M. Robson ² and B.E. Narayanaswamy ³

¹ School of Environmental Sciences, University of Liverpool, 4 Brownlow Street, Liverpool, Merseyside, L69 3GP, UK

² Joint Nature Conservation Committee, Monkstone House, City Road, Peterborough, PE1 1JY, UK

³ Scottish Association Marine Science, Scottish Marine Institute, Oban Argyll PA37 1QA, UK

EXECUTIVE SUMMARY

- UK deep-sea habitats are currently undersampled compared to shelf ecosystems, e.g. the North Sea.
- There are no consistently sampled long-term (>30 years) datasets from UK deep-sea habitats that document the extent of natural environmental and biological variability over time.
- UK deep-sea habitats are, and will continue to be, exposed to climate-driven changes, including: variability in food supply, temperature, oxygen, pH and hydrographic features.
- UK deep-sea habitats have been subject to inter-decadal variability in temperature and accumulation of atmospheric CO₂ throughout the water column.
- The Aragonite Saturation Horizon (ASH) has shoaled by 10–15 m in the subpolar North-East Atlantic.
- Models predict that Particulate Organic Carbon (POC) flux to the seafloor in the Atlantic will decrease by up to 15%, resulting in a reduction in benthic biomass of 7% (under Representative Concentration Pathway (RCP) 8.5).
- Models predict a decrease in pH of 0.2 units below 500 m in the North Atlantic, shoaling of the ASH (>1000 m) and exposure of ~85% of cold-water corals in the North-East Atlantic to corrosive waters by 2060.
- Sustained observatories and monitoring programmes are urgently required in UK deep-sea habitats, both at the seafloor and in the water column, to better understand variability of both environmental conditions and biological communities in time and space, and to detect and monitor the impact of climate change. This will enable more-accurate future climate-change predictions and can support progress in conservation measures for the deep sea through the development of appropriate management measures for Marine

Citation: Jeffreys, R.M., Robson, L.M. and Narayanaswamy, B.E. (2020) Impacts of climate change on deep-sea habitats relevant to the coastal and marine environment around the UK. *MCCIP Science Review 2020*, 293–321.

doi: 10.14465/2020.arc14.dsh

Submitted: 07 2019
Published online: 15th January 2020.

Protected Areas (MPAs) and improvements to long-term biodiversity monitoring programmes to assess and mitigate for anthropogenically-induced changes in biodiversity status.

1. INTRODUCTION

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 ~2200 m, located in the Rockall Trough (Figure 1). A wide diversity of 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 (Figure 1). Evidence for fluid venting at the seafloor within UK waters has also been documented, specifically in the Porcupine Seabight, Rockall Plateau and Darwin Mound regions (Hovland, 1990; Masson *et al.*, 2003). In 2013, the first evidence of chemosynthetic fauna associated with fluid venting in UK waters came to light (Oliver and Drewery, 2013), which was further explored via camera survey in 2015 (Neat *et al.*, 2018).

In addition to seafloor habitat, the overlying water column (pelagic zone) also provides habitat for biological communities. Specific deep-sea habitats within the pelagic zone include the mesopelagic, with a depth range of 200 m to 1000 m, and the bathypelagic, with a depth range of 1000 m to 4000 m. Together the meso- and bathy-pelagic zones represent a vast habitat for zooplankton, which includes both the holo- and mero-plankton (resident and larval zooplankton), micronekton, cephalopods, fish and sharks, marine mammals and reptiles. Many of these animals may be resident to UK waters, whereas some will also be visitors undertaking migrations. Deep-sea communities living within both the pelagic and benthic realms consist of a diverse range of fauna, in terms of both size and species diversity, including: archaea, bacteria, fungi, foraminifera, invertebrates, vertebrates and marine mammals.

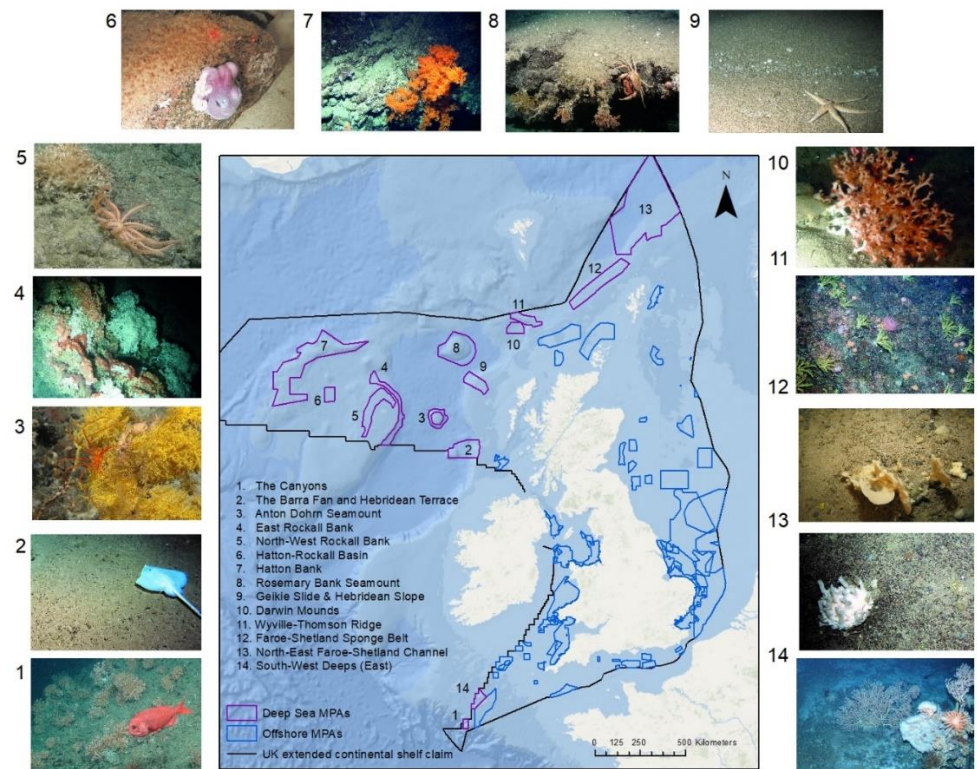


Figure 1: Map of Marine Protected Areas (MPAs, blue polygons) and deep-sea specific MPAs (purple polygons), within offshore waters of the UK extended continental shelf claim (including joint inshore/offshore sites). Photographs represent the diversity of seabed habitats and communities within the deep-sea MPAs. Map and Images from Defra/JNCC. Bathymetry from World Ocean Base (Esri). Copyright: UKCS: Contains public sector information, licensed under the Open Government Licence v.3.0, from the United Kingdom Hydrographic Office.

Despite technological advances in survey and sampling equipment (see Hughes and Narayanaswamy, 2013; Danovaro *et al.*, 2014), optics, image processing and the use of ‘deep learning’ in image analysis (Schoening *et al.*, 2012; Ismail *et al.*, 2018; Lu *et al.*, 2018; Siddiqui *et al.*, 2018) our knowledge of deep-sea habitats is still limited in relation to the extensive area of unexplored UK waters. To illustrate this paucity of knowledge, records were extracted from the Ocean Biogeographic Information System (OBIS: iobis.org) for two key phyla, echinoderms and polychaetes, and were compared for the UK deep sea (depth range 200–2215 m) and the North Sea (depth range 20–162 m). Records of both echinoderms (Figure 2a) and polychaetes (Figure 2b) were higher in the North Sea than in UK deep-sea habitats (Table 1).

Table 1: Number of OBIS records of echinoderms and polychaetes for both UK deep-sea habitats (200 m–2215 m) and the North Sea (20 m–162 m)

	UK Deep-Sea		North Sea
Polychaete records	2236		32 752
Echinoderm records	860		4910

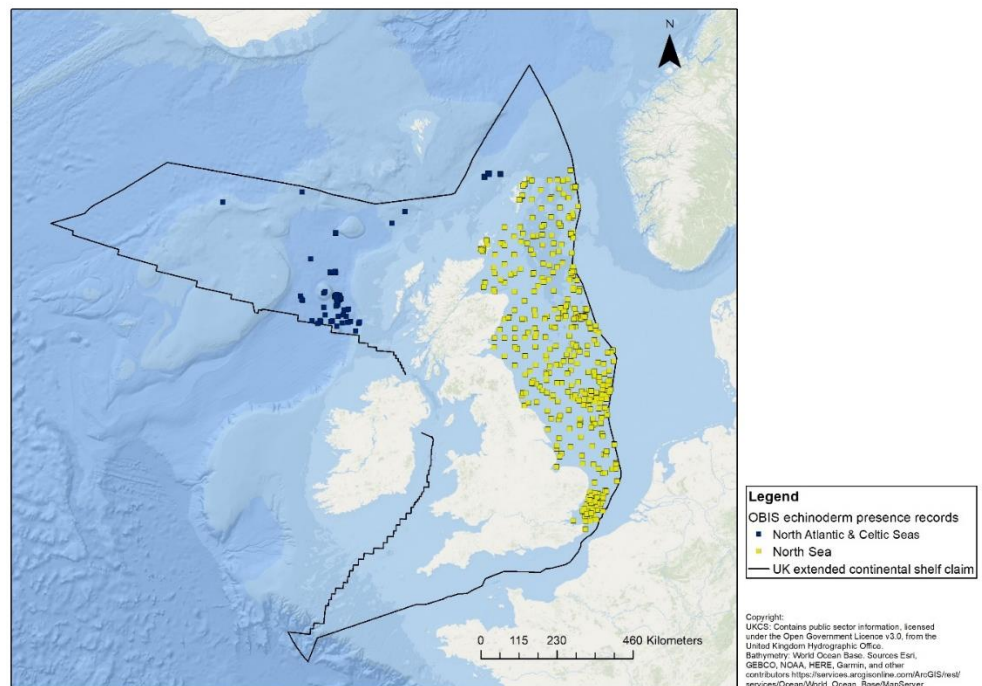


Figure 2a: Ocean Biogeographic Information System (OBIS: iobis.org) presence records for echinoderms within the UK extended continental shelf claim for UK deep-sea waters (purple symbols) and the North Sea (yellow symbols).

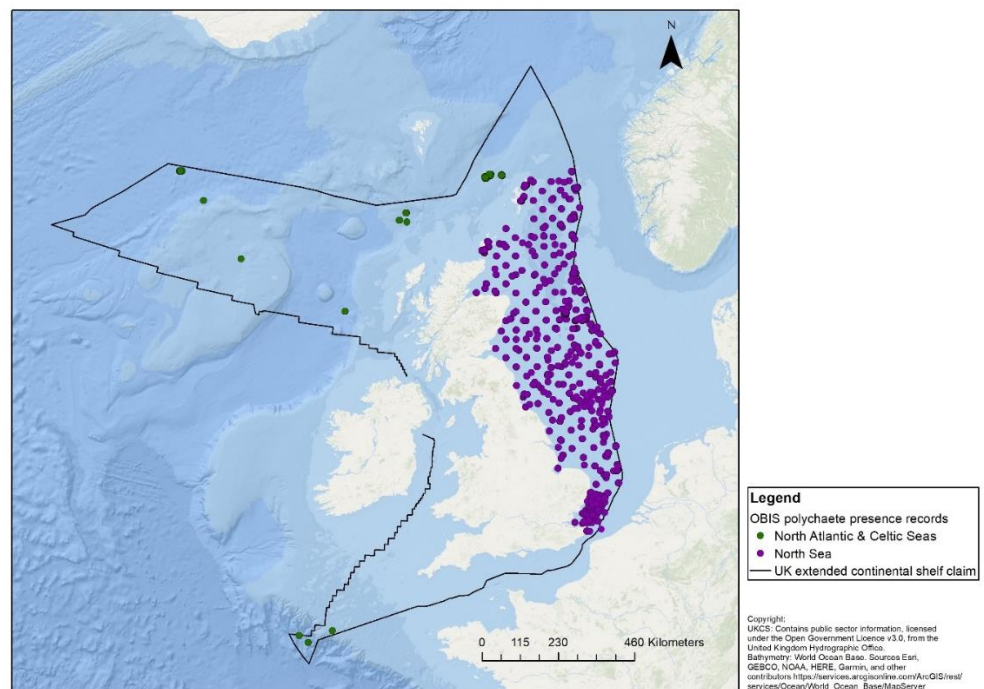


Figure 2b: Ocean Biogeographic Information System (OBIS: iobis.org) presence records for polychaetes within the UK extended continental shelf claim for UK deep-sea waters (green symbols) and the North Sea (purple symbols). (Map from Defra/JNCC.)

