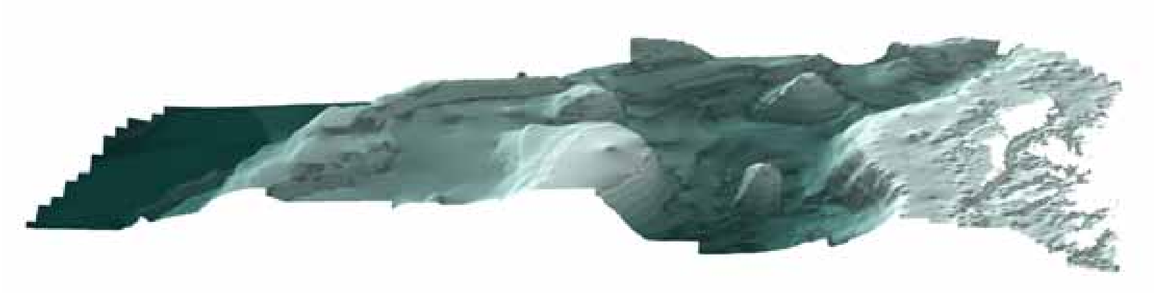
An Introduction to the Benthic Ecology of the Rockall - Hatton Area (SEA 7)



Executive Summary
2006

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and

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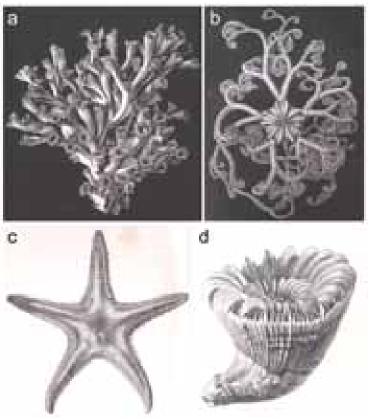
Summary

The Strategic Environmental Assessment area 7 (SEA 7) is based on the UK's exclusive fisheries zone and is bounded from SEA 4 to the north by the Wyville Thomson Ridge and from SEA 6 to the south between Kintyre, Scotland and Murlough Bay, Northern Ireland. SEA 7 extends westwards from the mainland UK at 5° W to 25° W, and lies between 55° N and 60° N. This area represents one of the largest extents of water within the UK's territorial seas and has been significant in the development of deep-sea biology since the late 19th century. The entire SEA 7 area is contained within the biogeographic region known as the Atlantic Deep-Sea Province, with most major oceanographic variables defined by the passage of North Atlantic Deep-Water. Several large bathymetric features characterise the area, the Rockall Trough, Hatton and Rockall Banks, the Wyville Thomson Ridge and three seamounts, Anton Dohrn, Rosemary Bank and the Hebrides Terrace are large geological features that contain a number of different benthic habitats and communities. Towards the northern boundary of SEA 7, recent surveys discovered a series of potentially unique geological and biological features which are now known as the Darwin Mounds.

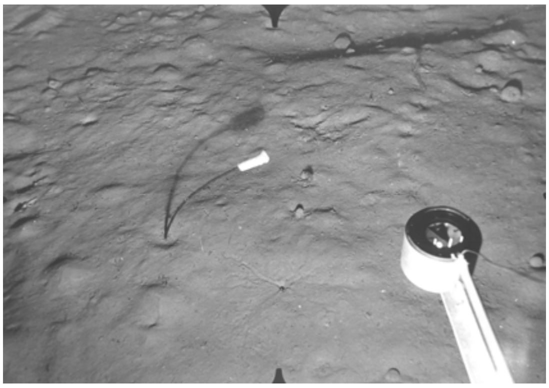
On the seafloor, the benthic biology in the SEA 7 area is well studied compared to other deep-sea regions. The first surveys of the area were conducted in the late 19th century, onboard the H.M.S. *Lightning* and H.M.S. *Porcupine* cruises revealing an array of previously un-described animal life. Modern researchers in the SEA 7 area and other deep-sea regions are still discovering un-described species. However, most current research is now being driven by the commercial exploitation of fisheries and hydrocarbons. Several large-scale reports have been generated within the SEA 7 area, including the Atlantic Frontier Environmental Network (AFEN) and the Oslo and Paris Convention (OSPAR) Quality Status Review. Smaller scale studies include environmental assessments for Enterprise Oil, the Brent Spar and Statoil. Academic work extends from projects including the Land Ocean Interaction Study - Shelf Edge Study (LOIS-SES, funded by the U.K. Natural Environmental Research Council), the Benthic Boundary Layer Experiment (BENBO, funded by the U.K. Natural Environmental Research Council), research conducted by the late Professor John Gage and colleagues at the Scottish Association for Marine Science (SAMS), as well as from various authors from the National Oceanography Centre, Southampton (NOCS) and staff of the former Institute of Oceanographic Sciences (IOS).



Engravings from of benthic fauna from Wyville Thomson's The Depths of the Sea (1874). (a) Lophelia prolifera, Pallas. (b) Asterophyton linckii, Müller and Troschel, (c) Archaster bifrons, Wyville Thomson. (d) Caryophyllia borealis, Fleming.

The benthic faunal composition is subdivided into different size spectra, classed as either megafauna, macrofauna or meiofauna based on taxonomic and sieve size definition. In the

SEA 7 area, the megafauna are dominated by species belonging to the phyla Echinodermata and Arthropoda, with other groups such as Porifera and Cnidaria comprising a lesser component. At depths between 1000 m and 1400 m megafauna communities are primarily composed of the hexactinellid sponge *Pheronema carpenteri*, overlapping with the ophiuroid *Ophiocten gracilis*. Within this depth range, populations of multinucleate xenophyophores are also particularly abundant. In deeper areas (2000 m), communities are comprised of octocorals such as *Acanella arbuscula* and other ophiuroids such as *Ophiomusium lymani*, abyssal megafauna (> 3500 m) are mostly composed of Holothurioidea, Actinaria and Pennatulacea. The macrofaunal community includes polychaetes, peracarid crustaceans, molluscs and other worm groups such as the Nemertea. On the Hebrides Slope in the SEA 7 area, much of the macrofaunal community is composed of polychaetes, crustaceans and molluscs, with polychaetes from the families Amphinomidae and Glyceridae consistently the most abundant at different depths.



Seabed photograph from the Hebrides Slope (DTI License Block 154/1) at 1295 m. In the foreground there is a stalked glass sponge, Hyalonema sp and also traces of Lebensspuren with small 'volcano' mounds and the radial marks around the burrow opening in the foreground caused by feeding and burrowing activity of relatively large animals.

The smaller meiofauna are dominated numerically by nematodes and harpacticoid copepods. In the SEA 7 area, nematodes often account for 80 - 95 % if the total meiofauna, with several numerically dominant genera including, *Sabatieria* spp. on the shelf and upper slopes and *Acantholaimus* spp. on the lower slopes with *Monhystera* spp. and *Daptonema* spp. dominant from the shelf to the lower slopes. Another important part of the meiofauna is the protozoan Foraminifera, an often overlooked part of the meiofauna which is numerically dominated by members of the suborder Allogromiina. In the SEA 7 area, the composition of benthic communities are strongly controlled by large-scale factors such as oceanic water masses, regional scale organic matter input and depth. These large scale variables are partly responsible for a community composition that is somewhat similar to other deep-sea regions in the North East Atlantic Ocean. On smaller scales, the major forcing factors are the level of hydrodynamic disturbance, the presence of habitat modifying species such as corals and sponges, local depth and topography, as well as localised organic matter input.

Commercial interest in the natural resources of the SEA 7 area is dominated by fisheries, hydrocarbon exploitation, waste disposal and the emerging possibilities of deep-sea mining and carbon dioxide storage. Even in well studied areas, many of the effects of such activities are unknown, especially in deep-sea regions. Immediate physical disturbance may cause destruction of habitats, whereas hydrocarbon exploitation and waste disposal may release contaminants over longer time-scales. The SEA 7 area is a continuing focus for deep-sea researchers, with research being undertaken for the DTI in 2005 in the SEA 7 area. Multi-disciplinary cruises are now becoming more common as scientists begin to recognise the importance of researching as many aspects of the deep-sea as possible.

