

Impacts of climate change on deep-sea habitats

David J. Hughes and Bhavani E. Narayanaswamy

Scottish Association for Marine Science, Oban, PA37 1QA, UK

EXECUTIVE SUMMARY

The UK's territorial deep sea covers a huge geographic area and supports a wide range of environments and biological communities. The deep sea is remote, difficult and expensive to study and as result our understanding of its ecology is still very limited, with detailed studies restricted to a small number of localities.

Deep-sea ecosystems carry out a range of ecosystem processes that are essential to global biogeochemical cycling (e.g. organic carbon turnover and burial).

There are no long-term datasets from the UK's deep sea showing the extent of natural biological variability over time. The lack of a natural baseline makes it difficult to predict future climate-driven changes.

Deep-sea organisms are largely reliant for food on plankton sinking from surface waters. Climate-driven changes in surface ocean productivity will therefore have a major impact on deep-sea ecosystems.

Studies on the Porcupine Abyssal Plain indicate that increases in the annual flux of detrital food reaching the deep-sea bed can trigger population explosions of some benthic invertebrate species. Deep-sea populations are therefore likely to be responsive to climate-driven changes in ocean primary production.

Ocean acidification poses a major long-term threat to deep-sea corals and other calcifying organisms. However, at present we have very few data on which to base predictions of future impacts.

1. WHAT IS ALREADY HAPPENING?

In UK territorial waters the "deep sea" is coincident with "Charting Progress" Region 8 (Atlantic North-West Approaches, Rockall Trough and Faroe-Shetland Channel). The south-west extremity of Region 4 (Western English Channel, Celtic Sea and South-West Approaches) crosses the shelf break and therefore extends marginally into the deep sea. Although Region 4 accounts for only a small fraction of the territorial deep sea, this small area contains the only UK submarine canyons, an important deep-sea habitat. Water depths range from ~200 m at the shelf break to >2000 m in the central Rockall Trough. Offshore areas of relatively shallow topography include the Anton Dohrn and Rosemary Bank Seamounts (summits 500-600 m) and the broad expanse of the north-eastern Rockall Plateau (~200 m). This area to the north and west of Scotland was the scene of some of the pioneering oceanographic surveys of the 19th century which helped lay the foundations of deep-sea science (Wyville Thomson, 1873; Gage and 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 plains using corers, dredges and trawls. Areas of rugged topography such as seamounts, reefs and steep slopes were generally avoided, the early manned submersible surveys by Wilson (1979) on deep-water coral distribution being a notable exception. Modern research vessels with precise satellite navigation systems, dynamic positioning, remotely operated vehicles (ROVs) and camera-guided samplers can now access difficult submarine terrain and our knowledge of these habitats in the UK's deep sea is expanding rapidly (Stewart *et al.*, 2009). 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 of the UK's seamounts and banks has been gained only within the last seven years (Narayanaswamy *et al.*, 2006; Howell *et al.*, 2007, 2010a,b; Howell, 2010; Stewart *et al.*, 2009). Assessment of climate change impacts in the UK's deep sea is therefore constrained by our limited understanding of ecosystem structure and functioning 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 on decadal change in this deep-sea region.

At depths >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 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 local thermocline, with a subsequent change in animal distributions.

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 sea (Smith *et al.*, 2008; Glover *et al.*, 2010).

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 >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 (Goody, 2002). Climatic oscillations such as El Niño and the North Atlantic Oscillation (NAO) have been shown to drive changes in organic flux to the deep-sea bed, with major consequences for benthic ecosystems (Smith *et al.*, 2006).

The ecological consequences of seasonality in phytodetrital flux to the deep-sea bed became a principal theme of research through the 1980s and 1990s. The EU-funded BENGAL programme (1996-1999) was a major international research initiative focusing on a 4850 m-deep station on the Porcupine Abyssal Plain (PAP), south-west of Ireland (Billett and Rice, 2001). An unexpected but highly significant outcome of this programme was the discovery that populations of several species of large benthic invertebrates (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 some deep-sea animals are highly variable and can change far more rapidly than previously thought. Sampling has continued at the site now designated as 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 from 1997 to 2000, but showed a second major peak in 2002, 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). 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 input 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 was followed by the second major abundance peak of *A. rosea* in 2002, a pattern supporting the hypothesis that community changes on the PAP are driven by interannual variation in the quantities of phytodetritus reaching the sea bed.