Although significant knowledge gaps remain in the UK deep sea, sufficient evidence has been collated to support designation of 14 deep-sea Marine Protected Areas (MPAs) around the UK for the protection of benthic habitats. Two Special Areas of Conservation (SAC) in the Scottish offshore were designated in 2008 and 2011 under the EC Habitats Directive (Darwin Mounds and North West Rockall Bank SACs). Since the 2013 MCCIP Report Card, four additional Special Areas of Conservation in the Scottish offshore and UK's extended continental shelf claim were designated in 2013. Further to this, six Nature Conservation MPAs were designated in 2014, and two Marine Conservation Zones (MCZs) in English offshore waters in 2013 and 2019, under the Marine & Coastal Access Act 2009 (Figure 1). In addition, the North East Atlantic Fisheries Commission (NEAFC) has implemented closures to bottom trawling to protect vulnerable marine ecosystems in five areas of the NEAFC Regulatory Area located within, or partially within, the UK extended continental shelf claim (Recommendation 19 2014: <http://extwprlegs1.fao.org/docs/pdf/mul165665.pdf>).

Deep-sea habitats and their associated communities are an integral part of a healthy ocean and provide valuable 'ecosystem services'. In UK waters, cold-water corals in the North-East Atlantic provide important habitats for fish (Costello *et al.*, 2005; Milligan *et al.*, 2016) as seen on the Hebrides Terrace Seamount, where the stony coral *Solenosmilisa variabilis* provides refuge for skate eggs (Henry *et al.*, 2016). Cold-water coral reefs are also important reservoirs for, and hotspots of, deep-sea biodiversity, for example Freiwald and Roberts, (2005) found that species richness and abundance of fish in the North-East Atlantic was greater on *Lophelia pertusa* reefs than on the surrounding sediment. Deep-sea habitats and communities are also important for the remineralisation of organic carbon and recycling of nutrients, carbon sequestration, and the provision of resources, e.g. oil and gas, and commercially exploited food, e.g. fisheries (Armstrong *et al.*, 2012; Thurber *et al.*, 2014). Recently, deep-sea sponges have been found to harbour important anti-microbial bacteria (Xu *et al.*, 2018). Changes to deep-sea habitats as a result of climate impacts will likely have an impact on the ecosystem services currently provided by the deep sea.

In order to confidently attribute changes in deep-sea habitats to climate change, it is essential to determine natural variation within these systems and establish baselines, and these require long-term temporally resolved observations from time-series studies. Two benthic time-series studies have been carried out by deep-sea scientists from the UK. John Gage and co-workers at the Scottish Association of Marine Science, formerly the SMBA, established 'Station M' at a water depth of 2200 m in the Rockall Trough in UK waters. 'Gage Station M', as it is now known, was sampled on an annual basis from 1973 to 1995 and has since been repeated by Narayanaswamy in 2013, 2015 and 2016. In parallel, the Ellett line, initiated in the Rockall Trough and now extending to Iceland, is a hydrographic time series established by David Ellett in 1975 (Holliday and Cunningham, 2013).

Outside of UK territorial waters, to the south-west of Ireland, the Porcupine Abyssal Plain Sustained Observatory (PAP-SO), established in 1989 at a depth of 4850 m, undertakes regular sampling and observations of the water column and seafloor (Lampitt *et al.*, 2010). More recently, a shorter time-series study (four years) has monitored cold-water coral abundance and diversity on the Irish margin (Boolukos *et al.*, 2019). These time-series records have been instrumental in understanding deep-sea habitats, their ecology and how these systems function and interact with the environment. Additionally, insight into how deep-sea communities have responded to climate change prior to modern deep-sea observational science can be gained from the geological record. However, this is only possible for certain taxa, e.g. scleractinian corals, ostracods and foraminifera.

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

Primary production

The majority of deep-sea communities meet their energetic requirements via primary production originating in the overlying surface waters. The vertical flux of Particulate Organic Carbon (POC) to the seafloor is an important parameter in regulating the standing stock (biomass and abundance), biodiversity and activity of deep-sea organisms from bacteria to megafauna (Rex *et al.*, 2006; Vadaro *et al.*, 2009; Woolley *et al.*, 2016). There is a high degree of natural variation in the quantity and quality of POC reaching the seafloor, which results in a high degree of variation in both the structure and functioning of deep-sea communities (Wolff *et al.*, 2011; Woolley *et al.*, 2016; Laguionie-Marchais *et al.*, 2016). Climate-induced ocean warming could lead to enhanced ocean stratification, reducing nutrient input to the upper euphotic zone and subsequently reducing the export of POC flux to the seafloor (Chust *et al.*, 2014; Doney *et al.*, 2014), which could lead to reductions in biomass of fauna at the seafloor (Jones *et al.*, 2014).

More recently, it has been demonstrated that microbial and archaeal fixation of dissolved inorganic carbon provides a substantial pool of new organic carbon, which is thought to sustain the mesopelagic, bathypelagic and sedimentary microbial food webs in the North Atlantic (Reinthal *et al.*, 2010; Guerrero-Feijóo *et al.*, 2018).

Temperature

Global mean sea-surface temperatures (the upper 75 m of the water column) have increased by 0.11°C per decade between 1971 and 2010 (IPCC, 2014) but temperatures in the deep sea are generally thought to be low and stable (McClain *et al.*, 2012; Levin and LeBris, 2015). However, the Intergovernmental Panel on Climate Change Assessment Report 5 (IPCC, 2014) states that it is “*virtually certain that the upper 700 m of the ocean warmed from 1971 to 2010, and it is likely that the ocean warmed from depths of 700 m to 2000 m from 1957 to 2009, and from depths of 3000 m to the seafloor from 1992 to 2005.*” Many biochemical and organismal processes are controlled by temperature, and metabolic rates of marine species are known to increase with temperature (Hochachka and Somero, 2002). The geological record has also demonstrated that temperature is considered to be a key environmental stressor for deep-sea communities at the higher and lower ends of the temperature scale in the deep sea (Yasuhara and Danovaro, 2016).

Oxygen

Oxygen is an essential requirement for respiration, sustaining metabolic processes and growth (Pörtner and Knust, 2007). However, dissolved oxygen has declined in the global ocean since the 1960s (IPCC, 2014; Oschlies *et al.*, 2018) and oxygen is predicted to decrease further during the 21st century in response to warming sea-surface temperatures because oxygen is less soluble in warm waters (Mahaffey *et al.*, 2020).

pH

Increases in ocean acidification (lowering of seawater pH via an increase in hydrogen ions) have been predicted by Earth system models under all Representative Concentration Pathways (RCPs; IPCC, 2014). Seawater pH has already decreased by 0.12 units compared to pre-industrial levels, as a result of absorption of anthropogenic CO₂ emissions by the oceans (Gattuso *et al.*, 2015; Perez *et al.*, 2018). The lowering of pH in the ocean results in a reduction and decreased saturation state of carbonate ions, which can lead to shoaling of the ‘aragonite saturation horizon’. Most calcifying organisms live above the aragonite saturation horizon, where calcium carbonate does not readily dissolve. Therefore, lowering of ocean pH, and the resultant effects on the aragonite saturation horizon, are likely to affect a number of deep-sea habitats and organisms including: cold-water corals, foraminifera, echinoderms and molluscs. These organisms use calcium carbonate (CaCO₃) to build their skeletons and shells, and ocean acidification will likely lead to their dissolution and decreased calcification. Lower pH has also been shown to lead to depressed feeding activity in deep-sea demosponges (Robertson *et al.*, 2017).

Hydrographic features

Many deep-sea benthic organisms produce larvae, that spend time in the water column (known as the ‘planktonic larval duration’) before settling to the seafloor as an adult. The planktonic larval duration can range from days to months. Whilst in the water column, planktonic larvae are exposed to different hydrodynamic conditions at different depths, examples of which include regional currents, internal waves, tidal currents and both upwelling and downwelling of water masses. The success and health of deep-sea communities and habitats is related to the successful recruitment and settlement of offspring, which could be adversely influenced by climate-induced changes to hydrodynamics.

Hydrographic features are also known to play a role in the delivery of POC to deep-sea habitats and the subsequent biogeochemical cycling of organic matter. For example, neap-spring tidal cycles at the PAP-SO have been shown to affect the aggregation of particles and biogeochemical cycling of organic matter in the benthic boundary layer (Turnewitsch *et al.*, 2017). Similarly, a hydraulic jump or downwelling has been demonstrated to bring fresh particles (food) to cold-water corals (Davies *et al.*, 2008; Roberts *et al.*, 2009; Soetaert *et al.*, 2016). Turbulence has also been shown to deliver oxygen rich waters to seafloor communities (Cyr and van Haren, 2016).

2. WHAT IS ALREADY HAPPENING?

Primary production

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) and increases in phytoplankton, specifically diatoms and coccolithophorids, have been observed (Beaugrand 2009; Hinder *et al.*, 2012; Rivero-Calle *et al.*, 2015). These shifts in phytoplankton have been coupled to shifts in community composition, abundance and distribution of zooplankton and higher trophic levels and linked to increased temperatures (Beaugrand 2009; Hátún *et al.*, 2009). Changes in phytoplankton and zooplankton communities will directly affect the flux of POC through the water column to the deep-sea floor, having an impact on both deep pelagic and benthic communities, e.g. from microbes to large vertebrates and sediment dwelling invertebrates.

Although not a UK deep-sea habitat, the Porcupine Abyssal Plain (PAP) has provided evidence of inter-annual variation in the quantity of POC arriving at the seafloor over two decades between 1989 and 2005 (Lampitt *et al.*, 2010), which have been linked to the North Atlantic Oscillation (Smith *et al.*, 2009). Megafaunal invertebrate densities have varied by several orders of magnitude

over this time period and have been linked to the changes in POC flux (Billett *et al.*, 2010). Inter-annual variation in faunal composition for polychaetes was also noted between 1991 and 1999, and was synchronous with changes in larger megafauna, specifically holothurians (Laguionie-Marchais *et al.*, 2013). 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).

The PAP time-series has provided important insights into how deep-sea communities vary over inter-annual time-scales but there is uncertainty as to whether or not this variability is a direct result of climate change or if it represents natural variability. Henson *et al.*, (2016) concluded that in order to detect a climate change trend in primary production in the surface waters, 32 years of continual sampling is required. The PAP time-series study now reaching its 30th year, but there have been gaps in sampling during this period and so it is not continuous. Furthermore, there is currently no comparable dataset for the variety of deep-sea habitats that exist within the UK continental shelf. Although Station M in the Rockall Trough was sampled continually from 1973 to 1995, it has not been sampled continuously since, and work is still ongoing to analyse those samples.