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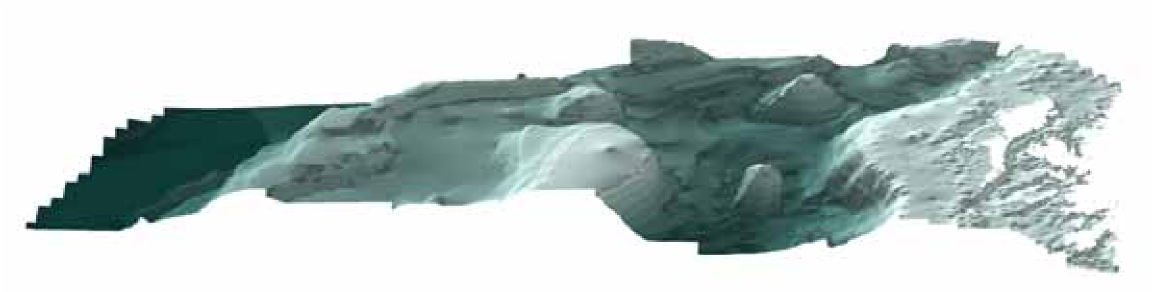

A Report for the DTI
March 2006

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1. Introduction

The boundary of the Strategic Environmental Assessment area 7 (SEA 7) is based on the UK's exclusive fisheries zone and represents one of the largest extents of water within the UK's territorial seas. It is separated from SEA 4 to the north by the Wyville Thomson Ridge whilst the boundary to the south extends from Kintyre, Scotland to Murlough Bay, Northern Ireland separating it from the SEA 6 area. SEA 7 extends westwards from the mainland UK at 5° W to 25° W, and lies between 55° N and 60° N (Figure 1).

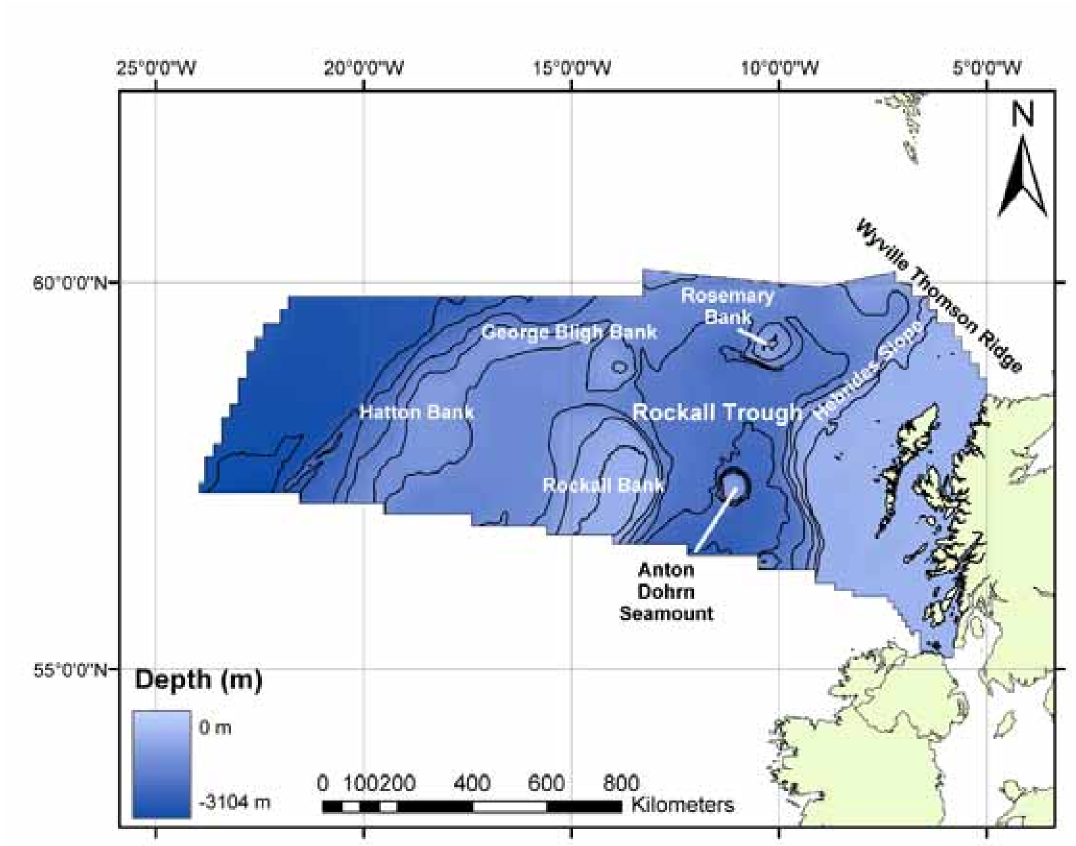

Figure 1: Map of the SEA 7 area, with major topographical features labelled (Mercator projection, contour lines represent 200 and 500 m intervals, bathymetry is from GEBCO 2001).

This area, especially the Hebrides slope and areas of the Rockall Trough have been significant in the development of deep-sea biology since the 19th century. In recent decades intensive sampling has been undertaken by researchers from UK institutions such as the Scottish Association for Marine Science (formerly the Scottish Marine Biological Association) and the National Oceanography Centre, Southampton (formerly Southampton Oceanography Centre and the Institute of Oceanographic Sciences).

The entire SEA 7 area is contained within the biogeographic region known as the Atlantic Deep-Sea Province, with the major oceanographic variables defined by the passage of North Atlantic Deep-Water. To the south, concentrated research efforts have taken place in areas such as the southern Rockall Trough, Porcupine Seabight and Porcupine Abyssal Plain. These encompass similar hydrographic and oceanic conditions to those of the SEA 7 area and form a basis for comparison.

A brief overview of the history of deep-sea research in the SEA 7 area is provided here, along with a summary of the physical environment. In this report, however, the main focus is the ecology of seafloor-dwelling organisms. To assist the reader, a section has been provided describing some of the techniques that are used in sampling deep-sea benthic communities. The ecology of benthic communities is described with respect to large-scale trends and is discussed in the context of how anthropogenic influences may affect the benthos. The final section discusses future planned research that may fill some of the gaps in our current knowledge.

2. Historical (19th century) and modern (1970s – 2000s) overview of information sources

It is over 150 years since Victorian scientists began to explore the deep sea systematically. Early scientists, such as the British naturalist Edward Forbes suggested that no life existed below 300 fathoms (550 m) (Forbes 1843). This was shortly disproved by the Norwegian naturalist Michael Sars who, along with his son, G.O. Sars, listed nearly 100 species of invertebrates living at depths greater than 600 m (Sars 1868). The first surveys into the deep seas of the North Atlantic were conducted by Charles Wyville Thomson aboard the vessels H.M.S. *Porcupine* and H.M.S. *Lightning*, which discovered animal life at depths of four kilometres and greater (Figure 2), almost all of which were new to science (Thomson 1874). These early cruises aboard the *Lightning* and *Porcupine* laid the basis for the largest survey of its time, a global circumnavigation aboard the H.M.S. *Challenger* (Thomson 1877) (Figure 2).

