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Deep-sea habitats and ecology

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EXECUTIVE SUMMARY

- The UK's territorial deep sea covers a huge geographical area and supports a wide range of environments and biological communities. The deep sea is remote, difficult and expensive to study and as a result our understanding of its ecology is still limited.
- Deep-sea ecosystems carry out a range of ecosystem processes which are essential to global biogeochemical cycling (e.g. carbon cycling).
- There are no long-term datasets showing the extent of natural biological variability over time in UK deep waters. This makes it difficult to predict future climate-driven changes.
- Deep-sea ecosystems are intricately linked to processes at the sea surface, as almost all deep-sea animals are dependent on plankton sinking from surface waters for food. Climate-driven changes in surface processes will therefore have a direct impact on deep-sea ecosystems.
- Studies on the Porcupine Abyssal Plain show that deep-sea communities are far more dynamic than once believed. Population explosions of some invertebrate species are thought to have been triggered by increases in the quantity of food reaching the sea-bed in particular years, which has been linked to climate variability.
- Plankton communities in the north-east Atlantic may already be demonstrating climate-driven changes. While corresponding changes in productivity will affect the supply of food material to the deep sea, it is difficult to predict the consequences for deep-sea ecosystems.
- While ocean acidification poses a major long-term threat to deep-sea corals and other calcifying organisms, at present we have very few data on which to base detailed predictions of future impacts.

FULL REVIEW

1. What is already happening?

In UK territorial waters the "deep sea" is coincident with "Charting Progress" Regions 7 (which includes part of the Wyville Thomson Ridge) and 8 (the Atlantic North-West Approaches, Rockall Trough and Faroe-Shetland Channel), together with a small region in the south-west of Region 4 (Western English Channel, Celtic Sea and Southwest Approaches surveyed by the Joint Nature Conservation Committee in 2007). Water depths range from approximately 200 m at the shelf break to 2500 m in the northern Rockall Trough, and > 3000 m in the Iceland Basin at the western extremity of Region 8. Offshore areas of relatively shallow topography include the summits of the Anton Dohrn and Rosemary Bank seamounts (500 – 600 m) and the broad expanse of the Rockall Bank, much of which is less than 500 m deep. The areas to the north and west of Scotland were the scene of some of the pioneering oceanographic surveys of the 19th century and played an important role in the birth of deep-sea science (Wyville Thomson, 1873; Gage & Tyler, 1991). Additional sampling, survey work or research activity of some kind has been conducted since the mid-1970s (reviewed in Hughes *et al.*, 2003; Davies *et al.,* 2006). Despite this, our knowledge of habitats, biodiversity and ecosystem functioning in the UK's territorial deep sea is still limited. Until recently, deep-sea sampling was heavily focused on relatively flat open slopes and abyssal plains using corers, dredges and trawls. Areas of rugged topography such as seamounts, reefs and steep slopes were generally avoided. Modern research vessels with precise satellite navigation systems, remotely operated vehicles (ROVs) and camera-guided samplers can now access difficult submarine terrain and our knowledge of these habitats in the UK's territorial deep sea is expanding rapidly. However, the number of sites sampled using these modern techniques is still small in relation to the huge extent of the region, and large areas are still barely explored. For example, most of the available information on biological communities in areas of difficult seabed terrain (e.g. seamounts, banks, ridges), where potentially vulnerable ecosystems are found, has been gained only within the last five years (Naryanaswamy *et al.,* 2006; Howell *et al.,* 2007). Assessment of climate change impacts in the UK's deep sea is therefore constrained by our limited understanding of ecosystem structure and function, and in particular by the lack of time-series data providing a baseline of natural variability. A benthic sampling time-series established by Gage and co-workers at two stations in the Rockall Trough (Gage *et al.*, 1980) ran from the mid-1970s to the early 1990s. This focused on growth rates and reproductive cycles of selected benthic invertebrate species rather than analysis of change at the community level, and the material collected has not so far been used to address this issue. However, the archive of data and unprocessed samples held at the Scottish Association for Marine Science is potentially a valuable source of historical information and efforts are underway to mobilize this with a view to re-starting the Rockall Trough time-series in the future.