Temperature

Within UK deep-sea habitats, bottom-water temperatures range from sub-zero, -0.7°C at 800 m in the Faroe Shetland Channel to $\sim 4.5^{\circ}\text{C}$ at 2300 m in the Rockall Trough (Bett, 2001; Holliday *et al.*, 2015). In the mesopelagic zone at 200 m, temperatures are higher at $7\text{--}9^{\circ}\text{C}$ (Bett, 2001; Holliday *et al.*, 2015). Regular time-series sampling of surface waters in the Rockall Trough has been carried out since 1948 by Ocean Weather Ships, the Extended Ellett Line time-series records and more recently with real-time observations by ocean gliders (Sherwin *et al.*, 2012). From these observations three specific periods have been noted: a warmer period from 1945 to 1972 with surface temperatures of $\sim 9.6^{\circ}\text{C}$, followed by a cooler period with temperatures of $\sim 9.1^{\circ}\text{C}$, and a warmer period since 1995 with temperatures of $\sim 10^{\circ}\text{C}$ (Sherwin *et al.*, 2012). However, it is not possible to determine if this is attributable to climate warming or inter-decadal natural variability (Sherwin *et al.*, 2012). Surface-water temperature changes in the Rockall basin are linked to movement and exchange of water masses in the North Atlantic (Sherwin *et al.*, 2012). Early observations of temperatures at 400 m in the Rockall Trough were $\sim 1^{\circ}\text{C}$ higher during the period 1948 to 1965 than between 1876 and 1915 (Smed, 1949; Ellett and Martin, 1973; Sherwin *et al.*, 2012). Periodic shifts in temperature regime within the North-east Atlantic have been coupled with changes in phytoplankton and zooplankton communities (Beaugrand, 2009; Hátún *et al.*, 2009), with potential implications for the POC flux.

Oxygen

Currently the North-east Atlantic Ocean is well-oxygenated compared to other oceanic regions (Sweetman *et al.*, 2017). Oxygen concentrations within the Rockall Trough are in the range of 6.2 mg/litre to 8.4 mg/litre (McGrath *et al.*, 2012) and bottom-water oxygen concentrations in the Porcupine Seabight and Rockall Trough are in the region of 5.7 mg/litre to 7.1 mg/litre (Dullo *et al.*, 2008; Henry *et al.*, 2014; Cyr and van Haren, 2016). Furthermore, in the Whittard canyon, which intersects the Celtic Sea, dissolved oxygen was found to range from 4.8 mg/litre to 10.4 mg/litre over a period of 22 days (Hall *et al.*, 2017). These concentrations are not considered to be hypoxic (i.e. < 2 mg/litre). However, there is some evidence that low oxygen concentrations could be stressful for certain species of UK deep-sea cold-water coral. For example, *Desmophyllum pertusum*, one of the main reef-forming corals found within the UK deep-sea, is typically found in areas with ambient dissolved oxygen concentrations of 6.60 mg/litre to 10.56 mg/litre but is not known to occur at concentrations below 3.38 mg/litre (Davies *et al.*, 2008). This suggests that decreased oxygen concentrations at these levels could have negative effects on this species and associated habitat.

pH

Observations and measurements from the Extended Ellett Line in the Rockall Trough have revealed accumulation of anthropogenic CO₂ throughout the water column, at a rate of 2.8 ± 0.4 mg carbon per m³ per year, double that of the global mean (Humphreys *et al.*, 2016). This has potential negative consequences for the aragonite saturation zone in the area. By comparison, in the Irminger Sea the concentration of carbonate ions has decreased, which has led to shoaling of the aragonite saturation zone by 10–15 metres per year (Perez *et al.*, 2018). In the North-East Atlantic, cold-water coral reefs are found at depths of 50–1000 m, above the aragonite saturation zone (located below 2000 m; Guinotte *et al.*, 2006; Jiang *et al.*, 2015). However, currently, one of the two most-suitable seafloor habitats globally for cold-water corals is located within the deeper aragonite saturation zone of the North-East Atlantic (Tittensor *et al.* 2010). Additionally, it has been found that transport of carbonate ions (required by reef building corals for their skeletons) to the North-East Atlantic deep ocean is now 44% lower than in pre-industrial times (Perez *et al.*, 2018).

Hydrographic features

A number of studies have highlighted that energetic near bottom processes, such as internal tides and waves, hydraulic jumps/flows and enhanced mixing, are important mechanisms for the delivery of POC and oxygen to cold-water coral reefs, sponge grounds and communities found on seamounts (Davies *et*

al., 2008; Duineveld *et al.*, 2012; Henry *et al.*, 2014; Mohn *et al.*, 2014; Cyr and van Haren, 2016; Howell *et al.*, 2016). Furthermore, internal wave reflection and sub-inertial waves are known to aid retention of suspended particulate organic matter at cold-water coral habitats (Hosegood and van Haren, 2004; White *et al.*, 2005; Cyr and van Haren, 2016). In addition, tidally generated internal waves are thought to be important mechanisms in upwelling nutrients to the surface waters and subsequently driving brief pulses of primary productivity above seamounts, which are later exported to depth (Turnewitsch *et al.*, 2016; Gove *et al.*, 2019).

Anthropogenic change is altering the mean state of the North Atlantic Oscillation (NAO; IPCC, 2014). The NAO is correlated with both current strength and circulation in the North Atlantic Ocean (Inall *et al.*, 2009; Chafik, 2012; Woolings *et al.*, 2014). Particle tracking models have shown that dispersal pathways of *Desmophyllum pertusum* larvae were consistent with circulation pathways within the North-East Atlantic and were strongly correlated with the dominant pattern of variability in the NAO (Fox *et al.*, 2016). When the NAO was in positive phase, connectivity of *D. pertusum* was increased within the UK MPA network (Figure 1). However, when the NAO was in negative phase, clusters of the MPA network were isolated and larvae were dispersed into the High Seas (Fox *et al.*, 2016). It is therefore likely that changes in the mean state of the NAO linked to anthropogenic climate change will have implications for dispersal of deep-sea species within UK waters.

The Atlantic Meridional Overturning Circulation (AMOC) is one of the global ocean's major circulation systems, and redistributes heat, nutrients and oxygen between different regions of the ocean. During the last 150 years, the AMOC has weakened and slowed (Caesar *et al.*, 2018; Thornalley *et al.*, 2018). The weakening of the AMOC could also have negative implications for delivery of oxygen and larval dispersal within UK deep-sea habitats.

3. WHAT COULD HAPPEN IN THE FUTURE?

Primary production

Globally, open-ocean primary production will decrease by 2100 (IPCC, 2014). A high greenhouse gas emission scenario (RCP 8.5) could lead to a reduction in primary production of between 6.3% to 8.1% by 2090 (Bopp *et al.*, 2013; Yool *et al.*, 2013; 2017). Reduced primary productivity would lead to an associated decline in export production, predicted to be in the order of 7% to 16% (Bopp *et al.*, 2013; Yool *et al.*, 2017). Declining export production in turn, could result in a reduction of POC at the seafloor, predicted to be around 4% by 2090 under RCP 8.5 (Yool *et al.*, 2017). However, larger declines in export production and seafloor POC have also been predicted. For example, Yool *et al.* (2013) predicted a larger decline in export production (at

1000 m) of up to 40.7% and attributed this to the associated effects of ocean acidification. Sweetman *et al.* (2017) predicted declines in seafloor POC flux from present day to 2100 of between 1.3% to 27% for abyssal habitats, and a change of +4.8% to –36.3% for bathyal seafloor habitats in the Atlantic, whilst Jones *et al.*, (2014) predicted a global reduction of 11.4% in seafloor POC by 2100 (Table 2).

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 deep-sea habitats will decline under future climate-change scenarios. Ultimately this will result in a reduction of food and chemical energy supply for deep-sea habitats both in the water column and at the seafloor.

Recent developments in benthic modelling have also enabled scientists to predict outcomes of future climate change on deep-sea communities at global and regional levels (Kelly-Gerreyn *et al.*, 2014; Jones *et al.*, 2014; Yool *et al.*, 2017). Using empirical analysis, coupled with the ocean biogeochemistry model NEMO-MEDUSA, Jones *et al.* (2014) predicted a global decline in seafloor biomass of up to 5.2% by 2090 (Table 2). This predicted decline in biomass was accompanied by a shift in seafloor community structure, with the largest predicted decrease in macrofaunal (250–520 μm) biomass, followed by megafauna (>10 mm, Jones *et al.*, 2014). Predictions from the BORIS model (a size-resolved benthic biomass model coupled to NEMO-MEDUSA, Yool *et al.*, 2017), were in close alignment with the output produced from the empirical analysis of Jones *et al.* (2014).

Under an RCP 8.5 emissions scenario, Yool *et al.* (2017) also predicted declines in global seafloor biomass between 1990 and 2090 of 0.8% at 200 m, 7.3% at 500 m, 17.8% at 1000 m, 28.9% at 2000 m and 32.0% at 5000 m. In the North-East Atlantic, specifically the Porcupine Abyssal Plain region, a 19.5% decline in benthic biomass is predicted to occur under an RCP 4.5 emissions scenario, decreasing further by 38.5% under the RCP 8.5 emissions scenario by 2090 (Jones *et al.*, 2014). Furthermore, areas with cold-water corals and seamounts, and areas that are heavily fished, are projected to have substantial declines in food availability (POC flux) and seafloor biomass by 2100 (Jones *et al.*, 2014; Table 2). These global and regional (PAP) predictions with emphasis on specific habitats e.g. cold-water corals, canyons and seamounts, demonstrate that UK deep-sea habitats could be adversely affected by the impact of climate change in terms of primary production, by 2100.

Declines in global seafloor biomass are also predicted for the near future i.e. 2020 and 2050 (Table 3). 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.

Table 2: Percentage changes in POC flux and seafloor biomass between 2006–2015 and 2091–2100 under scenario RCP 4.5 and RCP 8.5. (Data from Jones et al., 2014.)

	POC flux to seafloor		Seafloor biomass	
	RCP 4.5	RCP 8.5	RCP 4.5	RCP 8.5
Global	-4.44	-11.4	-2.08	-5.21
Atlantic	-6.86	-15.4	-3.07	-7.23
Bathyal	-4.42	-10.9	-2.26	-5.75
Abyssal	-4.83	-11.9	-2.05	-5.13
Areas with seamounts	-5.44	-13.8	-2.40	-6.06
Areas with cold-water corals	-10.7	-20.9	-3.78	-8.64
Areas with canyons	-4.85	-11.2	-2.34	-5.64
Areas with fishing	-6.11	-14.5	-2.73	-6.44

Table 3: Percentage change in seafloor biomass between 2006–2015 and 2091–2100 under RCP 4.5 and RCP 8.5 for 2020, 2050 and 2080. (Data from Jones et al., 2014.)

Year	RCP 4.5	RCP 8.5
2020	-0.77	-0.99
2050	-2.34	-3.22
2080	-3.46	-5.85

Temperature

The ocean has absorbed > 90% of excess heat in the climate system between 1971 and 2010 (IPCC, 2014). Approximately 30% of this ocean warming has occurred below 700 m and 19% below 2000 m (Balmaseda *et al.*, 2013; Talley *et al.*, 2015). Modelled changes in seafloor temperatures in the Atlantic are predicted to be within the range of -0.4°C to $+1^{\circ}\text{C}$ for abyssal regions (>3000 m) and -0.3°C to $+4.4^{\circ}\text{C}$ for bathyal regions (200 m to 3000 m, Sweetman *et al.*, 2017). The lack of continuous time-series observations for basic physical parameters such as temperature within the UK deep sea, and the lack of knowledge of the thermal tolerance of many deep-sea organisms (Yasuhara and Danovaro, 2016) hampers future predictions of the effect of temperature on deep-sea communities. However, experimental laboratory work and the geological record has provided some insight into the response of deep-sea habitats to temperature. The main focus of this work to date has been on cold-water corals, i.e. *D. pertusum*, which is of specific relevance for UK deep-sea habitats. The optimal temperature range of *D. pertusum* is $4\text{--}12^{\circ}\text{C}$ (Rogers, 1999), however, there is conflicting evidence for the effect of elevated temperatures. Mortality has been observed in *D. pertusum* from the Gulf of Mexico at ambient temperature $+2^{\circ}\text{C}$ (Lunden *et al.*, 2014), whilst, increased growth rates were observed in *D. pertusum* from Norwegian reefs at ambient temperature $+4^{\circ}\text{C}$ (Büscher *et al.*, 2017). At the Mingulay reef

complex POLCOMS-ERSEM models predict that summer water temperatures will increase from 9.6°C to 17.25°C at the surface (0–20 m), and from 9.3°C to 14°C at 100–120 m water depth, by 2080 (Findlay *et al.*, 2013), which is at the upper limit of the thermal tolerance of *D. pertusum* (Brooke and Young, 2009).