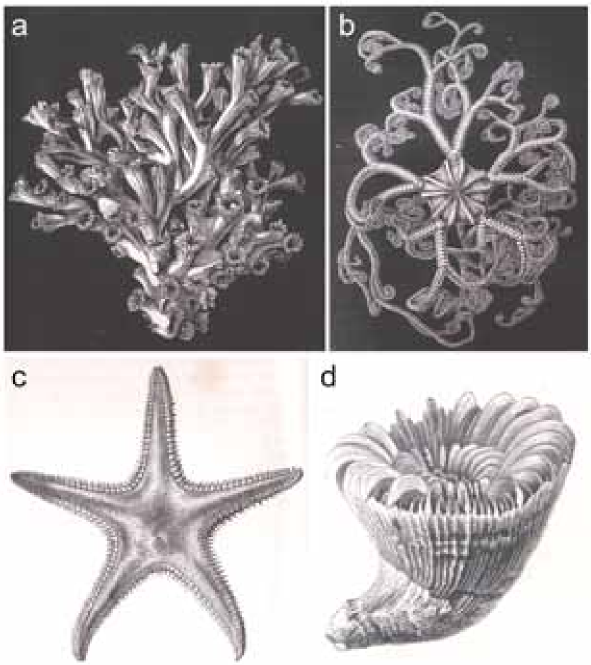

Figure 2: Engravings from of benthic fauna from Wyville Thomson's The Depths of the Sea (1874). (a) *Lophelia prolifera*, Pallas. (b) *Asterophyton linckii*, Müller and Troschel, (c) *Archaster bifrons*, Wyville Thomson. (d) *Caryophyllia borealis*, Fleming.

These pioneering surveys proved that the deeper waters off Britain and Ireland held a wide diversity of animal life. However, it was not until the middle of the 20th century that scientists discovered the true extent of the abundance and diversity of the small fauna inhabiting seafloor sediments. Russian biologists sampled the sediments of the Pacific and other oceans during the 1950s, using equipment adapted from coastal surveys and by following a programme of quantitative sampling, they established general rules about the geographical and bathymetric distribution of benthic biomass in the deep sea (Spärck 1951; Vinogradova 1959; Zenkivitch *et al.* 1971). The next major progression in deep-sea biology was during the 1960s and 1970s, when American deep-sea research began into the ecology of the many different life forms found on the seafloor. Using fine-meshed trawls, Sanders and Hessler discovered unexpectedly high species diversity in the previously undersampled small fauna of deep-sea sediments (Hessler & Sanders 1967; Sanders & Hessler 1969). Today, the emphasis in deep-sea research is on quantitative sampling, using newer technological developments such as the USNEL box corer (Hessler & Jumars 1974) (Figure 3a) and hydraulically damped corers such as the SMBA multiple corer (Barnett et al. 1984) and megacorer (Figure 3b). Use of these technologies became widespread in the latter half of the 20th century, allowing the generation and testing of hypotheses about the geographical distribution of benthic biomass and abundance throughout the deep sea (Gage & Tyler 1991; Rex *et al.* 1997).

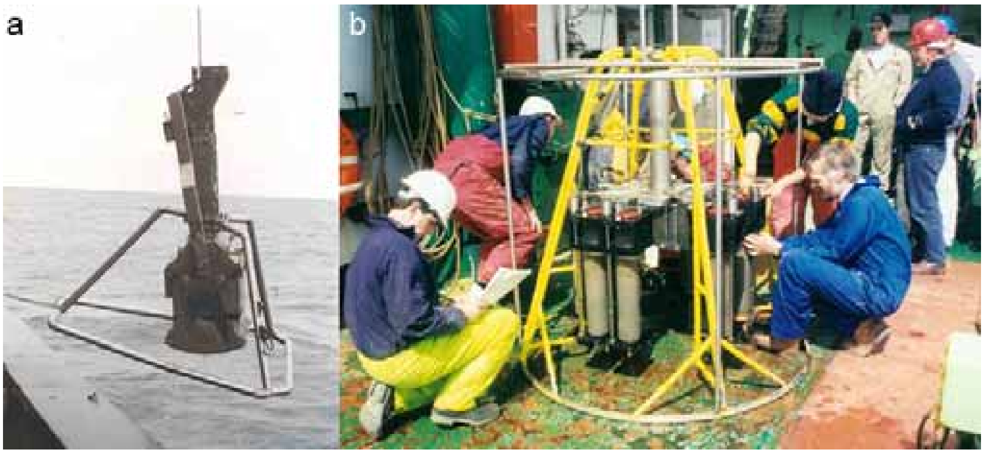

Figure 3: Modern deep-sea sampling equipment; (a) USNEL Box-corer, (b) Megacorer, (both images courtesy B.E. Narayanaswamy, 1998).

The setting for modern research into the SEA 7 area and the wider region which makes up the north-east Atlantic has been driven by the pressure of commercial exploitation of fisheries and hydrocarbons in ever deeper waters. Several major large-scale reports have been generated within the SEA 7 area, including the Atlantic Frontier Environmental Network (AFEN) (AFEN 2000; Bett 2001) and the Oslo and Paris Convention (OSPAR) Quality Status Review (OSPAR 2000). Localised environmental assessments have been conducted for the oil and gas industry, including Enterprise Oil (Jones et al. 1998), Statoil (Black 1998) and Brent Spar (Anon. 1994a, b). Academic work extends from projects including the Land Ocean Interaction Study - Shelf Edge Study (LOIS-SES, funded by the U.K. Natural Environmental Research Council), the Benthic Boundary Layer Experiment (BENBO, funded by the U.K. Natural Environmental Research Council), research from various authors from the National Oceanography Centre, Southampton (NOCS) and staff of the former Institute of Oceanographic Sciences (IOS) and over 25 years of research conducted by Professor John Gage and colleagues at the Scottish Association for Marine Science (SAMS) (See Figure 4 and Table 1 for details of the major research published within the SEA 7 area).