At depths greater than 200 m, ecosystems are not directly affected by climate-driven factors such as sea surface temperature, storm surge or significant wave height. Deep-sea organisms experience far more stability in terms of water temperature, salinity and currents than do their shallow-water counterparts and may not tolerate even small changes in these environmental parameters. Bottom water temperature in the deep sea is low but generally stable, although changes may occur in response to future shifts in the pattern of global thermohaline circulation such as, for example, reduction in the rate of deep water formation in the Norwegian-Greenland Sea brought about by freshening of the ocean surface at high latitudes. This area of the north-east Atlantic generates a large fraction of global deep water and the regional deep-sea ecosystem may therefore be the first to show the effects of climate change, with eventual consequences for the deep ocean worldwide. In the last 50 years there has been a 50% decrease in the southward transport of North Atlantic Deep-Water at 25°N (Bryden *et al.*, 2005); it is not clear what effect this may have had on deep-sea benthic ecosystems. Changes in thermohaline circulation may not affect all deep-water areas equally. For example, in the Faroe–Shetland Channel (Region 8) cold (subzero) waters occupy the deeper parts of the channel (>600 m), with warmer water above. This has a substantial influence on the distribution and diversity of the benthic fauna (Bett, 2001). While there is continuous variation in the fauna with depth, warm- and cold-water faunas are nonetheless quite distinct. Changes in the thermohaline circulation may alter the depth of this thermocline, with a subsequent change in the distribution of animals.

Over the next few decades the most significant impact of climate change on the UK's deep sea ecosystems is likely to be indirect, via changes in surface ocean primary productivity and the supply of organic matter to the deep-sea bed. Research into this fundamental ecological process has provided the best evidence that climate-driven changes are currently taking place in the deep ocean (Smith *et al.*, 2008).

The vast majority of deep-sea life is dependent on organic matter produced in surface waters, supplied either by vertical sinking through the water column or by advection down the continental slope from coastal and shelf seas. Until the early 1980s, organic flux to the deep-sea bed was thought to be essentially steady-state and largely decoupled from cycles of primary production in the euphotic zone. Studies in the Porcupine Seabight, off south-west Ireland, showed, in contrast, that aggregates of phytoplankton cells can sink rapidly following the spring bloom in surface waters and accumulate on the deep-sea bed at depths of over 4000 m. Deposition occurs with a time-lag of about eight weeks at 4000 m depth, imparting a distinct seasonal signal to the supply of organic matter (Lampitt,1985). Episodic deposition of partially-degraded phytoplankton (phytodetritus) has since been recorded at many deep-sea locations around the world (Beaulieu, 2002) and has been shown to trigger a range of short-term ecosystem responses including enhanced sediment community respiration, population “blooms” of opportunist foraminiferan species and rapid burial of organic-rich food particles by burrowing macrofauna (Gooday, 2002). Climatic oscillations such as El Niño and the North Atlantic Oscillation (NAO) have been shown to drive changes in organic flux to the abyssal seabed, with major consequences for benthic ecosystems (Smith *et al.*, 2006).

The ecological consequences of seasonality in phytodetrital flux to the abyssal seabed became a principal theme of deep-sea research through the 1980s and 1990s. The EU-funded *BENGAL* programme of 1996-1999 was a major international research initiative focusing on a station on the Porcupine Abyssal Plain (PAP), south-west of Ireland (48^0 50’ N, 16^0 30’ W, 4850 m depth), (Billett & Rice, 2001). An unexpected but highly significant outcome of this programme was the demonstration that populations of several species of benthic invertebrates (epibenthic megafauna) had increased massively in comparison with samples from the same area taken prior to 1996 (Billett *et al.,* 2001). In particular, seabed photographs showed that the small holothurian (sea cucumber) *Amperima rosea* occurred at densities of >6000 individuals ha^{-1} in 1997, an approximately 1000-fold increase since the early 1990s (Bett *et al.,* 2001). The striking population explosion of this formerly rare species led to the phenomenon being termed the “*Amperima* Event”. Trawl samples showed that the increase was not confined to the central study site but had occurred over a wide area of the PAP.