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 sea bed (Ruhl and 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 NAO, 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. However, we still have very limited information on the natural variability of deep-sea communities against which to measure the projected impacts of anthropogenic climate change.

2. WHAT COULD HAPPEN?

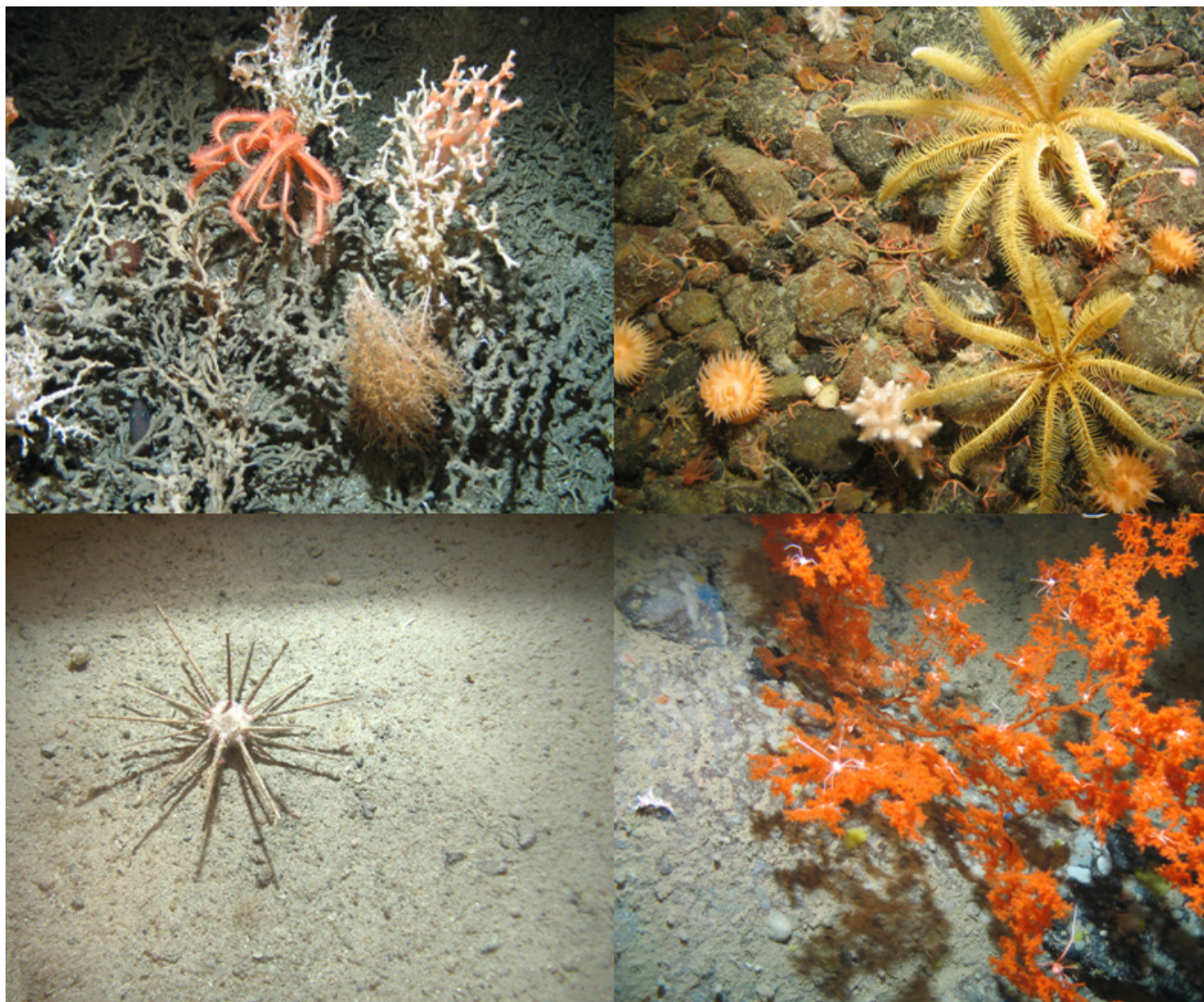
Future impacts of climate change on deep-sea ecosystems are likely to be driven by two main factors: 1) changes in surface ocean productivity, and 2) ocean acidification and other physico-chemical changes in water mass structure. These are likely to affect all UK sea areas that contain deep-water ecosystems.