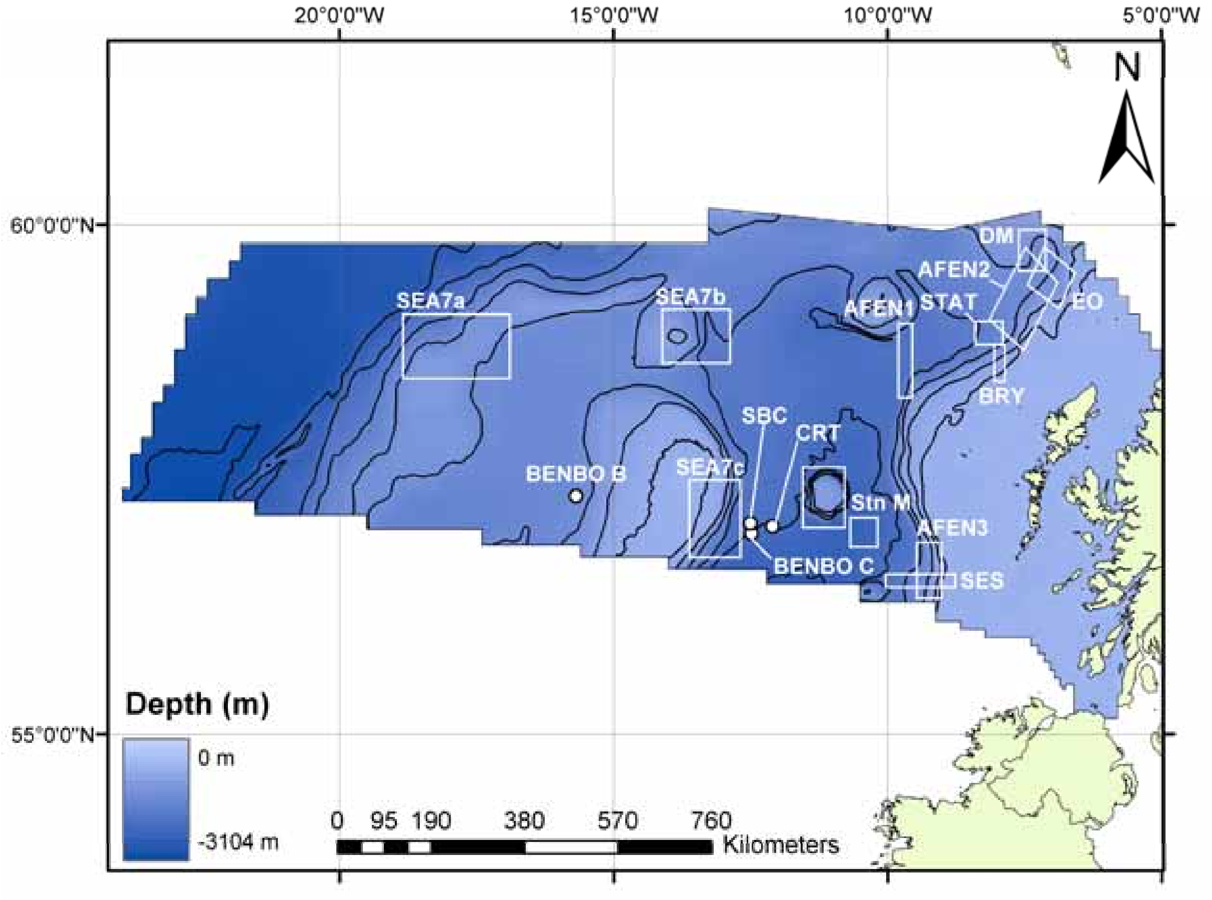

Figure 4: Map of sampling locations within the SEA 7 area, key is directly referenced to Table 1. (Mercator projection, contour lines represent 200 and 500 m intervals, bathymetry is from GEBCO 2001).

Table 1: Summary of readily available literature and data from research projects conducted in the SEA 7 area. (Key: ^{a} epibenthic sledge, ^{b} Agassiz trawl, ^{c} single warp trawl, ^{d} semi-balloon otter trawl, ^{e} USNEL box corer, ^{f} Barnett-Watson multiple corer, ^{g} mega corer, ^{h} rock dredge, ^{i} anchor box dredge, ^{j} day grab, ^{k} video assisted grab, ^{l} unspecified; Cameras, ^{m} epibenthic sledge camera, ^{n} bed hop camera, ^{o} sonar, ^{p} ROV stills or video. SBP; Seabed photography; Map Ref. is linked with Figure 4).

				Size class				
Location	Year	Depth (m)	Map Ref.	*Mega*	*Macro*	*Meio*	SBP	Reference
Hebrides shelf								
	1975-1995	401-2900	HST		e			(Gage et al. 2000)
	1998	570-1300	BRY		b, e, h			(Hughes 2001)
	1998	570-1311	EO	b, h	e, h		n	(Jones et al. 1998)
	1998	200-2000	AFEN 1, 2, 3		g, e, j	e, g, j	o	(AFEN 2000; Bett 2001)
	1998	1289-1496	STAT	b	g, f		n	(Black 1998)
	1995-1996	134-2071	SES				n	(LOIS-SES 1999)
Rockall Trough								
	1973-1980	1000-2900	Stn M	a				(Gage & Tyler 1982)
	1973-1985	1632-2300	Stn M	a, b c, d				(Gage & Tyler 1985)
	1978-1981	2170-2300	Stn M	b, c				(Pain et al. 1982)
	1973-1983	0-3000	Stn M	l				(Gage et al. 1985b)
	1973-1985	1000-2900	Stn M	a, b, e				(Gage & Billett 1986)
	1973-1982	630-2500	Stn M	a, b, e, i				(Gage et al. 1983)
	1973-1982	630-2500	Stn M	a, b e, i				(Gage et al. 1985a)
	1998	1920	BENBO C	a, m	e, g	e, g	m, n	(Hughes & Gage 2004)
	1998	1920	BENBO C		f	f		(Gooday & Hughes 2002)
	1998	1889-1987	SBC		e			(Gage et al. 2001)
	1976	2000	CRT	b				(Gage et al. 2004)
	2005	163-1771	SEA7c				n, o, p	(Narayanaswamy et al. 2006)
Hatton-Rockall Basin								
	1998	1100	BENBO B	a, m	e, g	e, g	m, n	(Hughes & Gage 2004)

	1998	1100	BENBO B	e				(Hughes et al. 2005)
	2005	425-1368	SEA7a, b				n, o, p	(Narayanaswamy et al. 2006)
Darwin Mounds								
	2000	904-960	DM			e, f		(Gooday et al. 2002)
	2000	947-958	DM			e		(Hughes & Gooday 2004)
	1998-2000	904-960	DM		e		o, p	(Masson et al. 2003)
	2000	900-999	DM		k			(Henry & Roberts 2004)
	2000	604-960	DM			f		(Van Gaever et al. 2004)

3. Overview of the Physical Environment

Bathymetry

The SEA 7 area is dominated by several large bathymetric features (nomenclature after Naylor et al. 1999) (Figures 5 and 6); the Rockall Trough being the most notable, including numerous banks such as the Hatton and Rockall Banks, the Wyville Thomson Ridge and three seamounts, Anton Dohrn, Rosemary Bank and Hebrides Terrace (Dietrich & Ulrich 1961; Howe *et al.* 2006). The easternmost point of the study area is bounded by the Hebrides Slope leading into the Rockall Trough. To the north-west, the Wyville Thomson Ridge separates the Faroe Bank Channel to the north from the Rockall Trough. The ridge rises to within 400 m of the surface at its crest, restricting the passage of cold Norwegian bottom water into the Rockall Trough (Hansen & Østerhus 2000).

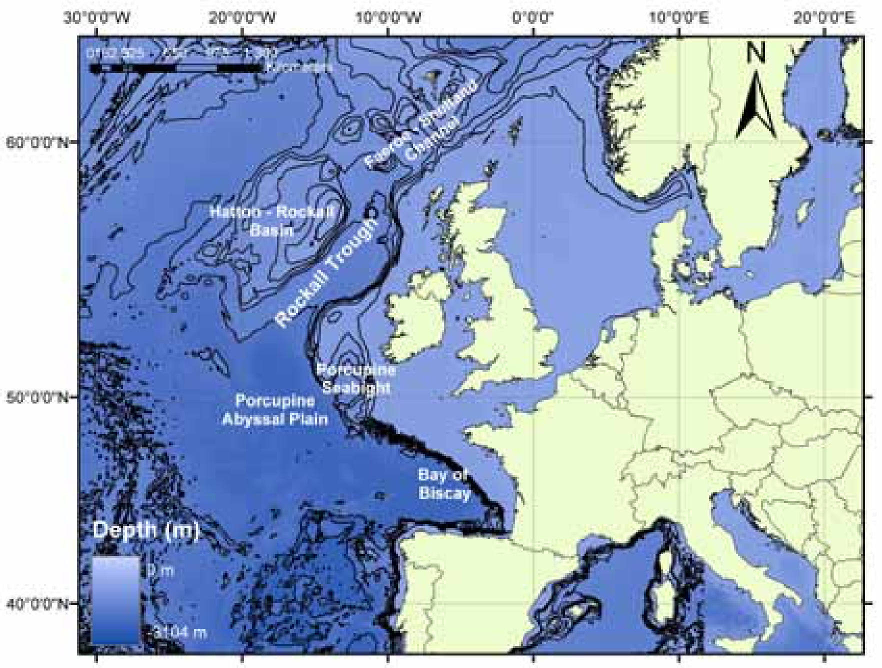

Figure 5: Map of the larger north-east Atlantic area, with major topographical features labelled (Mercator projection, contour lines represent 200 and 500 m intervals, bathymetry is from GEBCO 2001).

The Rockall Trough divides the Scottish and Irish continental slopes from the Rockall Plateau in the west; this steep sided, deep-water basin reaches depths of over 2000 m. To the west of the study area the Rockall Bank marks the beginning of the Rockall Plateau. In the centre of the plateau lies the Hatton-Rockall Basin, bounded by Rockall Bank to the east, Hatton Bank to the west and George Bligh Bank to the north-east and deepening from 900 m in the north-east to 1600 m at the southwest (Edwards 2002).