The discovery of the “*Amperima* Event” provided evidence that populations of deep-sea animals are highly dynamic and can change far more rapidly than previously thought. Sampling has continued at the site now designated the *Porcupine Abyssal Plain Sustained Observatory* (PAP-SO), which lies just outside the UK’s territorial deep sea. Data on other components of the benthic ecosystem have been analysed since the end of the *BENGAL* programme, with results (to 2005) summarized by Billett *et al*. (2010). Megafaunal populations declined steadily after 1997 to 2000, but showed a second major peak in 2002 (Fig. 1), as before largely driven by increased densities of *A. rosea* (Billett *et al.,* 2010). Peaks in density were correlated with reductions in mean body size, indicating that the increases were caused by large-scale recruitment events. Analysis of data from the BENGAL programme showed that macrofaunal polychaetes and metazoan meiofauna, particularly nematodes, also showed significant increases in density during the “*Amperima* Event” of 1996-1999 (Kalogeropoulou *et al.,* 2010; Soto *et al.*, 2010).

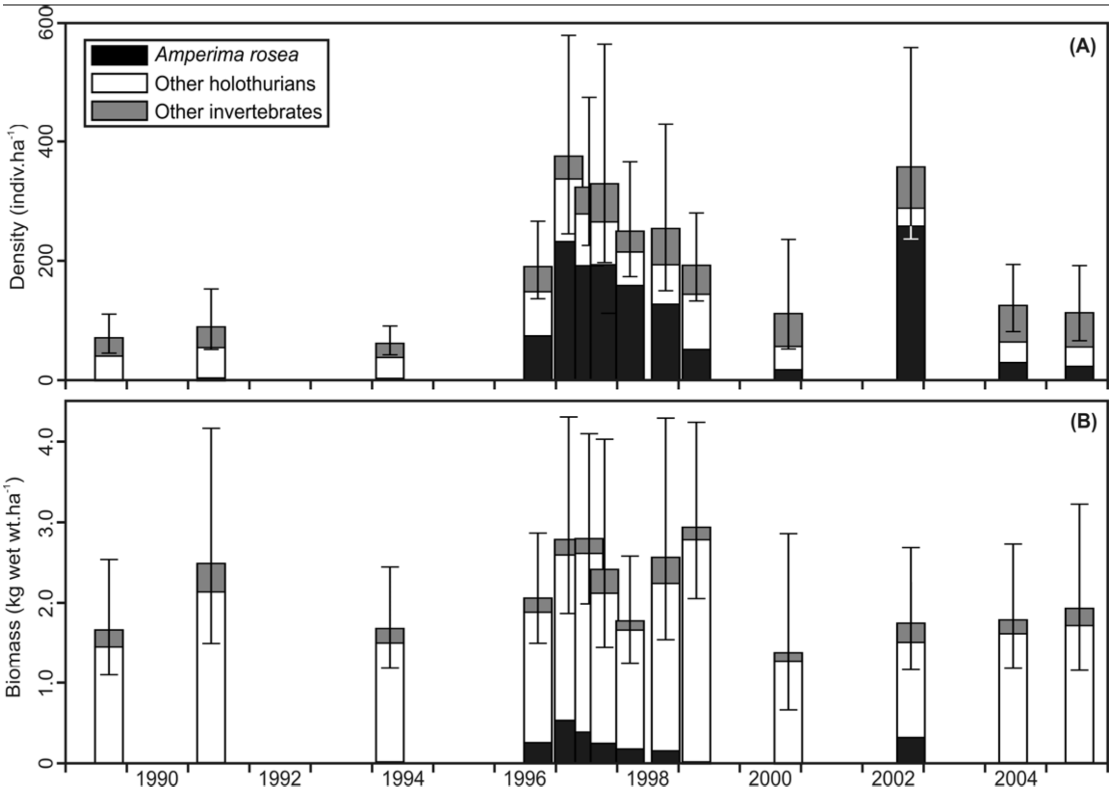


Figure 1. *Histograms illustrating temporal variations in (A) density and (B) biomass of selected megafaunal groups at the Porcupine Abyssal Plain Sustained Observatory site. Means ± 95% confidence intervals are shown. The cluster of bars from 1996-1999 represents the original "Amperima Event" detected during the BENGAL programme. Figure reproduced from Billett et al. (2010).*