The geological record has shown that cold-water coral reef-mound development varied during glacial-interglacial cycles, with warming bottom-waters limiting coral growth in the Gulf of Mexico (Roberts and Kohl, 2018). Geological studies of cold-water corals within the North-East Atlantic (Rockall and Porcupine Seabight) demonstrate that multiple factors are important for cold-water coral mound growth during glacial and interglacial time periods including: temperature, water mass structure and food supply (Raddatz *et al.*, 2014; Bonneau *et al.*, 2018).

Changing ocean temperature will also have a direct influence on larval survival, dispersal, population connectivity, community structure and regional to global scale patterns of biodiversity (O'Connor *et al.*, 2007; Ashford *et al.*, 2018). Many deep-sea species produce larvae with a planktonic life stage and temperature is known to be an important determinant of planktonic larval duration and development (O'Connor *et al.*, 2007; Ouellet and Sainte-Marie, 2018). The rate of early development of *D. pertusum* is temperature dependent, and in a study by Strömberg and Larrson (2017) on the larval behaviour of *D. pertusum* under different environmental conditions, development time was found to be 50% quicker at 11–12°C compared to 7–8°C. Rising ocean temperatures will also have implications for cold-water coral dispersal as planktonic larval development times decreases.

Temperature is also an important determining factor for export flux. The quantity of particulate organic carbon reaching the deep seafloor is dependent on the rate of remineralisation by zooplankton and microbes which degrade the sinking POC in the water column, and this remineralisation rate is dependent on temperature (Iverson and Ploug, (2013). Furthermore, model predictions for declining POC export by 2100 were found to be two-fold greater when temperature-driven metabolic changes to microbial respiration were taken into account, than for model predictions that did not take these effects into account (Cavan *et al.*, 2019).

Oxygen

Declining oxygen in warming oceans poses a serious threat to deep-sea habitats. A detailed discussion of the effects of declining oxygen on marine organisms can be found in Mahaffey *et al.*, (2020). Dissolved oxygen in the Atlantic is predicted to either: (a) remain the same, (b) increase at bathyal depths by 0.03 mg/litre or (c) decline by 0.04 mg/litre at both abyssal and bathyal depths by 2100 (Sweetman *et al.*, 2017). A decline in dissolved

oxygen of 0.04 mg/litre in the Rockall Trough region would result in oxygen concentrations of 4.76 mg/litre to 5.66 mg/litre at the seafloor, compared with current concentrations of 6.2 mg/litre to 8.4 mg/litre (McGrath *et al.*, 2012).

Not many studies have determined oxygen thresholds for North-east Atlantic deep-sea species. Laboratory studies have shown that *D. pertusum* is not able to maintain normal aerobic function below 4.65 mg/litre (Dodds *et al.*, 2007) and complete mortality was observed in laboratory experiments with *D. pertusum* from the Gulf of Mexico at dissolved oxygen concentrations of 2.24 mg/litre (Lunden *et al.*, 2014). However, the predicted decline in dissolved oxygen for the Atlantic by 2100 is still within the previously observed lower dissolved oxygen threshold of 3.38 mg/litre to 4.65 mg/litre for this species (Dodds *et al.*, 2007; Davies *et al.*, 2008; Lunden *et al.*, 2014). The effects of declining oxygen will depend on an organism's sensitivity and tolerance and can be compounded by its thermal tolerances (Pörtner and Knust, 2007). Small decreases in oxygen below an organisms' threshold can be physiologically challenging, for example in demersal fish (Gallo and Levin, 2016).

Periods of cold-water coral presence have alternated over geological history in the Mediterranean Sea (Fink *et al.*, 2012; Stalder *et al.*, 2018). Mediterranean cold-water corals underwent temporary extinction events over several periods, when dissolved oxygen concentrations, reconstructed from the geological record, fell below 2.85 mg/litre (Fink *et al.*, 2012; Stalder *et al.*, 2018). Declining oxygen concentrations in UK deep-sea habitats are likely to have consequences for many organisms, particularly since many species are not adapted to low oxygen environments. A weakened AMOC is likely to impact dissolved oxygen concentrations further.

pH

Models predict that by 2100 the pH at the seafloor in the Atlantic will decrease by a maximum of 0.13 units at abyssal depths, and 0.37 units at bathyal depths (Sweetman *et al.*, 2017). Predictions for seven fully coupled earth system models show that deep-sea habitats below 500 m in the North Atlantic region will experience a reduction in pH of 0.20 units by 2100, and more than 17% of the North Atlantic will likely be affected (Gehlen *et al.*, 2014). Palaeo-evidence suggests that the critical threshold for fauna experiencing a reduction in pH is a decrease of 0.10 to 0.20 units (Gehlen *et al.*, 2014), which indicates that effects on deep-sea fauna could be severe. Within their projections ~ 23% of deep-sea canyons and ~8% of seamounts are expected to experience a reduction of 0.20 pH units, whilst ~15% of canyons and ~3% of seamounts are expected to experience a reduction of 0.30 pH units (Gehlen *et al.*, 2014).

Perez *et al.* (2018) also predict that a doubling of atmospheric anthropogenic CO₂ over the next three decades will reduce the transport of carbonate ions to

the deep subpolar north Atlantic by 64 to 79%. The reduction in the concentration of carbonate ions will cause the aragonite saturation horizon to shoal by 1000 m to 1700 m by 2060 (Perez *et al.*, 2018).

Concomitantly, the AMOC could transfer acidified water southwards, endangering UK cold-water corals and other deep-sea habitats. It has been estimated that ~85% of the North-east Atlantic cold-water corals are likely to be exposed to corrosive waters by 2050 to 2060 (Jackson *et al.*, 2014; Perez *et al.*, 2018). Habitat suitability models predict a substantial decrease in seafloor habitat suitability for cold-water corals in the northern North Atlantic (~30° to 60° N) as a result of predicted changes in ocean carbonate chemistry (IS92a, business as usual by 2099, Tittensor *et al.*, 2010).

Results from the Proudman Oceanographic Laboratory Coastal Ocean Modelling System (POLCOMS), coupled with the European Regional Seas Ecosystem Model (ERSEM), predicts that by 2080 summertime pH will decrease by 0.20 units in both surface and bottom waters at the Mingulay reef complex (Findlay *et al.*, 2013). Therefore, UK deep-sea habitats are likely to be at risk from the effects of ocean acidification, as reductions in pH are below the critical threshold established by Gehlen *et al.* (2014). However, habitat suitability modelling also predicts that seamounts could act as refugia for certain species of cold-water corals in the North-East Atlantic (Tittensor *et al.*, 2010). In geological time there have been several periods of high atmospheric CO₂, which have led to extinctions of corals and other deep-sea fauna and it has been postulated that seamounts acted as temporal refugia for both cold-water corals and other deep-sea fauna during these periods (Vernon *et al.*, 2008; Tittensor *et al.*, 2010).

Numerous laboratory experiments have investigated the response of cold-water corals to ocean acidification (e.g. Maier *et al.*, 2009; Hennige *et al.*, 2014; Lunden *et al.*, 2014). These studies have demonstrated that cold-water corals, e.g. *D. pertusum*, are generally flexible in their response to multiple stressors such as warming and ocean acidification, and can maintain positive growth rates (Lunden *et al.*, 2014). However, when cold-water corals are exposed to conditions of aragonite undersaturation, calcification of the skeletons is close to zero and significant changes in skeletal biomineralisation have been observed (Hennige *et al.*, 2015; Büscher *et al.*, 2017). Higher energetic demands will probably be required in order to sustain calcification of cold-water coral skeletons (Büscher *et al.*, 2017). Thus, ocean acidification at the seafloor is likely to lead to degradation of UK cold-water coral habitats.

Ocean acidification is also likely to impact other taxa.

Experiments conducted at 650 m at the seafloor revealed increased foraging times for the deep-sea echinoid *Strongylocentrotus fragilis*, being 4.7 times longer under high CO₂ conditions (0.46 pH units lower) compared to ambient

conditions (Barry *et al.*, 2014). Thus, ocean acidification can also lead to changes in behaviour, foraging and fitness of taxa.

Oceanic uptake of anthropogenic CO₂ has also altered calcium carbonate concentrations at the seafloor. Observations coupled with a rate model have demonstrated that significant dissolution of sedimentary CaCO₃ has occurred in the western North Atlantic compared to pre-industrial times as a result of anthropogenic CO₂ (Sulpis *et al.*, 2018). Although the North-East Atlantic is currently not experiencing high dissolution of sedimentary CaCO₃ (Sulpis *et al.*, 2018), the acidification of water masses within the Atlantic meridional overturning circulation (Perez *et al.*, 2018) could lead to increased dissolution of sedimentary CaCO₃ within the North-East Atlantic.

Hydrographic features

Reliable predictions of how hydrographic features, such as downwelling, internal tides and internal waves could change in the future are lacking. In nearshore coastal locations, hydrographic features could be affected via stratification. At the Mingulay reef complex, tidal downwelling could be maintained or intensified by 2080 if stratification increases (Lowe *et al.*, 2009; Findlay *et al.*, 2013). Both nearshore- and open-ocean stratification could intensify as the ocean warms (Capotondi *et al.*, 2012). In addition, the interaction of ocean tides with seabed topography leads to internal waves and turbulent mixing, which can also determine the intensity and extent of stratification in the ocean (Jayne *et al.*, 2004) and in turn feedback to primary production.

Cumulative effects of multiple stressors

Many of the climate induced changes discussed here are inextricably linked. Laboratory studies have demonstrated that multiple concurrent stressors, e.g. pH, temperature, dissolved oxygen and food availability could be detrimental to a species' survival (Lunden *et al.*, 2014; Hennige *et al.*, 2015; Büscher *et al.*, 2017). For example, although increased food availability was shown to reduce the impact of ocean acidification on the fitness of *D. pertusum* (Bücher *et al.*, 2017), under an RCP 8.5 emissions scenario, food availability (quality and quantity) is predicted to decline alongside increases in seawater pH, shoaling of the aragonite saturation horizon, lower oxygen concentrations and higher temperatures. This could thus prove fatal for some UK deep-sea habitats.

Other concurrent stressors for UK deep-sea habitats include impacts from anthropogenic activities, for example: oil and gas extraction, deep-water fisheries, and plastic and microplastic pollution. Oil and gas exploration and extraction can lead to indirect pressures (e.g. noise and light), direct physical pressures (e.g. smothering from drill cuttings and abrasion from drilling rig mooring-anchors) and chemical contamination (e.g. from drill cuttings and produced water, Cordes *et al.*, 2016). Visible impacts on habitats (with

associated reductions in megafaunal density and diversity) have been observed at a distance of 100–200 m away from well-heads in the North-East Atlantic (Gates and Jones, 2012) and ecological effects on sensitive species have been detected at ~ 1–2 km from the discharge source (Paine *et al.*, 2014). However, oil and gas projects within Marine Protected Areas are subject to the Environmental Impact Assessment process, which includes identification of potential impacts and mitigation measures. Furthermore, resulting environmental management strategies to avoid or minimise impact may become conditions of operation (Cordes *et al.*, 2016).