On a local scale, within these large banks and basins, the SEA 7 area contains numerous smaller bathymetric features resulting from past volcanic, glacial and sedimentary processes (Figure 6). Rosemary Bank is a volcanic seamount situated in the northern Rockall Trough, with steep flanks of up to 20 °. It is broadly domed in profile, encircled by a moat of between 150 and 200 m depth (Roberts et al. 1974) and has a maximum vertical relief of 2000 m (Howe et al. 2006). The Anton Dohrn seamount lies further south at a water depth of 2000 m in the Rockall Trough, with a flat summit near 550 m (C. Jacobs pers. comm.). Both seamounts have significant moat features at the base (Dietrich & Ulrich 1961; Jones *et al.* 1994; Howe *et al.* 2006), likely to have been formed by high current activity and bottom scour (Roberts et al. 1974), processes which are probably still active today (Armishaw et al. 1998). The Hebrides Terrace Seamount lies further south in the Rockall Trough and is the smallest of all the seamounts within the SEA 7 area with a summit rising 1000 m above the seafloor in approximately 2000 m of water. It is likely that the structure of this seamount is similar to the others, with exposed flanks and bedrock (Graham et al. 2001).

Recently, on an even smaller scale, a series of mound formations were discovered during the 1998 AFEN survey (Bett 2001; Masson *et al.* 2003). The Darwin Mounds are potentially unique geological and biological features and occur in a small area south of the Wyville Thomson Ridge. The mounds were discovered between 900 and 1060 m water depth and are typically up to 75 m in diameter and up to 5 m high (Masson et al. 2003). The centre of the mound appears to be blocky rubble, with the cold-water coral *Lophelia pertusa* usually present (Bett 2001; Masson *et al.* 2003). The origin of these mounds is currently unclear, but hypotheses range from localised current regime to fluid or gas escape, either at present or sometime in the past (Masson et al. 2003).

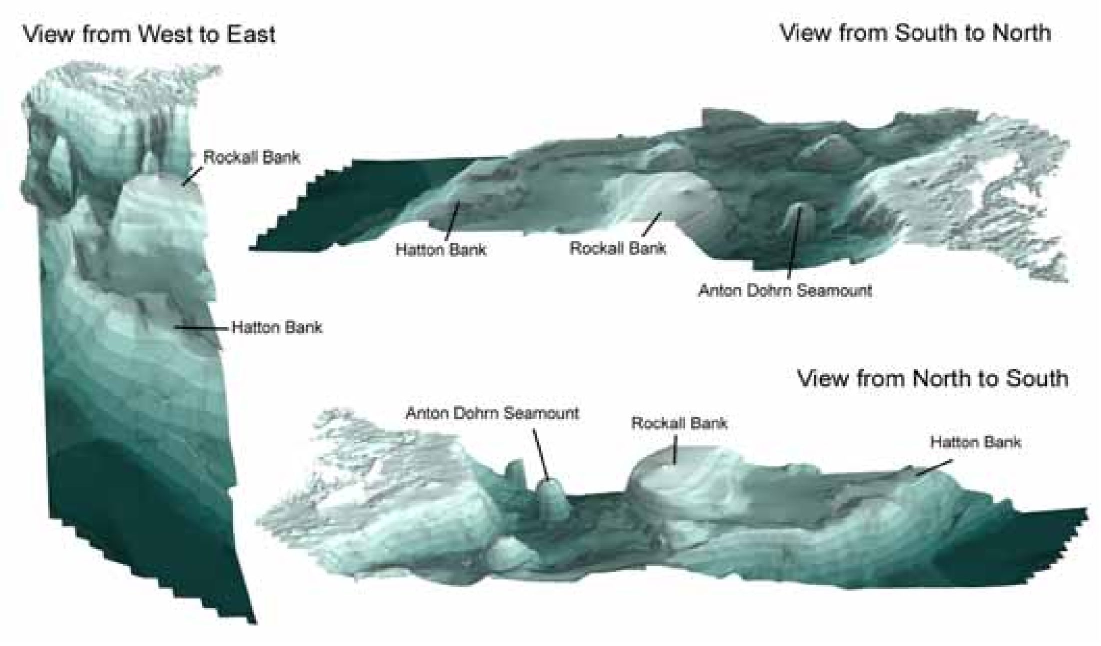

Figure 6: A series of three-dimensional bathymetric maps revealing sub-surface features within the SEA 7 area (WGS 84 projection, bathymetry from GEBCO 2001, white = land, pale = 200 m, dark = >3000 m).

Hydrography

The surface hydrography of the Rockall Trough is dominated by two main water masses; the uppermost extends from the surface to depths of 1200 - 1500 m and derives from North Atlantic Water; beneath this the lower water mass generally originates from the Labrador Sea and is centred on a salinity and oxygen maximum at about 1600 to 1900 m (Ellett et al. 1986) (Figure 7). The main upper water mass is the temperate North Atlantic Deep Water which, originates from the south and over lies two other deep-water masses, the upper Arctic Intermediate Water (AIW) and the lower Norwegian Sea Deep Water (NSDW) which enter the area from the north in limited amounts, restricted by the region’s complex topography. The circulation of these waters is reviewed in detail by

Ellett *et al*. (1986) and covered in numerous recent studies (e.g. see Turrell *et al.* 1999; Hansen & Østerhus 2000; Holliday *et al.* 2000). In general, the cold bottom waters move south from northerly latitudes, bringing cold dense water in to the Rockall Channel. The Wyville Thomson Ridge limits the volume of water entering the Rockall Trough to a small steady flow over the central depression and the north west of the ridge. In addition, there are often overflow events which can last for days at a time increasing the influx of cold, dense water (Arhan *et al.* 1994; Sherwin & Turrell 2005).

Localised hydrodynamic disturbances can occur on a much smaller scale than the large-scale oceanic currents which drive broad-scale temperature and salinity conditions (Holliday et al. 2000). The principal causes of disturbance to the seafloor are near-seabed currents, originating either from large-scale thermohaline sources such as the passage of dense water masses (Lonsdale & Hollister 1979; Ellett *et al.* 1986), which may become superimposed with currents originating from the semi-diurnal tidal cycle. These currents can cause local disturbance, as observed in the deep north-east Atlantic where tidal velocities have been recorded at 10 cm s^{-1} with rapid changes in direction and velocity (Heezen & Hollister 1971). Local topography often interacts with these principal forces, focusing currents and leading to the generation of amplified current flow or eddies (Walter et al. 2005). Internal waves generated as a result of the stratification of water bodies can break on sloping or irregular topography causing mixing between the stratified layers. This may be important for some sessile organisms (Rice *et al.* 1990; Frederiksen *et al.* 1992). Other less predictable disturbances may arise from surface storms and downslope cascades of cooled dense water over the shelf edge (Gage 1997).