Major changes in abundance occurred simultaneously in all size fractions of the PAP faunal community, indicating that the faunal changes were driven by environmental factors rather than being stochastic fluctuations in population size of a few species (Billett *et al.*, 2010). Early explanations of the "*Amperima* Event" focused on the feeding preferences of *A. rosea* (as indicated by gut content phytopigment profiles) and the possibility of changes in the composition (rather than total quantity) of phytodetritus reaching the PAP seabed (Wigham *et al.,* 2003). However it is now believed that interannual variation in the total quantity of organic flux to the deep-sea bed may be the causal factor behind the observed benthic community changes. The extended time-series at PAP-SO includes sediment trap measurements of settling organic matter. Results show that organic flux to the abyssal seabed can differ by an order of magnitude between years, a much wider range of variability than expected from previous studies (Lampitt *et al.*, 2010). The large deposition of organic carbon recorded in the late summer of 2001 (Fig. 2) was followed by the second major abundance peak of *A. rosea* in 2002 (Fig. 1), a pattern supporting the hypothesis that community changes on the PAP are driven by interannual variation in the quantities of phytodetritus reaching the seabed.

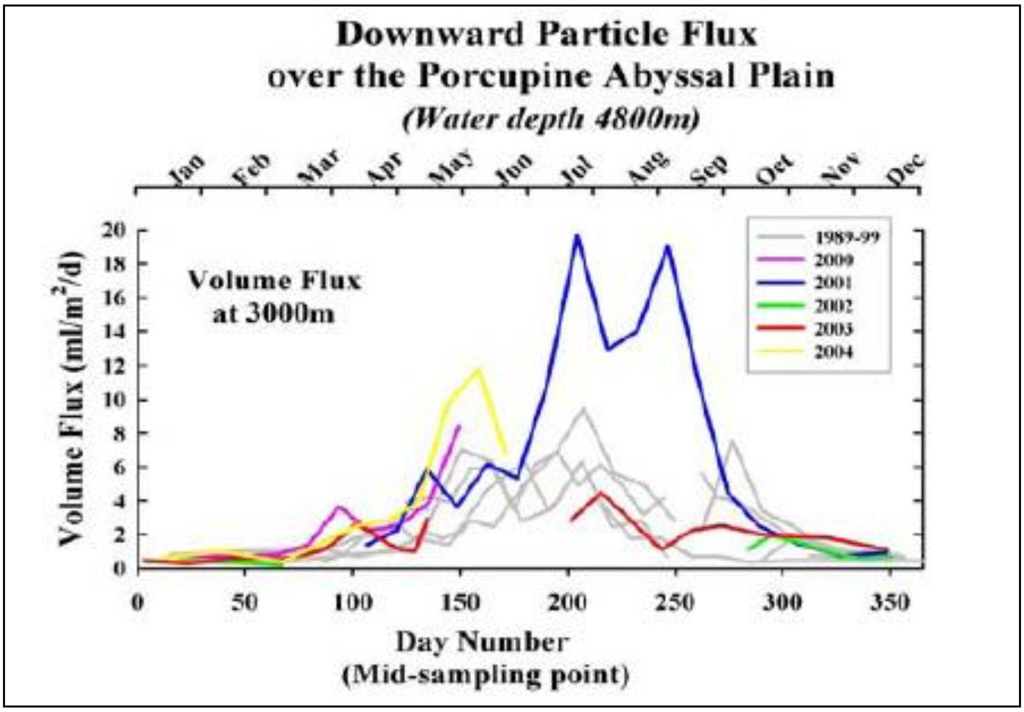


Figure 2*. Particle flux at the PAP-SO, 1989 – 2004, measured from sediment traps at 3000 m depth. Data from R. Lampitt, NOC.*

The detail and frequency of scientific observations at the PAP-SO are unique for the deep north-east Atlantic, and we have no comparable information from the Rockall Trough or Faroe-Shetland Channel. However, major ecosystem changes, involving large shifts in abundance of both invertebrate megafauna and fish species have been recorded from time-series studies at an abyssal locality in the north-east Pacific (Bailey *et al*., 2006; Ruhl, 2007). These changes also appear to be related to the quantities of surface-produced organic matter reaching the abyssal seabed (Ruhl & Smith, 2004) reinforcing the hypothesis that this is the causal factor behind the events observed on the PAP.