Deep-water fisheries for roundnose grenadier, blue ling, anglerfish (monkfish) and Greenland halibut occur in UK waters to the west of Scotland in the Rockall Trough, and in the Faroe-Shetland Channel (Priede, 2018). Benthic-pelagic fishes from the UK and Irish continental slope, including the roundnose grenadier, perform an important short-term ecosystem function by storing carbon within their biomass over their lifetime, estimated to be 1 million tonnes of CO₂ every year (Trueman *et al.*, 2014). Deep-water fisheries within the UK deep sea are subject to commercial exploitation pressures (Victorero *et al.*, 2018), which will affect the amount of carbon captured and stored by these fish. Additionally, deep-water habitats, primarily sessile, fragile communities, such as cold-water coral reefs, may also be impacted by commercial deep-water fishing through pressures such as seabed abrasion and siltation, particularly from deep-water trawling (Clark *et al.*, 2016) and to a lesser extent, long-lining (Fosså *et al.*, 2002; Sampedro *et al.*, 2012). The introduction of the EU deep-sea access regulation (EU) 2016/2336 has put in place a ban on bottom trawling in areas deeper than 800 m, which will reduce impact on habitats occurring at these depths. Furthermore, fishing with bottom gears below 400 m depth will be prohibited in areas where Vulnerable Marine Ecosystems occur or are likely to occur, based on best available evidence (Food and Agriculture Organisation of the United Nations, 2009, <http://www.fao.org/3/a-i5952e.pdf>).

There is convincing evidence of ingestion of microplastics by benthic invertebrates during the last four decades at Station M in the Rockall Trough (Courtenes-Jones *et al.*, 2019). Microplastics are known to affect feeding, growth, and reproduction of fish and invertebrates (Foley *et al.*, 2018). Similarly, deep-sea fish from the Rockall Trough have been shown to accumulate persistent organic pollutants, e.g. PCBs in their tissues (Webster *et al.*, 2014). The roundnose grenadier and black dogfish had PCB concentrations above the environmental assessment criteria (Webster *et al.*, 2014). Accumulation of microplastics, their associated chemicals and persistent organic pollutants could have toxic effects for deep-sea fauna at high concentrations.

Specific deep-sea habitats, e.g. seamounts and cold-water corals, have been outlined as vulnerable to the effects of climate change (Jones *et al.*, 2014; Gehlen *et al.*, 2014). These habitats are also areas where pressures from

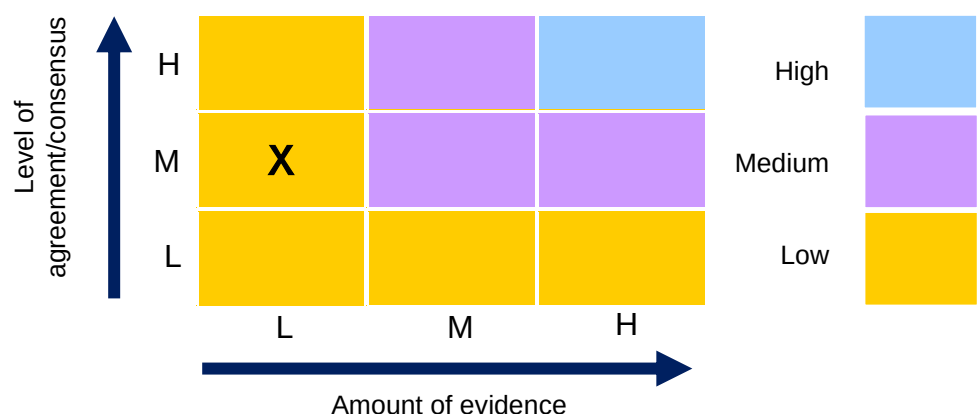
multiple concurrent stressors are in effect, e.g. fishing and resource extraction. Multiple concurrent stressors will likely amplify the negative effects of climate change as deep-sea ecosystems are slow to recover as a result of long generation times and slow population growth rates.

Socio-economic impacts

Deep-sea environments provide direct economic benefits to society through provision of oil and gas, minerals, fisheries and bioprospecting (Armstrong *et al.*, 2012; Thurber *et al.*, 2014). Indirect socio-economic impacts include sequestration of carbon, nutrient regeneration, waste absorption and detoxification (Armstrong *et al.*, 2012; Thurber *et al.*, 2014). However, there is limited knowledge on the monetary economic value of the deep sea (Folkersen *et al.*, 2018). Proposed changes to the Common Fisheries Policy for regulating deep-sea fish stocks outlined in EC COM 371 Final, 2012, was predicted to lead to a short-term reduction of landings of fish in the UK of 6540 tonnes, reducing the value by £3.3 million (Mangi *et al.*, 2016). A recent survey of the Scottish public revealed that the public were prepared to pay on average £70 to £77 for protection of deep-sea species and species with high potential for medicinal products (Jobstvagt *et al.*, 2014). This demonstrates that the public value deep-sea species and environments. Deep-sea habitats and ecosystems are clearly valuable as supporting systems for life on Earth in addition to the provisioning services they provide. However, there are large gaps in our knowledge that prevent a monetary assessment of the value of deep-sea habitats (Armstrong *et al.*, 2012).

4. CONFIDENCE ASSESSMENT

What is already happening?

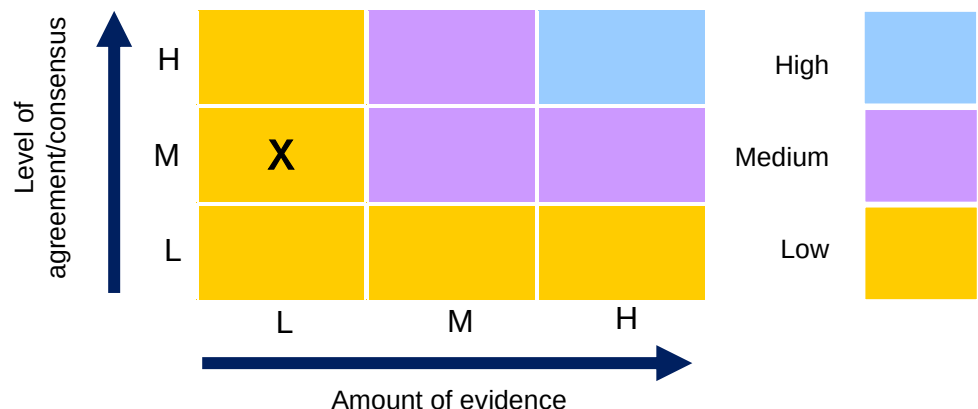


There is a high level of agreement and medium level of evidence concerning how the environment (food supply, physical oceanography) structures and shapes deep-sea communities and ecosystems. However, there is a medium

level of agreement and low amount of evidence concerning how deep-sea habitats are currently being affected by climate change. Repeat sampling at the PAP has demonstrated that deep-sea communities change in relation to variations in food supply, which is driven by the physical environment and potentially the NAO. The level of assessment has changed because the PAP time-series has not been continuously sampled for a sufficient time-period to confidently state that changes in benthic community structure at the PAP are driven by climate change. There is a similar level of uncertainty regarding changes in deep-sea temperatures along the Extended Ellett Line transect. There is good agreement with a low level of evidence for decreasing pH in UK deep-sea waters.

Finally, deep-sea habitats in UK waters are generally poorly sampled in time and space with the exception of Station M in the Rockall Trough and the Mingulay reef complex, although both of these sites lack systematic repeat sampling. However, the time-series data from Station M requires further analysis and the data from the time-series have not yet been published. There is also a lack of detailed knowledge of deep pelagic habitats within UK waters. In order to improve confidence in assessment of the current risks of climate change to UK deep-sea habitats, comprehensive whole ecosystem, e.g. euphotic zone, mesopelagic, bathypelagic, abyssopelagic and benthic, time-series stations need to be set up in strategic locations, e.g. important commercial fishery and biodiversity hotspots and within MPAs.

What could happen in the future?



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. The amount of evidence is low because most of

the models provide global or ocean basin level predictions, with few studies providing regional predictions, e.g. North Atlantic. Additionally, models incorporating the benthos and seafloor are relatively recent and still in development. In order 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, e.g. specifically within UK waters. Models predicting the effects of changing POC flux on deep-sea habitats need to encompass measurements of POC flux to the seafloor, as current models use measured export flux at 100 m below the surface. Experiments determining critical thresholds for fauna and their larvae, e.g. for oxygen, pH, temperature, could further enhance our understanding of how deep-sea habitats will be affected by climate change.

5. KEY CHALLENGES AND EMERGING ISSUES

1. There is a need to improve knowledge on the physical environment influencing UK deep-sea communities. Specifically, with respect to temporal and spatial variability of the hydrographic features influencing seafloor communities, how variable are these features over days, weeks and annual timescales? There is some limited information regarding this for the Mingulay reef complex and on the Irish margin (Davies *et al.*, 2008; Duineveld *et al.*, 2012 and Findlay *et al.*, 2013; Boolukos *et al.*, 2019). Additionally, how variable is temperature, dissolved oxygen, pH and POC flux for UK deep-sea habitats? For example, increased knowledge of POC flux reaching the seafloor will aid better parameterisation of models, as many current models use export flux at 100 m to predict flux of POC to the seafloor, which is likely to lead to incorrect assessment of climate impacts. The PAP time-series provides insight into POC flux and other environmental parameters over decadal timescales but this is outside of the UK continental shelf. Time-series stations and observatory networks within UK deep-sea habitats and for a variety of different habitats are urgently needed. Additionally, in order to predict how deep-sea habitats and communities will respond to climate change, in-situ experiments are required to test responses of deep-sea communities to specific and combined stressors. Environmental information is key to successful management of MPAs in a changing climate see: Gehlen *et al.* (2014) and Fox *et al.* (2016). EU and NERC funded programmes, e.g. ATLAS (<https://www.eu-atlas.org>) and DEEPLINKS (<https://deeplinksproject.wordpress.com>) and the recently funded iAtlantic (<http://www.iatlantic.eu>) are providing insight into the health of deep-sea ecosystems and best practice on management of an ecologically coherent network of MPAs, whilst the NERC funded CLASS project (<https://projects.noc.ac.uk/class/>) will continue to provide insight into how deep-sea habitats are changing within a changing Atlantic Ocean.

2. Knowledge of deep-sea biological communities and ecosystem functioning is still lacking for large areas of the UK deep-sea. Co-evolution of technology and research has led to enhanced understanding of biological communities within Monterey Bay (Robison *et al.*, 2017), particularly for mid-water species. The majority of research in UK deep-sea habitats has focused on seafloor habitats and yet the UK deep-sea is undersampled compared to the North Sea (Figure 1). The largest habitat in the UK deep-sea by volume is the pelagic realm, specifically the meso- and bathy-pelagic, and both have been largely overlooked. Fundamental baseline studies of UK deep-sea habitats are required in order to better understand and predict how UK deep-sea habitats will respond to climate change. In conjunction, experimental studies determining deep-sea species tolerances to key stressors, e.g. temperature, oxygen, pH and food availability are also necessary.
3. Advances in benthic modelling have revealed for the first time how deep-sea benthic biomass will respond to declining primary production predicted under future climate change scenarios (Jones *et al.*, 2014; Yool *et al.*, 2017). Most model outputs to date have been large scale e.g. global or basin scale. Regional predictions are required to understand specifically how UK deep-sea habitats will respond to future climate change. Models must also take into account multiple concurrent stressors, e.g. pH, dissolved oxygen and temperature. Models predictions should also take into account pelagic habitats.