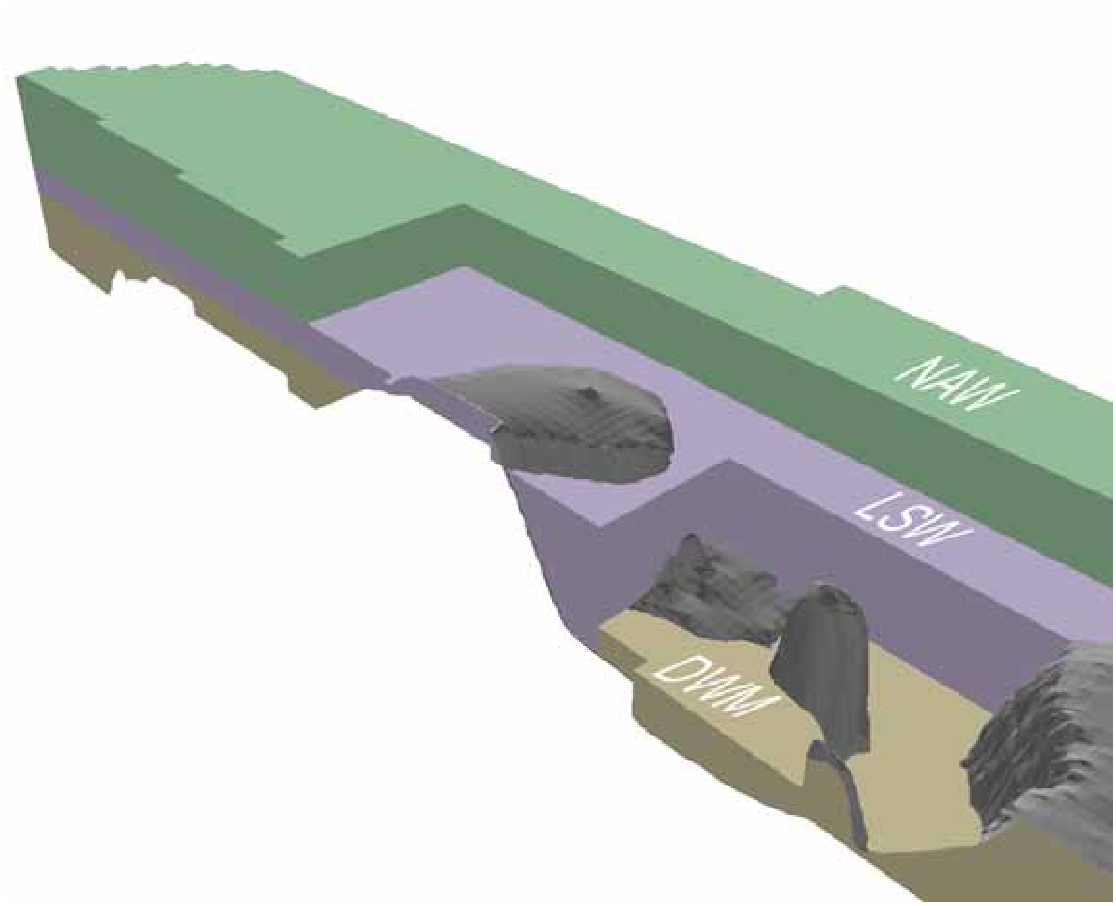

Figure 7: Simplistic representation of the hydrography of the SEA 7 area, extending from the Hebrides Shelf at the right to the Rockall Bank in the centre and the Hatton Bank to the left. Abbreviations used NAW, North Atlantic Water; LSW, Labrador Sea Water; DWM, Deep Water Masses (Drawn using data from Ellett *et al*. 1986).

Geology & Sedimentology

Seafloor topography within the SEA 7 area developed as a result of variable crustal thickness arising from Late Mesozoic to Early Cenozoic rifting and magmatism that occurred during the opening of the North Atlantic Ocean (Knott *et al.* 1993; Doré *et al.* 1999). During this time the British and Irish continental margins were stretched westwards, developing into deep-water banks, troughs and plateaux. To the north, the Wyville Thomson Lineament resulted in inversion folds forming the present-day Wyville

Thomson Ridge and Bill Bailey Bank (Tate et al. 1999). Subsequent plate reorganisation events during the Palaeogene and Neogene further contributed to the formation of the Rockall Trough area, with kilometre scale uplift (Rohrman & van der Beek 1996; Japsen & Chalmers 2000) and periods of rapid deepening (Cloetingh et al. 1990). The Anton Dohrn and Rosemary Bank seamounts are of volcanic origin, with some Maastrichtian deposits indicating the mounts were most likely formed during the Late Cretaceous period (Jones *et al.* 1974; Morton *et al.* 1995).

The modern Rockall Trough is a sediment-starved deep-water basin, principally containing sediments deposited during the late Quaternary at the end of the last glaciation (Stoker 1997). Since then, sediment input has been low, with present day sediment distribution determined by strong currents during the Holocene (Jones *et al.* 1970; Stoker *et al.* 1998). The thickest sediment deposits occur in the eastern Rockall Trough and Hebrides Slope, with the thinnest on the western margin and the Rockall Plateau (Stoker & Gillespie 1996). The sediments on the Hebrides Slope show a clear decrease in grain size with depth. The shelf and upper slope (140 – 300 m) have a coarse cover consisting of 25 % cobbles and boulders (2 – 20 cm, maximum 50 cm diameter) (Armishaw et al. 1998). Sands persist to depths of 700 m and from 700 to 1000 m the sediment composition changes from silty mud to mud, with rare gravel patches and even rarer cobbles and boulders (maximum 25 cm diameter) (Armishaw et al. 1998) (Figure 8). Towards the bottom of the slope, extending into the Rockall Trough, the sediments are mainly mud with some coarse sands and gravel (Armishaw et al. 1998). In contrast, the western flank of the Rockall Bank has been starved of sediment by erosive processes that have persisted since the Pliocene (Howe *et al.* 2001; Stoker *et al.* 2001). To the north-east flank of the Rockall Bank, bathymetric highs such as the George Bligh Bank and Wyville Thomson Ridge are locally exposed and overlain by a thin veneer of gravel lag and muddy-sandy contourite deposits (Howe et al. 2001).

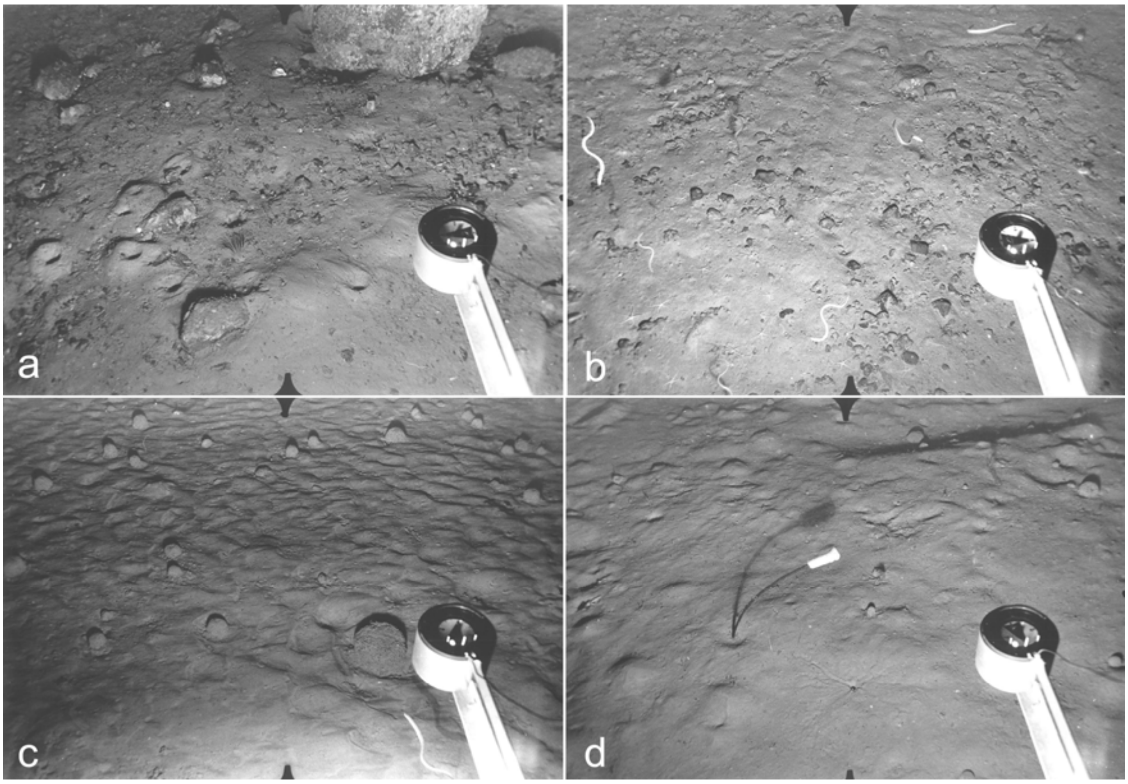

Figure 8: Photographs from the Hebrides Shelf Transect A, Enterprise Oil block 154/1 (Reproduced from Roberts et al. 2000). (a) At 721 m, the seabed is a mixture of sand and mud showing several burrow openings that were possibly produced by a crustacean. A ceranthid anthozoan is visible in the centre of the frame. To the top right, a boulder, which is probably a glacial dropstone, is half a metre in diameter. (b) At 885 m, small stones are still visible on the seabed and the ophiuroid *Ophiocten gracilis* can be clearly seen. There are nine cut-throat eels (*Synaphobranchus kaupi*) swimming close to the seabed. (c) Dense fields of xenophyophores (possibly *Syringammina fragilissima*) were found on the muddy sediments at 1108 m, achieving densities of up to 10 m^{-2}. (d) The muddy sediment at 1295 m shows signs of active bioturbation. There are several cone-like mounds and the characteristic spoke pattern associated with the feeding activity of an echiuran worm can be seen. The stalked organism is a glass sponge (*Hyalonema* sp.) photographed bending in the current (Roberts et al. 2000).