Smith *et al.* (2006) suggest that variations in export flux in the north-east Atlantic are related to the North Atlantic Oscillation, which is in turn linked to global climate, and present a model to estimate carbon flux to the deep sea from climatic indices and satellite measurements of surface primary production. This approach, which provides a link between atmospheric/surface ocean parameters and the supply of food to the abyss may allow prediction of the timing of future changes in deep-sea ecosystems.

2. What could happen in the future?

The future impacts of climate change on deep-sea ecosystems may be through two main factors: i) Ocean acidification, and ii) Changes in surface ocean productivity. These are likely to affect all UK sea areas that contain deep-water ecosystems equally.

i. Ocean acidification

Acidification arising from the increased flux of anthropogenic carbon dioxide to the ocean is thought likely to have signficant ecological effects by the mid to late 21st century (Orr *et al.,* 2005, IPCC, 2007). Ocean pH has already fallen by 0.1 units since pre-industrial times and is set to fall another 0.3-0.4 units by the year 2100 if fossil fuel burning continues at its current rate. Acidification will trigger significant changes in oceanic carbonate chemistry with major adverse effects on calcifying organisms. In the deep sea, attention has so far been focused on reef-forming corals (Turley *et al.,* 2007), which may be particularly affected by the shoaling of the aragonite saturation horizon (the depth separating saturated and under-saturated waters). It is estimated that 70% of known scleractinian cold-water coral ecosystems will be in under-saturated water by 2100 (Guinotte *et al.*, 2006). There have been no published experimental results on the impact of higher seawater CO_2 concentrations on deep-water corals. However, if deep-water corals respond in the same way as warm-water species, a substantial decrease in calcification would occur as a result of acidification (Kleypas *et al.*, 2006). Other deep-sea calcifying organisms such as molluscs, crustaceans and many benthic Foraminifera will also be sensitive to ocean acidification but the full extent of future impacts is still uncertain. The North Atlantic is a major sink for atmospheric CO_2 and may therefore be particularly vulnerable to the effects of acidification (Sabine *et al.,* 2004).

ii. Changes in surface ocean productivity

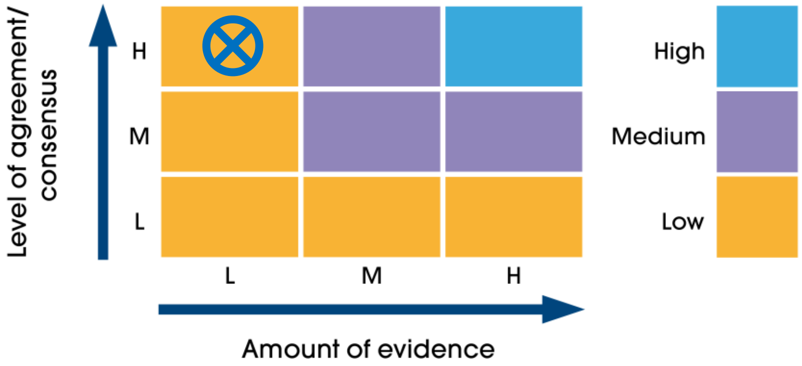
Given the uncertain influence of climate change on upper ocean processes, predicting the specific impacts on deep-sea ecosystems is difficult (Smith & Hughes, 2008). Some predicted broad-scale changes certainly would have catastrophic consequences on deep-sea life. The likely reorganisation in the global thermohaline circulation caused by climate change (Schmittner & Stocker, 1999; Bryden *et al.*, 2005) would have considerable impact on deep-sea fauna. These effects could be similar to the diversity fluctuations during the Cenozoic and Quaternary revealed by the microfossil (foraminifera and ostracod) record preserved in deep-sea sediments (Thomas & Gooday, 1996; Hunt *et al.*, 2005). At least in some cases, reductions in diversity were caused by changes in thermohaline circulation and must have had a substantial impact on ecosystem functioning (Danovaro *et al.*, 2008). In addition, climate-driven changes in upper-ocean biogeochemistry (Orr *et al.*, 2005) will alter the quantity and quality of food arriving at the sea-floor, driving changes in deep-sea benthic community composition (Billett *et al.*, 2001; Ruhl & Smith, 2004). Benthic biomass and abundance, bioturbation depth and rates have all been shown to be affected by food supply (Smith & Demopoulos, 2003). Changes in the rates of these ecosystem functions are likely to affect the sequestration and burial of carbon.