2.1 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 and Hughes, 2008; Glover *et al.*, 2010). Some predicted broad-scale changes certainly would have catastrophic consequences for deep-sea life. The likely reorganization in the global thermohaline circulation caused

by climate change (Schmittner and Stocker, 1999; Bryden *et al.*, 2005) would have considerable impact on deep-sea ecosystems. These effects could be similar to the diversity fluctuations during the Cenozoic revealed by the microfossil (foraminiferan and ostracod) record preserved in deep-sea sediments (Thomas and Gooday, 1996; Hunt *et al.*, 2005). At least in some cases, reductions in diversity were associated with 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 deep-sea floor, driving changes in benthic community composition (Billett *et al.*, 2001; Ruhl and Smith, 2004). Benthic biomass and abundance, rates and depth of bioturbation have all been shown to be affected by food supply (Smith and Demopoulos, 2003). Changes in these indices of ecosystem functioning are likely to affect the sequestration and burial of organic carbon at the sea floor.

The studies summarized above demonstrate that deep-sea ecosystems are much more responsive to upper-ocean processes than once believed. Recently-published results from the deep Catalanian 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 growing body of data it is very difficult to predict the course of future climate-driven changes in the UK's territorial deep sea. 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 to the deep sea (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 organic flux to the deep sea, to one characterized by picoplankton, microzooplankton and lower export efficiency (Smith *et al.*, 2008). Warmer, more strongly stratified surface waters may also lead to reduced particle sinking rates which will further limit the supply of food to the deep sea. 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 others exploiting older, more refractory material (Iken *et al.*, 2001). The timescale over which such changes might occur is unclear. In the abyssal north-east Pacific, measured carbon flux to the sea bed declined over the 1989-1996 period 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 be unsustainable in the long term. It is uncertain how benthic metabolism was maintained during the period of reduced carbon supply, but at this station the deficit was “corrected” by increased organic carbon flux after 1998. This example illustrates the difficulty of predicting the behaviour of the poorly-understood deep-sea ecosystem.



Photographs illustrating the diversity of seabed habitats and communities in the UK's territorial deep sea. [Images from Defra/JNCC]: Upper left: Brisingid seastar and patches of living cold-water coral (*Lophelia pertusa*) on sediment-covered coral rubble, Hatton Bank, 630 m depth. Upper right: Yellow crinoids (*Heliometra glacialis*) with anemones, white branching sponge and numerous brittlestars on gravel seabed, northern Wyville Thomson Ridge, 850 m depth. Lower left: Pencil urchin (*Cidaris cidaris*) on coarse sand, summit of Anton Dohrn Seamount, 660 m depth. Lower right: Black coral (*Leiopathes* sp.) colony with small chirostyliid crabs on silty bedrock slope, George Bligh Bank, 1280 m depth.

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 UK's deep sea in Region 8 occupies a much more complex topographic setting, which includes 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 and Smythe-Wright, 2001). This huge area supports a diverse range of deep-sea habitats and species (e.g. Bett 2001; Narayanaswamy *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.

2.2 Ocean acidification

Acidification arising from the increased flux of anthropogenic carbon dioxide to the ocean is thought likely to have significant 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. In the Rockall Trough a pH decrease of ~0.04 units for subsurface waters down to 1000 m depth, with further reductions below this has been recorded for the 1991–2010 period (McGrath *et al.*, 2012). 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 waters by 2100 (Guinotte *et al.*, 2006). So far, there are few published data of the effects of acidification on cold-water corals or other deep-sea organisms (Thresher *et al.*, 2011; Lunden *et al.*, 2013), and projected effects are largely based on analogies with better-studied shallow-water ecosystems. Several research programmes are currently underway to address these data gaps, including the UK's Ocean Acidification Programme, funded by NERC, and the European Commission's 7th Framework Programmes EPOCA and the recently-completed HERMIONE. If deep-water corals respond in the same way as tropical reef species, a substantial decrease in calcification may 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 and timescale of future impacts is difficult to predict. The North Atlantic is a major sink for atmospheric carbon dioxide and may therefore be particularly vulnerable to the effects of acidification (Sabine *et al.*, 2004).