4. Sampling and describing the benthos

Sampling methods

The early voyages of Sars and Wyville Thomson used coarse mesh trawls and dredges secured on hemp ropes which were lowered and raised by hand (Sars 1868; Thomson 1874, 1877) (Figure 9). Even with these constraints the trawls were effective in collecting samples from depths of almost 5500 m (Thomson 1877). Since these pioneering days, trawls and dredges remain largely similar in structure but deployment mechanisms have improved and a finer mesh capable of retaining smaller organisms is also used (Gage & Tyler 1991). One of the main trawls still being used since it was developed in the last century is the Agassiz trawl, a double sided beam trawl adapted from gear used by coastal fishermen. The main net consists of a 20 mm mesh, with a finer mesh of 10 mm towards the cod-end, and is principally used for collecting benthic megafauna and benthopelagic fauna (Gage & Tyler 1991).

Trawls are limited in the fauna that can be sampled, collecting only epibenthic and benthopelagic megafauna. To address this limitation, the epibenthic sled (Hessler & Sanders 1967; Aldred *et al.* 1976; Rice *et al.* 1982), was originally designed to strip the surface sediment, but in practice the sleds became rapidly clogged with sediment, rendering samples useless. Minor modifications involving adjustable cutting blades which could be set to sample slightly above the seafloor enabled the sampling of the sediment-water interface. The sled also served as a protective body for the use of a finer mesh of 1 mm, allowing small fauna to be retained relatively undamaged (Gage 1975). The development of the epibenthic sled improved the quality and quantity of specimens, but the main limitation was the lack of quantitative data collected. Semi-quantitative samples could be collected using the Anchor Dredge, which was able to penetrate to known depths in the sediment and allowed the sampled area to be calculated from the volume of obtained sediment divided by the biting depth (Sanders et al. 1965). The dredge was successful but often under-sampled the small-bodied fauna capable of swimming and often became clogged, preventing further material from entering the dredge (Gage 1975).

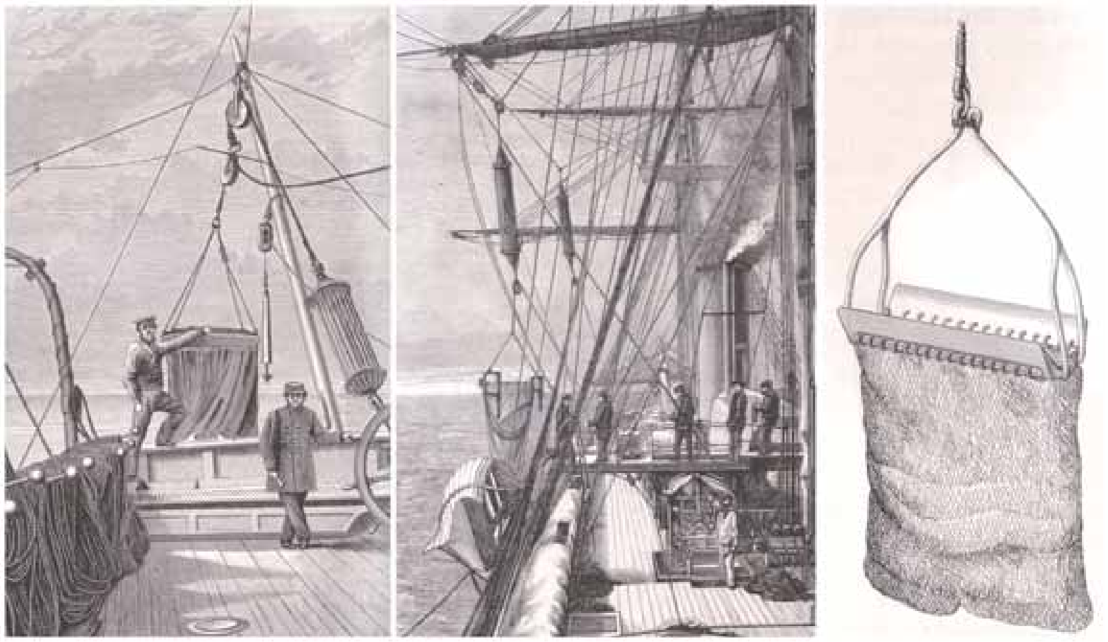

Figure 9: Illustrations from Wyville Thomson (a, c, 1874) (b, 1877), (a) The Stern of the H.M.S. Porcupine, showing the ‘accumulator’, the dredge and the mode of stowing the rope. (b) The dredging and sounding arrangements onboard the H.M.S. Challenger. (c) Ball’s Dredge, the frame is 18 inches long, with scrapers 7 inches apart, tapering to an opening of 3 inches.

Effective quantitative sampling began with the widespread use of corers. The most significant development was the United States Naval Electronic Laboratory (USNEL) box-corer developed by Hessler and Jumars (1974). The USNEL box-corer allows for quantitative sampling of smaller fauna over an area of 0.25 m² (50 x 50 cm) and is capable of penetrating to the full depth of the sampler (50 cm) (Figure 3a). A successful sample usually retains the undisturbed water immediately above the sampled sediment. These advantages have led to the USNEL corer becoming the standard quantitative sampler in deep-sea investigations world-wide (Gage & Tyler 1991). The SMBA multiple-corer was developed at the Scottish Marine Biological Association and is capable of collecting small diameter cores (56.5 mm) with an area of 25.1 cm², virtually free of bow-wave bias (Barnett et al. 1984). The USNEL corer was not without limitations; some bow-wave bias was evident and in some circumstances considerably under-sampled the fauna towards the edges of the collected sample (Jumars 1975a) and in comparison to multiple-corer (Barnett et al. 1984) and megacorer samples (Bett *et al.* 1994; Hughes & Gage 2004).

Grabs and corers provide highly detailed localised information, which is difficult to generalise to a larger scale. Remotely sensed information in the form of sonar or photography can address this issue by providing both local and regional scale information about the bathymetry, sedimentology and composition of the deep-sea area. Seabed photographs can be obtained from frame mounted cameras that are triggered by contact with the seafloor (e.g. Howe & Humphery 1995; Roberts *et al.* 2000), free-vehicle camera systems which can be deployed over long periods of time (Lampitt & Burnham 1983), lander-based time-lapse records (Lampitt 1983; Bett *et al.* 2001; Roberts *et al.* 2005b) or cameras mounted on submersibles and remotely operated vehicles (Rowe & Sibuet 1983; Rumohr 1995; Parry *et al.* 2003). Acoustic mapping technologies such as side-scan and multibeam sonar have been extensively used in seabed surveys over the last decade. In deep-water settings, these technologies can reveal seabed features (e.g. Masson & Jacobs 1998; Roberts *et al.* 2005a), produce accurate bathymetry (e.g. Howe et al. 2006) and characterise the sediment and geology of the area (Wynn & Stow 2002; Orpin & Kostylev 2006).