The studies summarized above demonstrate that deep-sea ecosystems are much more responsive to processes occurring in surface waters than once believed. Recently-published results from the deep Catalonian slope in the western Mediterranean also document shifts in benthic community structure that may be related to NAO-driven climate changes affecting food supply to the benthos (Cartes *et al.*, 2009). Despite this gradually-emerging pattern it is difficult to predict the course of future climate-driven changes in the UK's territorial deep sea, and it is impossible to predict how these may affect the different sea areas. Continuous Plankton Recorder (CPR) time-series data indicate shifts in north-east Atlantic plankton communities that may reflect a response to changing climate on a decadal timescale (Reid *et al.,* 1998). However, it is uncertain how these changes will be transmitted through the marine ecosystem (Beaugrand, 2009). One possible scenario is that a warmer, more stratified surface ocean with reduced upwelling will be associated with a shift from a planktonic system dominated by diatoms and large zooplankton, with high particulate organic carbon flux to the deep sea, to one characterized by picoplankton, microzooplankton and lower export efficiency (Smith *et al.*, 2008). A decline in organic carbon flux to the deep-sea bed would be expected to result in lower faunal biomass and a shift in community body size spectrum towards smaller organism size-classes. Benthic deposit-feeders specializing in a diet of fresh phytodetritus might be expected to be affected more rapidly than those exploiting older, more refractory organic material (Iken *et al.,* 2001). The time-scale over which such changes might occur is unclear. In the abyssal north-east Pacific, measured carbon flux to the sea-bed steadily declined over the period from 1989 to 1996 while sediment community oxygen demand (a measure of benthic biological metabolism) remained constant (Smith *et al.*, 2001). Such a deficit between ecosystem organic carbon supply and demand would not be sustainable in the long term. In the north-east Pacific the deficit was “corrected” by increased organic carbon flux after 1998, but the example illustrates the difficulty of predicting the behaviour of the poorly-understood deep-sea ecosystem.

The faunal changes observed on the PAP (and the parallel events in the north-east Pacific) took place in topographically simple abyssal plain ecosystems remote from continental influences and entirely dependent on organic matter sinking from the overlying euphotic zone. The deep-sea regions in “Charting Progress” Regions 4, 7 and 8 occupy a much more complex topographic setting, including seamounts, offshore banks, a steep continental margin and the deep basins of the Rockall Trough and Faroe-Shetland Channel. The physical oceanography of the region is also complex (New & Smythe-Wright, 2001). This huge area supports a diverse range of deep-sea habitats and species (e.g., Bett, 2001; Naryanaswamy *et al.,* 2006; Howell *et al.,* 2007), with biological communities changing markedly across gradients of water depth, substratum type and hydrodynamics (Gage, 2002). Assessment of potential climate change impacts mediated by changes in planktonic primary production is therefore even more difficult than in the case of abyssal plain ecosystems and no detailed predictions can be made at this time.

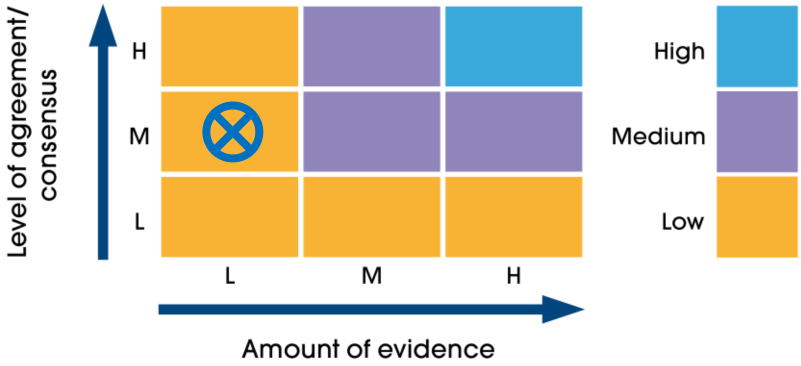
3. Confidence in the science

What is already happening: Low



We have clear evidence that major benthic community changes have occurred on the Porcupine Abyssal Plain and there is compelling evidence that these changes are related to changes in export flux of organic matter from the surface waters related to climate variations (i.e. the North Atlantic Oscillation). Export flux, seasonality and rate of organic matter recycling in the euphotic zone, are likely to be significantly affected by climate-driven changes in the surface ocean in UK waters. However, the “Amount of evidence” is rated as Low to reflect the fact that the available north-east Atlantic data are confined to the PAP and we have no comparable information from any other localities in the UK’s territorial deep sea.