3. KNOWLEDGE GAPS

a. *Lack of baseline data on natural temporal variability of deep-sea biological communities in Region 8:* The only currently-available source of information is the archive of data and unprocessed samples from the SAMS Rockall Trough stations, surveyed from 1973-1995. Support should be provided to process and analyse this material, which represents a unique historical dataset of benthic community change in the deep sea. Establishment of new monitoring time-series in a range of environments in the UK's territorial deep sea should also be a priority.

b. *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 of important ecological processes such as organic carbon turnover and burial, bioturbation, food web dynamics and reproductive output of benthic organisms.

c. *Limited information on the distribution and structure of deep-sea biological communities in Region 8:* The baseline surveys carried out under the Strategic Environmental Assessment (SEA) programme in the Rockall Trough and Faroe-Shetland Channel should be expanded to provide a more comprehensive mapping and classification of deep-sea ecosystems in this region, which accounts for almost all of the UK's territorial deep sea.

4. SOCIO-ECONOMIC IMPACTS

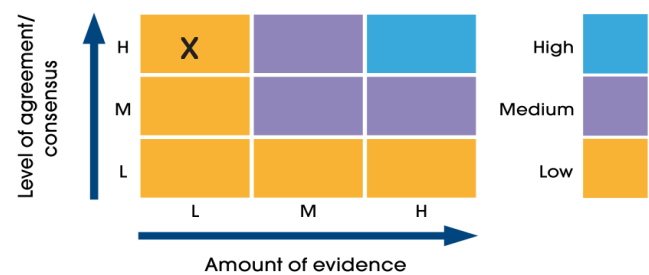
Attaching a monetary value to the deep sea is problematic for several reasons: the limited knowledge of deep-sea ecosystems and the goods and services they provide, the complexity of the ecological processes as well as the broad time- and spatial scales over which they operate, and the fact that very few people have first-hand experience of the deep sea, 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 ecosystem into the geological record.

Certain components of the Total Economic Value of the deep seas such as oil and gas extracted or fish harvested are relatively straight forward to value through market prices. The majority of deep-water biotic resources have slow growth rates such that their exploitation is analogous to that of an abiotic resource, i.e. effectively 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. Fish such as these are the only living resources currently exploited in the UK's deep sea. Stocks have already 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 very low levels (Neat and Burns, 2010).

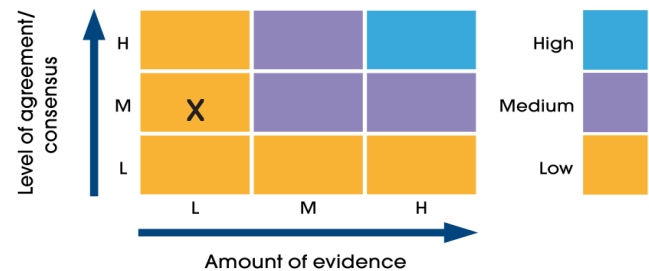
5. CONFIDENCE ASSESSMENT

What is already happening?



We know that major benthic community changes have occurred on the Porcupine Abyssal Plain (PAP) and there is strong evidence that these changes are driven by interannual variation in export flux of phytodetritus from surface waters (hence, "Level of Agreement" = High). This interannual variation may be related to climate-sensitive processes such as the North Atlantic Oscillation. Export flux, seasonality and rate of organic matter recycling in the euphotic zone are significantly affected by future climate-driven changes in surface waters around the UK. 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?



The lack of any long-term datasets giving information on background temporal variation in deep-sea ecosystems of Region 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 ocean productivity and acidification are likely to occur, with consequences for deep-sea ecosystems, although detailed predictions of the pattern of change are not possible.

CITATION

Please cite this document as:

Hughes, D.J. and B. E. Narayanaswamy (2013) Impacts of climate change on deep-sea habitats, *MCCIP Science Review 2013*, 204-210, doi:10.14465/2013.arc21.204-210