REFERENCES

- Armstrong, C.W., Foley, N.S., Tinch, R. and van den Hove, S. (2012) Services from the deep: Steps towards valuation of deep sea goods and services. *Ecosystem Services*, **2**, 2–13, doi: 10.1016/j.ecoser.2012.07.001
- Ashford, O.S., Kenny, A.J., Barrio Froján, C.R.S., Bonsall, M.B., Horton, T., Brandt, A., Bird, G.J., Gerken, S. and Rogers, A.D. (2018) Phylogenetic and functional evidence suggests that deep-ocean ecosystems are highly sensitive to environmental change and direct human disturbance. *Proceedings of the Royal Society, B*, **285**, 20180923, doi:10.1098/rspb.2018.0923
- Balmaseda, M.A., Trenberth, K.E. and Källén, E. (2013) Distinctive climate signals in reanalysis of global ocean heat content. *Geophysical Research Letters*, **40**(1) 754–759, doi: 10.1002/grl.50382
- Barry, J.P., Lovera, C., Buck, K.R., Peltzer, E.T., Taylor, J.R., Walz, P., Whaling, P.J. and Brewer, P.G. (2014) Use of a Free Ocean CO₂ Enrichment (FOCE) system to evaluate the effects of ocean acidification on the foraging behaviour of a deep-sea urchin. *Environmental Science and Technology*, **48**, 9890–9897, doi: 10.1021/es501603r
- 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
- Bett, B.J. (2001) UK Atlantic Margin environmental survey: Introduction and overview of bathyal benthic ecology. *Continental Shelf Research*, **21**, 917–956.
- Billett, D.S.M., Bett, B.J., Reid, W.K.D., Boorman, B. and Priede, I.M. (2010) Long-term change in the abyssal NE Atlantic: The ‘Amperima Event’ revisited. *Deep-Sea Research II*, **57**, 1406–1417, doi: 10.1016/j.dsr2.2009.02.001
- Bonneau, L., Colin, C., Pons-Branchu, E., Mienis, F., Tisnérat-Laborde, N., Blamart, D., Elliot, M., Collart, T., Frank, N., Foliot, L. and Douville, E. (2018) Imprint of Holocene climate variability on cold-water coral reef growth at the SW Rockall Trough Margin, NE Atlantic. *Geochemistry, Geophysics, Geosystems*, **19**, 2437–2452, doi: 10.1029/2018GC007502

- Boolukos, C.M., Lim, A., O’Riordan, R.M. and Wheeler, A. (2019) Cold-water corals in decline – A temporal (4 year) species abundance and biodiversity appraisal of complete photomosaiced cold-water coral reef on the Irish margin. *Deep-Sea Research I*, **146**, 44–54, doi: 10.1016/j.dsr.2019.03.004
- Bopp, L., Resplandy, L., Orr, J.C., Doney, S.C., Dunne, J.P., Gehlen, M., Halloran, P., Heinze, C., Ilyina, T., Séférian, R., Tjiputra, J. and Vichi, M. (2013) Multiple stressors of ocean ecosystems in the 21st century: projections with CMIP5 models. *Biogeosciences*, **10**, 6225–6245, doi: 10.5194/bg-10-6225-2013
- Brooke, S. and Young, C.M. (2009) Direct measurements of in situ survival and growth of *Lophelia pertusa* in the northern Gulf of Mexico. *Marine Ecology Progress Series*, **397**, 153–161.
- Büscher, J., 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**, 101, doi: 10.3389/fmars.2017.00101
- Caesar, L., Rahmstorf, S., Robinson, A., Geulner, G. and Saba, V. (2018) Observed fingerprint of a weakening Atlantic Ocean overturning circulation. *Nature*, **556**, 191–196.
- Capotondi, A., Alexander, M.A., Bond, N.A., Curchitser, E.N. and Scott, J.D. (2012) Enhanced upper ocean stratification with climate change in the CMIP3 models. *Journal of Geophysical Research*, **117**, C04031, doi: 10.1029/2011JC007409
- Cavan, E.L., Henson, S.A. and Boyd, P.W. (2019) The sensitivity of subsurface microbes to ocean warming accentuates future declines in particulate carbon export. *Frontiers in Ecology and Evolution*, **6**, 230, doi: 10.3389/fevo.2018.00230
- Chafik, L. (2012) The response of the circulation in the Faroe-Shetland Channel to the North Atlantic Oscillation. *Tellus A*, **64**, 18423, doi: 10.3402/tellusa.v64i0.18423
- Clark, M.R., Althaus, F., Schlacher, T.A., Williams, A., Bowden, D.A. and Rowden, A. (2016) The impacts of deep-sea fisheries on benthic communities: a review. *ICES Journal of Marine Science*, **73**, i51–i69, doi: 10.1093/icesjms/fsv123
- Chust, G., Allen, J.I., Bopp, L., Schrun, C., Holt, J., Tsiaras, K. *et al.* (2014) Biomass changes and trophic amplification of plankton in a warmer ocean. *Global Change Biology*, **20**, 2124–2139, doi: 10.1111/gcb.12562
- Cordes, E.E., Jones, D.O.B., Schlacher, T.A., Amon, D.J., Bernardino, A.F., Brooke, S. *et al.* (2016) Environmental impacts of the deep-water oil and gas industry: a review to guide management strategies. *Frontiers in Environmental Science*, **4**, 58.
- 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.
- Courteney-Jones, W., Quinn, B., Ewins, C., Gary, S.F. and Narayanaswamy, B.E. (2019) Consistent microplastic ingestion by deep-sea invertebrates over the last four decades (1976–2015), a study from the North East Atlantic. *Environmental Pollution*, **244**, 503–512.
- Cyr, F. and van Haren, H. (2016) Observations of small-scale secondary instabilities during the shoaling of internal bores on a deep-ocean slope. *Journal of Physical Oceanography*, **46**, 219–231, doi: 10.1175/JPO-D-15-0059.1
- Danovaro, R., Snelgrove, P.V.E. and Tyler, P. (2014) Challenging the paradigms of deep-sea ecology. *Trends in Ecology and Evolution*, **29**, 8, doi: 10.1016/j.tree.2014.06.002
- Davies, A.J., Wisshak, M. and Roberts, J.M. (2008) Predicting suitable habitat for the cold-water coral *Lophelia pertusa* (Scleractinia). *Deep-Sea Research*, **55**, 1048–1062.
- Davies, A.J., Duineveld, G.C.A., Lavaleye, M.S.S., Bergman, M.J.N., van Haren, H. and Roberts, M.J. (2009) Downwelling and deep-water bottom currents as food supply mechanisms to the cold-water coral *Lophelia pertusa* (Scleractinia) at the Mingulay Reef complex. *Limnology and Oceanography*, **54**, 620–629.
- 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**, 205–214.
- Doney, S.C., Bopp, L. and Long, M.C. (2014) Historical and future trends in ocean climate and biogeochemistry. *Oceanography*, **27**, 108–119, doi: 10.5670/oceanog.2014.14
- Duineveld, G.C.A., Jeffreys, R.M., Lavaleye, M.S.S., Davies, A.J., Bergman, M.J.N., Watmough, T. and Witbaard, R. (2012) Spatial and tidal variation in food supply to shallow cold-water coral reefs of the Mingulay Reef complex (Outer Hebrides, Scotland). *Marine Ecology Progress Series*, **444**, 97–115, doi: 10.3354/meps09430
- Dullo, W.C., Flögel, S. and Rüggeberg, A. (2008) Cold-water coral growth in relation to the hydrography of the Celtic and Nordic European continental margin. *Marine Ecology Progress Series*, **371**, 165–176, doi: 10.3354/meps07623

- Ellett, D.J. and Martin, J.H. (1973) The physical and chemical oceanography of the Rockall Channel. *Deep-Sea Research*, **20**, 819–835.
- EurOBIS data. European node of the Ocean Biogeographic Information System (EurOBIS). www.eurobis.org. Consulted on 2019-01-18.
- Findlay, H.S., Artioli, Y., Navas, J.M., Hennige, S.J., Wicks, L.C., Huvenne, V.A.I., Woodward, 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**, 2708–2719, doi: 10.1111/gcb.12256
- Fink, H.G., Wienberg, C., Hebbeln, D., McGregor, H.V., Schmiedl, G., Taviani, M. and Freiwald, A. (2012) Oxygen control on Holocene cold-water coral development in the eastern Mediterranean Sea. *Deep-Sea Research*, **62**, 89–96, doi: 10.1016/j.dsr.2011.12.013
- Foley, C.J., Feiner, Z.S., Malinich, T.D. and Höök, T.O. (2018) A meta-analysis of the effects of exposure to microplastics on fish and aquatic invertebrates. *Science of the Total Environment*, **631**, 550–559, doi: 10.1016/j.scitotenv.2018.03.046
- Folkersen, M.V., Fleming, C.M. and Hasan, S. (2018) The economic value of the deep sea: A systematic review and meta-analysis. *Marine Policy*, **94**, 71–80, doi: 10.1016/j.marpol.2018.05.003
- Fosså, J.H., Mortensen, P.B. and Furevik, D.M. (2002) The deep-water coral *Lophelia pertusa* in Norwegian waters: distribution and fishery impacts. *Hydrobiologia*, **471**, 1–12.
- Fox, A., Henry, L.-A., Corne, D.W. and Roberts, J.M. (2016) Sensitivity of marine protected area network connectivity to atmospheric variability. *Royal Society Open Science*, **3**, 160494, doi:10.1098/rsos.160494
- Freiwald, A. and Roberts, J.M. (2005) *Cold-Water Corals and Ecosystems*. Springer, Heidelberg.
- Gallo, N.D. and Levin, L.A. (2016) Fish ecology and evolution in the World's oxygen minimum zones and implications of ocean deoxygenation. *Advances in Marine Biology*, **74**, 117–198, doi: 10.1016/bs.amb.2016.04.001
- Gates, A.R. and Jones, D.O.B. (2012) Recovery of benthic megafauna from anthropogenic disturbance at a hydrocarbon drilling well (380 m depth in the Norwegian Sea). *PLoS One*, **7**(10), e44114, doi: 10.1371/journal.pone.0044114
- Gattuso, J.-P., Magnan, A., Billé, R., Cheung, W.W.L., Howes, E.L., Joos, F. *et al.* (2015) Contrasting futures for ocean and society from different anthropogenic CO₂ emissions scenarios. *Science*, **349**, aac4722.
- Gehlen, M., Séférian, R., Jones, D.O.B., Roy, T., Roth, R., Barry, J. *et al.* (2014) Projected pH reductions by 2100 might put deep North Atlantic biodiversity at risk. *Biogeosciences*, **11**, 6955–6967, doi: 10.5194/bg-11-6955-2014
- 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.
- Gove, J.M., McManus, M.A., Neuheimer, A.B., Polovina, J.J., Drazen, J.C., Smith, C.R., Merrifield, M.A., Friedlander, A.M., Ehlers, J.S., Young, C.W., Dillon, A.K. and Williams, G.J. (2019) Near-island biological hotspots in barren ocean basins. *Nature Communications*, **7**, 10581, doi: 10.1038/ncomms10581
- Guinotte, J.M., Orr, J., Cairns, S., Freiwald, A., Morgan, L. and George, R. (2006) Will human-induced changes in seawater chemistry alter the distribution of deep-sea scleractinian corals? *Frontiers in Ecology and the Environment*, **4**, 141–146.
- Guerrero-Feijóo, E., Sintes, E., Herndl, G.J. and Varela, M.M. (2018) High dark inorganic carbon fixation rates by specific microbial groups in the Atlantic off the Galician coast (NW Iberian margin). *Environmental Microbiology*, **20**, 602–611, doi: 10.1111/1462-2920.13984
- Hall, R.A., Aslam, T. and Huvenne, V.A.I. (2017) Partly standing internal tides in a dendritic submarine canyon observed by an ocean glider. *Deep-Sea Research I*, **126**, 73–84, doi: 10.106/j.dsr.2017.05.015
- 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 bio-geographical 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
- Hennige, S.J., Wicks, L.C., Kamenos, N., Bakker, D.C.E., Findlay, H.S., Dumousseaud, C. and Roberts, J.M. (2014) Short term metabolic and growth responses to the cold-water coral *Lophelia pertusa* to ocean acidification. *Deep-Sea Research II*, **99**, 27–35, doi: 10.1016/j.dsr2.2013.07.005
- 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*, **282**, 20150990, doi: 10.1098/rspb.2015.0990