What could happen: ***Low***



The lack of any long-term data sets giving information on background temporal variability of deep-sea biological communities in Regions 4, 7 and 8 justifies a Low rating for “Amount of evidence”. “Level of agreement” is rated as Medium to reflect the general consensus that climate-driven changes in surface ocean primary productivity and export flux are likely to occur and will have consequences for deep-sea ecosystems, although detailed predictions of the pattern of change are not possible.

4. Knowledge gaps

The top priority knowledge gaps that need to be addressed in the short term to provide better advice to be given to policy makers are:

1. *Lack of baseline data on natural temporal variability of deep-sea biological communities in Region 8.* There is an urgent need for more time-series data to detect and monitor ecosystem change. The archived data and unprocessed samples from the SAMS Rockall Trough stations, surveyed at intervals from 1973 to 1995, should be analysed with a view to re-starting this time-series. Long-term monitoring should also be established in the domain of Arctic water outflow in the Faroe-Shetland Channel/Wyville Thomson Ridge Region.
2. *Limited understanding of the ecosystem effects of benthic community changes in the deep sea.* This should be addressed by maintaining the PAP-SO time-series sampling of phytodetrital flux and benthic population abundance/biomass, supplemented by measurements, *in situ* experiments and ecological modelling (as appropriate) of important ecological processes such as organic carbon turnover and burial, bioturbation, food web dynamics and reproductive output of benthic organisms.
3. *Limited information on the distribution and structure of benthic biological communities in Region 8.* While the baseline surveys carried out under the Strategic Environmental Assessment (SEA) programme in the Faroe-Shetland Channel (SEA4) and Rockall Trough (SEA7) there is still a lack of data on the range and distribution of deep-sea faunal communities within UK waters.

5. Socio-economic impacts

Attaching a monetary value to the deep-sea is problematic for several reasons: the limited knowledge of deep-sea ecosystems and the goods and services they provide, the complexity of the ecological processes as well as the broad time- and spacescales over which they operate, the nature of deep-sea ecosystems, especially those with significant option-use values for which it is difficult to derive a monetary value, and the fact that people have practically no first-hand experience of deep-sea ecosystems, so valuation methods based on preferences are likely to be biased or irrelevant (van den Hove, 2007).

While there are unlikely to be any direct socio-economic impacts arising from the ecosystem changes discussed here, the deep sea provides a number of important ecosystem functions which may alter in response to climate change. In particular, the deep sea plays an important role in the global carbon cycle, and mediates the removal of carbon from the global carbon cycle into the geological record. The deep-sea also provides a range of ecosystem goods and services (i.e. human benefits directly or indirectly derived from ecosystem functions). Maintenance of biodiversity is thought to be essential to ecosystem stability, so that loss of species may detrimentally influence ecosystem function, and therefore the provision of goods and services (van den Hove, 2007).

Certain components of the Total Economic Value of the deep seas such as oil and gas extracted or fish harvested are relatively straightforward to value through market prices. However, the majority of deep-water biotic resources have slow growth rates such that their exploitation is much like that of abiotic resources; that is, they should be considered as non-renewable. Climate-driven changes in the deep sea of Region 8 are likely to affect commercially-exploited demersal fish species such as orange roughy (*Hoplostethus atlanticus*), roundnose grenadier (*Coryphaenoides rupestris*) and deep-water sharks. This is the only living resource currently exploited in the UK's deep sea. Stocks of these fish species have been massively depleted by unsustainable levels of trawling (Gordon, 2003; Bailey *et al.*, 2009). Current fishing pressure is much reduced, with populations possibly stabilizing at much reduced levels (Neat & Burns, 2010).

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