REFERENCES

- Bailey, D.M., Ruhl, H.A. and Smith, K.L. Jr. (2006) Long-term change in benthopelagic fish abundance in the abyssal northeast Pacific Ocean. *Ecology*, **87**, 549-555.
- Bailey, D.M., Collins, M.A., Gordon, J.D.M., Zuur, A.F. and Priede, I.G. (2009) Long-term changes in deep-water fish populations in the northeast Atlantic: a deeper-reaching effect of fisheries? *Proc. R. Soc. Lond. B*, **276**, 1965-1969.
- Beaugrand, G. (2009) Decadal changes in climate and ecosystems in the North Atlantic Ocean and adjacent seas. *Deep-Sea Res. II*, **56**, 656-673.
- Beaulieu, S.E. (2002) Accumulation and fate of phytodetritus on the sea floor. *Oceanogr. Mar. Biol. Ann. Rev.*, **40**, 171-232.
- Bett, B.J. (2001) UK Atlantic Margin Environmental Survey: Introduction and overview of bathyal benthic ecology. *Continental Shelf Res.*, **21**, 917-956.
- Bett, B.J., Malzone, M.J., Narayanaswamy, B.E. and Wigham, B.D. (2001) Temporal variability in phytodetritus and megabenthic activity at the seabed in the deep Northeast Atlantic. *Prog. Oceanogr.*, **50**, 349-368.
- Billett, D.S.M. and Rice, A.J. (2001) The BENGAL programme: introduction and overview. *Prog. Oceanogr.*, **50**, 13-25.
- Billett, D.S.M., Bett, B.J., Rice, A.J., Thurston, M.H., Galéron, J., Sibuet, M. and Wolff, G.A. (2001) Long-term change in the megabenthos of the Porcupine Abyssal Plain (NE Atlantic). *Prog. Oceanogr.*, **50**, 325-348.
- Billett, D.S.M., Bett, B.J., Reid, W.D.K., Boorman, B. and Priede, I.G. (2010) Long-term change in the abyssal NE Atlantic: the “Amperima” Event revisited. *Deep-Sea Res. II*, **57**, 1406-1417.
- Bryden, H.L., Longworth, H.R. and Cunningham, S.A. (2005) Slowing of the Atlantic meridional overturning circulation at 250 N. *Nature*, **438**, 655-657.
- Cartes, J.E., Maynou, F., Fannelli, E., Papiol, V. and Lloris, D. (2009) Long-term changes in the composition and diversity of deep-slope megabenthos and trophic webs off Catalonia (western Mediterranean): are trends related to climatic oscillations? *Prog. Oceanogr.*, **82**, 32-46.
- Danovaro, R., Gambi, C., Dell’Anno, A., Corinaldesi, C., Fraschetti, S., Vanreusel, A., Vincx, M. and Gooday, A.J. (2008) Exponential decline in deep-sea ecosystem functioning linked to benthic biodiversity loss. *Current Biology*, **18**, 1-8.
- Davies, A.J., Narayanaswamy, B.E., Hughes, D.J. and Roberts, J.M. (2006) *An introduction to the benthic ecology of the Rockall-Hatton area (SEA7)*. http://www.offshore-sea.org.uk/consultations/SEA_7/SEA7_Benthos.pdf
- Gage, J.D. (2002) *Benthic biodiversity across and along the continental margin: patterns, ecological and historical determinants, and anthropogenic threats*. In: Wefer, G., Billett, D., Hebbeln, D., Jørgensen, B.B., Schlüter, M. and Van Weering, T. (eds.) *Ocean Margin Systems*. Springer-Verlag, Berlin and Heidelberg, pp. 307-321.