- Henry, L.-A., Vlad, J., Findlay, H.S., Murillo, J., Milligan, R. and Roberts, J.M. (2014) Environmental variability and biodiversity of megabenthos on the Hebrides Terrace Seamount (Northeast Atlantic). *Scientific Reports*, **4**, 5589, doi:10.1038/srep05589
- Henry, L.-A., Stehmann, M.F.W., De Clippele, L., Findlay, H.S., Golding, N. and Roberts, J.M. (2016) Seamount egg-laying grounds of the deep-water skate *Bathyraja richardsoni*. *Journal of Fish Biology*, **89**, 1473–1481, doi: 10.1111/jfb.13041
- Henson, S.A., Beaulieu, C. and Lampitt, R. (2016) Observing climate change trends in ocean biogeochemistry: when and where? *Global Change Biology*, **22**, 1561–1571.
- 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
- Hochachka, P.A. and Somero, G.N. (2002) *Biochemical Adaptation: Mechanism and Process in Physiological Evolution*. Oxford University Press, New York.
- Holliday, N.P. and Cunningham, S. (2013) The extended Ellett Line: Discoveries from 65 years of marine observations west of the UK. *Oceanography*, **26**, 156–163, doi: 10.5670/oceanog.2013.17
- Holliday, N.P., Cunningham, S., Johnson, G.S.C., Griffiths, C., Read, J.F., and Sherwin, T. (2015) Multidecadal variability of potential temperature, salinity and transports in the eastern subpolar North Atlantic. *Journal of Geophysical Research*, **120**, 5945–5967, doi: 10.5194/essdd-8-57-2015
- Hosegood, P. and van Haren, H. (2004) Near-bed solibores over the continental slope in the Faeroe-Shetland Channel. *Deep-Sea Research II*, **51**, 2942–2971.
- Hovland, M. (1990) Do carbonate reefs form fluid seepage? *Terra Nova*, **2**, 8–18.
- Howell, K., Piechaud, N., Downie, A.L. and Kenny, A. (2016) The distribution of deep-sea sponge aggregations in the North Atlantic and implications for their effective spatial management. *Deep-Sea Research I*, **115**, 309–320.
- Hughes, D.J. and Narayanaswamy, B.E. (2013) Impacts of climate change on deep-sea habitats. *MCCIP Science Review* 2013, 204–210, doi: 10.14465/2013.arc21.204-210
- Humphreys, M.P., Griffiths, A.M., Achterberg, E.P., Holliday, N.P., Rérolle, V.M.C., Barraqueta, J.-L.M., Couldrey, M.P., Oliver, K.I.C., Hartman, S.E., Esposito, M. and Boyce, A.J. (2016) Multidecadal accumulation of anthropogenic and remineralized dissolved inorganic carbon along the Extended Ellett Line in the northeast Atlantic Ocean. *Global Biogeochemical Cycles*, **30**, 293–210, doi: 10.1002/2015GB005246
- Inall, M., Gillibrand, P., Griffiths, C., MacDougall, N. and Blackwell, K. (2009) On the oceanographic variability of the North-West European Shelf to the west of Scotland. *Journal of Marine Systems*, **77**, 210–226, doi: 10.1016/j.jmarsys.2007.12.012
- IPCC (2014) *Climate change 2014: Synthesis report*. Contribution of working groups 1, II and III to the fifth assessment report of the intergovernmental panel on climate change [Pachauri, R.K. and Meyer, L.A. (eds.)]. IPCC, Geneva, Switzerland, 151 pp.
- Ismail, K., Huvenne, V. and Robert, K. (2018) Quantifying spatial heterogeneity in submarine canyons. *Progress in Oceanography*, **169**, 181–198, doi: 10.1016/j.pcean.2018.03.006
- Iverson, M.H. and Ploug, H. (2013) Temperature effects on carbon-specific respiration rate and sinking velocity of diatom aggregates: potential implications for deep ocean export processes. *Biogeosciences*, **10**, 4073–4085, doi: 10.5194/bg-10-4073-2013
- Jackson, E.L., Davies, A.J., Howell, K.L., Kershaw, P.J. and Hall-Spences, J.M. (2014) Future-proofing marine protected area networks for cold water coral reefs. *ICES Journal of Marine Science*, **71**, 2621–2629.
- Jayne, S.R., St. Laurent, L.C. and Gille, S.T. (2004) Connections between ocean bottom topography and Earth's climate. *Oceanography*, **17**, 65–74.
- Jiang, L.-Q., Feely, R.A., Carter, B.R., Greeley, D.J., Gledhill, D.K. and Arzayus, K.M. (2015) Climatological distribution of aragonite saturation state in the global oceans. *Global Biogeochemical Cycles*, **29**, 1656–1673.
- Jobstvogt, N., Hanley, N., Hynes, S., Kenter, J. and Witte, U. (2014) Twenty thousand sterling under the sea: Estimating the value of protecting deep-sea biodiversity. *Ecological Economics*, **97**, 10–19, doi: 10.1016/j.ecolecon.2013.10.019
- Jones, D.O., Yool, A., Wei, C.-L., Henson, S.A., Ruhl, H.A., Watson, R.A., Gehlen, M. (2014) Global reductions in seafloor biomass in response to climate change. *Global Change Biology*, **20**, 1861–1872, doi: 10.1111/gcb.12480
- Kelly-Gerreyn, B.A., Martin, P.A., Bett, B.J., Anderson, T.R., Kaariainen, J.I., Main, C.E. and Yool, A. (2014) Benthic biomass size spectra in shelf and deep-sea sediments. *Biogeosciences*, **11**, 6401–6416, doi: 10.5194/bg-11-6401-2014
- Laguionie-Marchais, C., Billett, D.S.M., Paterson, G.L.J., Bett, B.J., Ruhl, H.A., Soto, E.H., Smith, K.L. and Thatje, S. (2013) Inter-annual dynamics of abyssal polychaete communities in the North

- East Pacific and North East Atlantic – A family-level study. *Deep Sea Research I*, **75**, 175–186, doi: 10.1016/j.dsr.2012.12.007
- Laguionie-Marchais, C., Paterson, G.L.J., Bett, B.J., Smith, K.L. and Ruhl, H.A. (2016) Inter-annual species-level variations in an abyssal polychaete assemblage (St. M, NE Pacific, 4000 m). *Progress in Oceanography*, **140**, 43–53, doi: 10.1016/j.pocean.2015.10.006
- Lampitt, R.S., Billett, D.S.M. and Martin, A.P. (2010) The sustained observatory over the Porcupine Abyssal Plain (PAP): Insights from time series observations and process studies. *Deep-Sea Research II*, **57**, 1267–1271.
- Levin, L.A. and LeBris, N. (2015) The deep ocean under climate change. *Science*, **350**, 766–768, doi: 10.1126/science.aad0126
- Lowe, J.A., Howard, T.P., Pardaens, A., Tinker, J., Holt, J., Wakelin, S., Milne, G., Leake, J., Wolf, J., Horsburgh, K., Reeder, T., Jenkins, G., Ridley, J., Dye, S. and Bradley, S. (2009) *UK Climate Projections Science Report: Marine and Coastal Projections*. Met Office Hadley Centre, Exeter, UK.
- Lu, H.M., Li, Y.J., Uemura, T., Ge, Z., Xu, X., He, L., Serikawa, S. and Kim, H. (2018) FDCNet: filtering deep convolutional network for marine organism classification. *Multimedia Tools App.*, **77**, 21847–21860, doi: 10.1007/s11042-017-4585-1
- Lunden, J.J., McNicholl, C.G., Sears, C.R., Morrison, C.L. and Cordes, E.E. (2014) Acute survivorship of the deep-sea coral *Lophelia pertusa* from the Gulf of Mexico under acidification, warming, and deoxygenation. *Frontiers in Marine Science*, **1**, 78, doi: 10.3389/fmars.2014.00078
- Mahaffey, C.M., Palmer, M., Greenwood, N. and Sharples, J. (2020) Impacts of climate change on dissolved oxygen concentrations relevant to the coastal and marine environment around the UK. *MCCIP Science Review 2020*, 31–53.
- Maier, C., Hegeman, J., Weinbauer, M.G. and Gattuso, J.-P. (2009) Calcification of the cold-water coral *Lophelia pertusa*, under ambient and reduced pH. *Biogeosciences*, **6**, 1671–1680, doi: 10.5194/bg-6-1671-2009
- Mangi, S.C., Kenny, A., Readdy, L., Posen, P., Ribeiro-Santos, A., Neat, F.C. and Burns, F. (2016) The economic implications of changing regulations for deep sea fishing under the European Common Fisheries Policy: UK case study. *Science of the Total Environment*, **562**, 260–269, doi: 10.1016/j.scitotenv.2016.03.218
- 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
- Masson, D.G., Bett, B.J., Billett, D.S.M., Jacobs, C.L., Wheeler, A.J. and Wynn, R.B. (2003) The origin of deep-water coral-topped mounds in the northern Rockall Trough, Northeast Atlantic. *Marine Geology*, **194**, 159–180.
- McClain, C.R., Allen, A.P., Tittensor, D.P. and Rex, M.A. (2012) Energetics of life on the deep seafloor. *Proceedings of the National Academy of Sciences USA*, **109**, 15366–15371, doi: 10.1073/pnas.1208976109
- McGrath, T., Kivimäe, C., Tanhua, T., Cave, R. C. and McGovern, E. (2012) Inorganic carbon and pH levels in the Rockall Trough 1991–2010. *Deep Sea Research I*, **68**, 79–91, doi: 10.1016/j.dsr.2012.05.011
- 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.
- Mohn, C., Rengstorf, A., White, M., Duineveld, G., Mienis, F., Soetaert, K. and Grehan, A. (2014) Linking benthic hydrodynamics and cold-water coral occurrences: a high-resolution model study at three cold-water coral provinces in the NE Atlantic. *Progress in Oceanography*, **122**, 92–104.
- Neat, F.C., Jamieson, A.J., Stewart, H.A., Narayanaswamy, B.E., Collie, N., Stewart, M., and Linley, T. (2018) Visual evidence of reduced seafloor conditions and indications of a cold-seep ecosystem from the Hatton–Rockall basin (NE Atlantic). *Journal of the Marine Biological Association of the UK*, 1–7, doi:10.1017/S0025315418000115.
- O'Connor, M.I., Bruno, J.F., Gaines, S.D., Halpern, B.S., Lester, S.E., Kinlan, B.P. and Weiss, J.M. (2007) Temperature control of larval dispersal and the implications for marine ecology, evolution and conservation. *Proceedings of the National Academy of Sciences USA*, **104**, 1266–1271.
- Oliver, P.G. and Drewery, J. (2013) New species of chemosymbiotic clams (Bivalvia: Vesicomidae and Thyasiridae) from a putative ‘seep’ in the Hatton-Rockall Basin, north-east Atlantic. *Journal of the Marine Biological Association of the UK*, **94**, 389–403.
- Oschlies, A., Brandt, P., Stramma, L. and Schmidtke, S. (2018) Drivers and mechanisms of ocean deoxygenation. *Nature Geoscience*, **11**, 467–473.
- Ouellet, P. and Sainte-Marie, B. (2018) Vertical distribution of snow crab (*Chionoecetes opilio*) pelagic stages in the Gulf of St. Lawrence (Canada) and effect of temperature on development and survival. *ICES Journal of Marine Science*, **75**, 773–784, doi: 10.1093/icesjms/fsx169