- Gage, J.D., Lightfoot, R.H., Pearson, M. and Tyler, P.A. (1980) An introduction to a sample time-series of abyssal macrobenthos: methods and principal sources of variability. *Oceanologia Acta*, **3**, 169-176.
- Gage, J.D. and Tyler, P.A. (1991) *Deep-Sea Biology: A Natural History of Organisms at the Deep-Sea Floor*. Cambridge University Press, 504 pp.
- Glover, A.G., Gooday, A.J., Bailey, D.M., Billett, D.S.M., Chevaldonné, P., Colaço, A., Copley, J., Cuvelier, D., Desbruyères, D., Kalogeropoulou, V. et al. (2010) Temporal change in deep-sea benthic ecosystems: a review of the evidence from recent time-series studies. *Adv. Mar. Biol.*, **58**, 1-95.
- Gooday, A.J. (2002) Biological responses to seasonally varying fluxes of organic matter to the ocean floor: a review. *J. Oceanogr.*, **58**, 305-332.
- Gordon, J.D.M. (2003) The Rockall Trough, Northeast Atlantic: the cradle of deep-sea biological oceanography that is now being subjected to unsustainable fishing activity. *J. Northwest Atl. Fishery Sci.*, **31**, 57-83.
- 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 Ecol. Env.*, **4**, 141-146.
- Howell, K.L. (2010) A benthic classification system to aid in the implementation of marine protected area networks in the deep/high seas of the NE Atlantic. *Biol. Cons.*, **143**, 1041-1056.
- Howell, K.L., Davies, J.S., Hughes, D.J. and Narayanaswamy, B.E. (2007) *Strategic Environmental Assessment/Special Area of Conservation*. Photographic Analysis Report. Report to the Department of Trade and Industry/GEOTEK, 82 pp.
- Howell, K.L., Davies, J.S. and Narayanaswamy, B.E. (2010a) Identifying deep-sea megafaunal epibenthic assemblages for use in habitat mapping and marine protected area network design. *J. Mar. Biol. Assoc. UK*, **90**, 33-68.
- Howell, K.L., Mowles, S.L. and Foggo, A. (2010b) Mounting evidence: near-slope seamounts are faunally indistinct from an adjacent bank. *Mar. Ecol.*, **31** (Suppl. S1), 52-62.
- Hughes, J.A., Narayanaswamy, B.E. and Bett, B.J. (2003) *SEA4: an overview of the benthic ecology of the Faroe-Shetland Channel*. http://www.offshoresea.org.uk/consultations/SEA_4/SEA4_TR_Benthos_SOC.pdf
- Hunt, G., Cronin, T.M. and Roy, K. (2005) Species-energy relationship in the deep sea: a test using the Quaternary fossil record. *Ecol. Lett.*, **8**, 739-747.
- Iken, K., Brey, T., Wand, U., Voight, J. and Junghans, P. (2001) Food web structure of the benthic community at the Porcupine Abyssal Plain (NE Atlantic): a stable isotope analysis. *Prog. Oceanogr.*, **50**, 383-405.
- IPCC (2007) *Climate Change 2007: The physical science basis*. Summary for policymakers. Contribution of Working Group I to the Fourth Assessment Report. The Intergovernmental Panel on Climate Change.
- Kalogeropoulou, V., Bett, B.J., Gooday, A.J., Lampadariou, N., Martinez Arbizu, P. and Vanreusel, A. (2010) Temporal changes (1989-1999) in deep-sea metazoan meiofaunal

- assemblages on the Porcupine Abyssal Plain, NE Atlantic. *Deep-Sea Res. II*, **57**, 1383-1395.
- Kleypas, J.A., Feely, R.A., Fabry, V.J., Langdon, C., Sabine, C.L. and Roggins, L.L. (2006) *Impacts of ocean acidification on coral reefs and other marine calcifiers: a guide for future research*. Report of workshop sponsored by NSF, NOAA and the US Geological Survey. http://www.ucar.edu/communications/Final_acidification.pdf
- Lampitt, R.S. (1985) Evidence for the seasonal deposition of detritus on the deep-sea floor and its subsequent resuspension. *Deep-Sea Res.*, **32A**, 885-897.
- Lampitt, R.S., de Cuevas, B., Hartman, S., Larkin, K. and Salter, I. (2010) Inter-annual variability in downward particle flux at the Porcupine Abyssal Plain Sustained Observatory. *Deep-Sea Res. II*, **57**, 1346-1361.
- Lunden, J.J., Georgian, S.E. and Cordes, E.E. (2013) Aragonite saturation states at cold-water coral reefs structured by *Lophelia pertusa* in the northern Gulf of Mexico. *Limnol. Oceanogr.*, **58**, 354-362.
- McGrath, T., Kivimäe, C., Tanhua, T., Cave, R.R. and McGovern, E. (2012) Inorganic carbon and pH levels in the Rockall Trough 1991-2010. *Deep-Sea Res. I*, **68**, 79-91.
- Narayanaswamy, B.E., Howell, K.L., Hughes, D.J., Davies, J.S. and Roberts, J.M. (2006) *Strategic Environmental Assessment Area 7 - Photographic Analysis*. Report to the Department of Trade and Industry/GEOTEK, 168 pp.
- Neat, F. and Burns, F. (2010) Stable abundance, but changing size structure in grenadier fishes (Macrouridae) over a decade (1998-2008) in which deepwater fisheries became regulated. *Deep-Sea Res. I*, **57**, 434-440.
- New, A.L. and Smythe-Wright, D. (2001) Aspects of the circulation in the Rockall Trough. *Continental Shelf Res.*, **21**, 777-810.
- Orr, J.C., Fabry, V.J., Aumont, O. *et al.* (2005) Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature*, **437**, 681-686.
- Reid, P.C., Edwards, M., Hunt, H.G. and Warner, A.J. (1998) Phytoplankton change in the North Atlantic. *Nature*, **391**, 546.
- Ruhl, H.A. (2007) Abundance and size distribution dynamics of abyssal epibenthic megafauna in the northeast Pacific. *Ecology*, **88**, 1250-1262.
- Ruhl, H.A. and Smith K.L. Jr. (2004) Shifts in deep-sea community structure linked to climate and food supply. *Science*, **305**, 513-515.
- Sabine, C.L., Feely, R.A., Gruber, N., Key, R.M., Lee, K., Bullister, J.L., Waningkhof, R., Wong, C.S., Wallace, D.W.R., Tilbrook, B. *et al.* (2004) The oceanic sink for anthropogenic CO₂. *Science*, **305**, 367-371.
- Schmittner, A. and Stocker, T.F. (1999) The stability of the thermohaline circulation in global warming experiments. *J. Clim.*, **12**, 1117-1133.
- Smith, C.R. and Demopoulos, A. (2003) *Ecology of the deep Pacific Ocean floor*. In: Tyler, P.A. (ed.) *Ecosystems of the World 28: Ecosystems of the Deep Ocean*. Elsevier, Amsterdam, pp. 181-220.
- Smith, C.R., De Leo, F.C., Bernardino, A.F., Sweetman, A.K. and Martinez Arbizu, P. (2008) Abyssal food limitation, ecosystem structure and climate change. *Trends Ecol. Evol.*, **23**, 518-528.
- Smith, K.L. Jr., Kaufmann, R.S., Baldwin, R.J. and Carlucci, A.F. (2001) Pelagic-benthic coupling in the abyssal eastern North Pacific: an 8-year time-series study of food supply and demand. *Limnol. Oceanogr.*, **46**, 543-556.
- Smith, K.L. Jr., Baldwin, R.J., Ruhl, H.A., Kahru, M., Mitchell, B.G. and Kaufmann, R.S. (2006) Climate effect on food supply to depths greater than 4000 metres in the northeast Pacific. *Limnol. Oceanogr.*, **51**, 166-176.
- Smith, T. and Hughes, J.A. (2008) *A review of indicators and identification of gaps: deep-sea habitats*. Report of work carried out on behalf of the Joint Nature Conservation Committee. National Oceanography Centre, Southampton, Consultancy Report No. 45, 72 pp.
- Soto, E.H., Paterson, G.L.J., Billett, D.S.M., Hawkins, L.E., Galéron, J. and Sibuet, M. (2010) Temporal variability in polychaete assemblages of the abyssal NE Atlantic Ocean. *Deep-Sea Res. II*, **57**, 1396-1405.
- Stewart, H., Davies, J., Long, D., Strömberg, H. and Hitchin, K. (2009) *JNCC Offshore Natura Survey Anton Dohrn Seamount and East Rockall Bank Areas of Search 2009/03*. JNCC Cruise Report Number CR/09/113.
- Thomas, E. and Gooday, A.J. (1996) Cenozoic deep-sea benthic foraminifers: tracers for changes in oceanic productivity? *Geology*, **24**, 355-358.
- Thresher, R.E., Tilbrook, B., Fallon, S., Wilson, N.C. and Adkins, J. (2011) Effects of chronic low carbonate saturation levels on the distribution, growth and skeletal chemistry of deep-sea corals and other seamount megabenthos. *Mar. Ecol. Prog. Ser.*, **442**, 87-99.
- Turley, C.M., Roberts, J.M. and Guinotte, J.M. (2007) Corals in deep water: will the unseen hand of ocean acidification destroy cold-water coral ecosystems? *Coral Reefs*, **26**, 445-448.
- Van den Hove, S. (2007) UNEP (2007) *Deep-Sea biodiversity and Ecosystems: a Scoping Report on their Socio-Economy, Management and Governance*. UNEP-WCMC Biodiversity Series, 28.
- Wigham, B.D., Hudson, I.R., Billett, D.S.M. and Wolff, G.A. (2003) Is long-term change in the abyssal Northeast Atlantic driven by qualitative changes in export flux? Evidence from selective feeding in deep-sea holothurians. *Prog. Oceanogr.*, **59**, 409-441.
- Wilson, J.B. (1979) 'Patch' development of the deep-water coral *Lophelia pertusa* (L.) on Rockall Bank. *J. Mar. Biol. Assoc. UK*, **59**, 165-177.
- Wyville Thomson, C. (1873) *The Depths of the Sea*. MacMillan and Co., London.