- Paine, M.D., DeBlois, E.M., Kilgour, B.W., Tracy, P., Pocklington, P., Crowley, R.D., Williams, U.P. and Janes, G.G. (2014) Effects of the Terra Nova offshore oil development on benthic macro-invertebrates over 10 years of development drilling on the Grand Banks of Newfoundland, Canada. *Deep Sea Research II*, **110**, 38–64.
- Perez, F.F., Fontela, M., García-Ibáñez, M.I., Mercier, H., Velo, A., Lherminier, P., Zunino, P., de la Paz, M., Alonso-Pérez, Guallart, E.F. and Padin, X.A. (2018) Meridional overturning circulation conveys fast acidification to the deep Atlantic Ocean. *Nature*, **554**, 515–518, doi: 10.1038/nature25493
- Pörtner, H.O. and Knust, R. (2007) Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science*, **315**, 95–97, doi: 10.1126/science.1135471
- Priede, I.M. (2018) Deep-sea fishes literature review. *JNCC Report*, No. 619, JNCC, Peterborough. ISSN 0963-8091.
- Raddatz, J., Rüggeberg, A., Liebetrau, V., Foubert, A., Hathorne, E.C., Fietzke, J., Eisenhauer, A. and Dullo, W.-C. (2014) Environmental boundary conditions of cold-water coral mound growth over the last 3 million years in the Porcupine Seabight, Northeast Atlantic. *Deep Sea Research II*, **99**, 227–236, doi: 10.1016/j.dsr2.2013.06.009
- Rex, M.A., Etter, R.J., Morris, J.S., Crouse, J. and McClain, C.R., Johnson, N.A., Stuart, C.T., Deming, J.W., Thies, R. and Avery, R. (2006) Global bathymetric patterns of standing stock and body size in deep-sea benthos. *Marine Ecology Progress Series*, **317**, 1–8.
- Reinthal, T., van Aken, H.M. and Herndl, G.J. (2010) Major contribution of autotrophy to microbial carbon cycling in the deep North Atlantic's interior. *Deep Sea Research II*, **57**, 1572–1580, doi: 10.1016/j.dsr2.2010.02.023
- 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
- Roberts, J.M., Davies, A.J., Henry, L.-A., Dodds, L.A., Duineveld, G.C.A., Lavaleye, M.S.S. *et al.* (2009) Mingulay reef complex: an interdisciplinary study of cold-water coral habitat, hydrography and biodiversity. *Marine Ecology Progress Series*, **397**, 139–151, doi: 10.3354/meps08112
- Roberts, H.H. and Kohl, B. (2018) Temperature control of cold-water coral (*Lophelia*) mound growth by climate-cycle forcing, Northeast Gulf of Mexico. *Deep Sea Research I*, **140**, 142–158.
- Robertson, L.M., Hamel, J.-F. and Mercier, A. (2017) Feeding in deep-sea demosponges: Influence of abiotic and biotic factors. *Deep Sea Research I*, **127**, 49–56, doi: 10.1016/j.dsr.2017.07.006
- Rogers, A.D. (1999) The biology of *Lophelia pertusa* (Linnaeus 1758) and other deep-water reef-forming corals and impacts from human activities. *International Review of Hydrobiology*, **84**, 315–406.
- Robison, B.H., Reisenbichler, K.R. and Sherlock, R.E. (2017) The coevolution of midwater research and ROV technology at MBARI. *Oceanography*, **30**, 26–37, doi: 10.5670/oceanog.2017.421
- Sampaio, Í., Braga-Henriques, A., Pham, C., Ocaña, O., De Matos, V., Morato, T., and Porteiro, F. (2012) Cold-water corals landed by bottom longline fisheries in the Azores (north-eastern Atlantic). *Journal of the Marine Biological Association UK*, **92**, 1547–1555, doi:10.1017/S0025315412000045
- Schoening T., Bergmann M., Ontrup J., Taylor J., Dannheim J., Gutt J., Purser A. and Nattkemper T.W. (2012) Semi-automated image analysis for the assessment of megafaunal densities at the Arctic deep-sea observatory HAUSGARTEN. *PLoS One*, **7**, e38179.
- Sherwin, T.J., Read, J.F., Holliday, N.P. and Johnson, C. (2012) The impact of changes in North Atlantic Gyre distribution on water mass characteristics in the Rockall Trough. *ICES Journal of Marine Science*, **69**, 751–757, doi: 10.1093/icesjms/fsr185
- Siddiqui, S.A., Salman, A., Malik, M.I., Shafait, F., Mian, A., Shortis, M.R. and Harvey, E.S. (2018) Automatic fish species classification in underwater videos: exploiting pre-trained deep neural network models to compensate for limited labelled data. *ICES Journal of Marine Science*, **75**, 374–389.
- Smed, J. (1949) Monthly mean temperatures of the surface water in the areas of the north-eastern North Atlantic during the years 1876–1939 and 1945–1948. *Annales Biologiques*, **5**, 10–15.
- Smith, K.L. Jr, Ruhl, H.A., Bett, B.J., Billett, D.S.M., Lampitt, R.S. and Kaufmann, R.S. (2009) Climate, carbon cycling, and the deep-ocean ecosystems. *Proceedings of the National Academy of Sciences USA*, **106**, 19211–19218, doi: 10.1073/pnas.0908322106
- Soetaert, K., Mohn, C., Rengstorf, A., Grehan, A. and van Oevelen, D. (2016) Ecosystem engineering creates a direct nutritional link between 600-m deep cold-water coral mounds and surface productivity. *Nature Scientific Reports*, **6**, 35057, doi: 10.1038/srep35057
- Stalder, C., Kateb, A.-E., Vertino, A., Rüggeberg, A., Camozzi, O., Pirkenseer, C.M., Spangenberg, J.E., Hajdas, I., Van Rooij, D. and Spezzaferri, S. (2018) Large-scale paleoceanographic variations in the western Mediterranean Sea during the last 34,000 years: From enhanced cold-water coral

- growth to declining mounds. *Marine Micropalaeontology*, **143**, 46–62, doi: 10.1016/j.marmicro.2018.07.007
- Strömberg, S.M. and Larsson, A.I. (2017) Larval behaviour and longevity in the cold-water coral *Lophelia pertusa* indicate potential for long distance dispersal. *Frontiers in Marine Science*, **4**, 411, doi: 10.3389/fmars.2017.00411
- Sulpis, (2018) Current CaCO₃ dissolution at the seafloor caused by anthropogenic CO₂. *Proceedings of the National Academy of Sciences, USA*, **115**, 46, doi: 10.1073/pnas.1804250115
- Sweetman, A.K., Thurber, A.R., Smith, C.R., Levin, L.A., Mora, C., Wei, C.-L. and Roberts, J.M. (2017) Global climate change effects on deep seafloor ecosystems. *Elementa, Science of the Anthropocene*, **5**, 4, doi: 10.1525/elementa.203
- Talley, L.D., Feely, R.A., Sloyan, B.M., Wanninkhof, R., Baringer, M.O., Bullister, J.L., (2015) Changes in ocean heat, carbon content, and ventilation: A review of the first decade of GO-SHIP global repeat hydrography. *Annual Review of Marine Science*, **8**, 185–215, doi: 10.1146/annurev-marine-052915-100829
- Thurber, A.R., Sweetman, A.K., Narayanaswamy, B.E., Jones, D.O.B., Ingels, J. and Hansman, R.L. (2014) Ecosystem functions and services in the deep sea. *Biogeosciences*, **11**, 3941–3963, doi: 10.5194/bg-11-3941-2014
- Thornalley, D.J.R., Oppo, D.W., Ortega, P., Robson, J.I., Brierley, C.M., Davis, R., Hall, I.R., Moffa-Sanchez, P., Rose, N.L., Spooner, P.T., Yashayaev, I. and Keigwin, L.D. (2018) Anomalously weak Labrador Sea convection and Atlantic overturning during the past 150 years. *Nature*, **556**, 227–230, doi: 10.1038/s41586-018-0007-4
- Tittensor, D.P., Baco, A.R., Hall-Spencer, J.M., Orr, J.C. and Rogers, A.D. (2010) Seamounts as refugia from ocean acidification for cold-water stony corals. *Marine Ecology*, **31**, 212–225, doi:10.1111/j.1439-0485.2010.00393x
- Trueman, C.N., Johnston, G., O’Hea and MacKenzie, K.M. (2014) Trophic interactions of fish communities at midwater depths enhance long-term carbon storage and benthic production on continental slopes. *Proceedings of the Royal Society B*, **281**, 20140669, doi: 10.1098/rspb.2014.0669
- Turnewitsch, R., Dale, A., Lahajnar, N., Lampitt, R.S. and Sakamoto, K. (2017) Can neap-spring tidal cycles modulate biogeochemical fluxes in the abyssal near-seafloor water column? *Progress in Oceanography*, **154**, 1–24.
- Turnewitsch, R., Dumont, Kiriakoulakis, K., Legg, S., Mohn, C., Peine, F. and Wolff, G. (2016) Tidal influence on particulate organic carbon export fluxes around a tall seamount. *Progress in Oceanography*, **149**, 189–213.
- Vadaro, M.F., Ruhl, H.A. and Smith, K.L. Jr (2009) Climate, carbon flux, and bioturbation in the abyssal North Pacific. *Limnology and Oceanography*, **54**, 2081–2088.
- Vernon J.E.N. (2008) Mass extinctions and ocean acidification: biological constraints on geological dilemmas. *Coral Reefs*, **27**, 459–472.
- Victorero L., Watling L., Deng Palomares M. L., and Nouvian C. (2018) Out of sight, but within reach: A global history of bottom-trawled deep-sea fisheries from >400 m depth. *Frontiers in Marine Science*, **5**, 98, doi: 10.3389/fmars.2018.00098
- White, M., Mohn, C., de Stiger, H. and Mottram, G. (2005) Deep water coral development as a function of hydrodynamics and surface productivity around the submarine banks of the Rockall Trough, NE Atlantic. In *Cold-water Corals and Ecosystems* [Freiwald, F. and Roberts, J.M. (eds)]. Springer-Verlag, Berlin, pp. 503–514.
- Webster, L., Russell, M., Walsham, P., Hussy, I., Lacaze, J.-P., Phillips, L., Dalgarno, E., Packer, G., Neat, F. and Moffat, C.F. (2014) Halogenated persistent organic pollutants in relation to trophic level in deep sea fish. *Marine Pollution Bulletin*, **88**, 14–27, doi: 10.1016/j.marpolbul.2014.09.034
- Wolff, G.A., Billett, D.S.M., Bett, B.J., Holtvoeth, J., FitzGeorge-Balfour, T., Fisher, E.H., Cross, I., Shannon, R., Salter, I., Boorman, B., King, N.J., Jamieson, A. and Chaillan, F. (2011) The effects of natural iron fertilisation on deep-sea ecology: the Crozet Plateau, Southern Indian Ocean. *PLoS One*, **6**, e20697, doi: 10.1371/journal.pone.0020697
- Woolings, T., Franzke, C., Hodson, D.L.R., Dong, B., Barnes, E.A., Raible, C.C. and Pinto, J.G. (2014) Contrasting interannual and multidecadal NAO variability. *Climate Dynamics*, **45**, 539–556, doi: 10.1007/s00382-014-2237-y
- Woolley S.N., Tittensor, D.P., Dunstan, P.K., Guillera, G.-A., Lahoz-Monfort, J.J., Wintle, B.A., Worm, B. and O’Hara, T.D. (2016) Deep-sea diversity patterns are shaped by energy availability. *Nature*, **533**, 393–396, doi:10.1038/nature17937
- Xu, D., Han, L., Li, C., Cao, Q., Zhu, D., Barrett, N.H., Harmody, D., Chen, J., Zhu, H., McCarthy, P.J., Sun, X. and Wang, G. (2018) Bioprospecting deep-sea actinobacteria for novel anti-infective natural products. *Frontiers in Microbiology*, **9**, 787 doi: 10.3389/fmicb.2018.00787

- Yasuhara M. and Danovaro, R. (2016) Temperature impacts on deep-sea biodiversity. *Biological Reviews*, **91**, 275–287, doi: 10.1111/brv.12169
- Yool, A., Popova, E.E., Coward, A.C., Bernie, D. and Anderson, T.R. (2013) Climate change and ocean acidification impacts on lower trophic levels and the export of organic carbon to the deep ocean. *Biogeosciences*, **10**, 5831–5854, doi: 10.5194/bg-10-5931-2013
- Yool, A., Martin A.P., Anderson, T.R., Bett, B.J., Jones, D.O. 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**, 3554–3566, doi: 10.1111/gcb.13680