Faunal size class definitions

The fauna of the seafloor can be divided into several categories based on physical size. The term megafauna is generally used to describe organisms that are > 10,000 µm, which are visible in seabed photographs (Gage 2001). Smaller organisms are subdivided into three size classes based on retained fauna when sieving samples collected from the sediment. In shallow water, macrofauna are usually defined as organisms greater than 1000 µm or 500 µm, any smaller organisms are called meiofauna. In the deep-sea, size classes are shifted downwards, with macrofauna defined as organisms retained on a 300 or 250 µm mesh including polychaetes, crustaceans, molluscs and smaller echinoderms. The meiofauna are fauna between 250 – 62 µm, however these also include nematodes, harpacticoids copepods and Foraminifera that may be retained on a 250 µm sieve. Taxonomic definitions are becoming increasingly used, and define meiofauna as Nematoda, Harpacicoida, Ostracoda, Foraminifera and other minor groups irrespective of size (e.g. Hughes & Gage 2004).

5. Benthic Ecology

The organisms inhabiting the seafloor can be described as either the epifauna, which live on the surface of the sediment or the infauna, which live buried within it. Benthic species can be further defined by their life styles, such as mobile species or sessile species which remain attached to the same area of seabed for the majority of their life history (Gage & Tyler 1991). Subdivision into different size spectra is useful, and the community can be divided into the megafauna, macrofauna, meiofauna and microfauna based on taxonomic and sieve size definitions (see section 4 for definitions). In this section, the ecology of the main size class divisions is discussed, with the emphasis on variation over bathymetric gradients and in relation to local hydrodynamic conditions and substratum type.

Megafauna

Within the north-east Atlantic, the conspicuous megafauna are mainly mobile or sessile. The most common mobile megafauna belong to the phyla Echinodermata and Arthropoda with other groups such as Porifera and Cnidaria comprising a less abundant component of the sessile megafauna (Gage & Tyler 1991). The most abundant Echinodermata are generally the Ophiuroidea followed by Asteroidea, Echinoidea and Holothurioidea (Gage 1986). For Arthropoda, the most abundant class is the Decapoda (Hessler *et al.* 1978; Gage & Tyler 1991). The composition of benthic communities is often variable, controlled by large-scale factors such as oceanic water masses, regional scale organic matter input, and depth (Rex et al. 1997). On a more local scale, important factors are the level of hydrodynamic disturbance (Gage 1979, 1997), the presence of habitat-modifying species such as corals or sponges (Gage 1986; Mortensen *et al.* 1995), depth (Carney et al. 1983) and input of organic matter (Gooday 2002; Hughes & Gage 2004).

Broad-scale patterns

Describing the wide-scale distributions of species is often difficult, with many different factors interacting. Large-scale oceanic processes are often overlain with many smaller scale factors which can further affect local species presence, diversity and abundance

(Rex et al. 1997). The north-east Atlantic Ocean falls mainly within a biogeographic region described as the Atlantic Deep-Sea Province (ADSP), which has relatively homogenous oceanic conditions extending throughout the entire SEA 7 area. This homogeneity is reflected in the broad distributional patterns of some megafauna at specific depths. Throughout the north-east Atlantic, communities characterised by the hexactinellid sponge *Pheronema carpenteri*, are generally restricted to a depth band of *ca*. 1000 m to *ca*. 1400 m (Rice *et al.* 1990; Duineveld *et al.* 1997; Flach *et al.* 1998; Hughes & Gage 2004), often overlapping with high abundances of the ophiuroid *Ophiocten gracilis* (Gage *et al.* 1983; Lamont & Gage 1998). Within this depth range, populations of multinucleate xenophyophores are also particularly abundant in areas with high surface productivity and high particle flux (Tendal & Gooday 1981; Bett 1999; Roberts *et al.* 2000). Extending deeper, to depths of *ca*. 2000 m, communities become characterised by the high abundance of the octocoral *Acanella arbuscula* and ophiuroids (Duineveld et al. 1997), specified in one location as *Ophiomusium lymani* (Hughes & Gage 2004). At abyssal depths (> 3500 m), the most abundant megafauna in the north-east Atlantic belong to the Holothurioidea, Actinaria and Pennatulacea (Rutgers van der Loeff & Lavaleye 1986; Christiansen & Thiel 1992; Thurston *et al.* 1994; Billett *et al.* 2001).

The deep-sea megafaunal communities of the north-east Atlantic demonstrate strong linear decreases in abundance and biomass with increasing water depth (Lampitt *et al.* 1986; Duineveld *et al.* 1997; Hughes & Gage 2004). Data from stations between 500 m and 4000 m water depth in the Porcupine Seabight, show the two common groups, Echinodermata and Crustacea both demonstrate this relationship, with the latter exhibiting a stronger gradient for both abundance and biomass (Lampitt et al. 1986). In comparison to the linear trends observed with abundance and biomass, increases in depth often result in a curvilinear pattern in species diversity, with a maximum usually at mid-depth (Rex et al. 1997). In the north Atlantic, this diversity maximum occurs at different depths for each taxonomic grouping, usually between 1800 m and 2300 m (Sibuet 1977; Rex 1981; Howell *et al.* 2002).

Individual species also respond strongly to depth, (Gage 1986; Rex *et al.* 1997) and this is most obviously observed within the Echinodermata. Many common species of ophiuroid and asteroid have wide bathymetric tolerances (Gage 1986), e.g. the asteroid *Pseudarchaster parelli* extends from shallow seas to depths of over 2500 m. However, the adult stage of the ophiuroid species *Ophicoten gracilis* occupies only a narrow depth range but disperses widely, with juvenile and post-larval recruitment recorded to depths of over 3000 m with variable survival success (Gage 1986). Compared to these groups, other echinoderm classes such as the echinoids and holothurians demonstrate a stronger restriction within certain depth bands. The majority of common species are restricted to depths of 500 m to 900 m and many do not demonstrate the wide, potentially wasteful dispersal which is observed in many ophiuroids and asteroids, with the exception of a few species such as the echinoid *Echinus affinis* (Gage & Tyler 1985).

Local-scale patterns

On a more local scale, the Hebrides slope has been intensively sampled at depths between *ca*. 400 m and 2900 m (Gage 1986; Gage *et al.* 2000). Seabed photographs show a clear transition of sediment type with depth, with shallower stations dominated by coarser sediments and deeper stations having much finer sediments. Marked current ripples occur at 1100 m (Jones *et al.* 1998; Roberts *et al.* 2000), potentially indicating a stronger current regime and increased occurrence of hydrodynamic disturbance (Howe & Humphery 1995). On the Hebrides slope, stations situated at 885 m or less contained mainly *O. gracilis*, although at a lower density than comparable sites within the north-east Atlantic, such as the Porcupine Seabight (Duineveld et al. 1997). The dominant species present on the fine sediments of deeper stations of *ca*. 1300 m, were the octocoral *A. arbuscula*, pennatulids such as *Kophobelemnon stelliferum* and hexactinellid sponges such as *Hyalonema* sp. (Jones *et al.* 1998; Roberts *et al.* 2000). Although the majority of the community on the Hebrides slope followed the expected distributional patterns for the north-east Atlantic, some species were found at unusual depths, for example, *A. arbuscula* is usually found at depths greater than 1500 m (Duineveld *et al.* 1997; Hughes & Gage 2004), rather than 1300 m from here. These differences are most likely explained by the local hydrodynamic regime and species association with the sediment types found throughout the area (Jones et al. 1998).

The Rockall Trough and Northern Feni Ridge at 1920 m depth, contains a community dominated by the octocoral *A. arbuscula* and the ophiuroid *Ophiomusium lymani* which was almost always seen in close association with *A. arbuscula* (Hughes & Gage 2004). Sessile suspension feeders were the most abundant within this site, accounting for 77 % of the total megafaunal standing stock biomass (e.g. *Phelliactis robusta*, *A. arbuscula*, ceriantharians and *Brisinga endecanemos*). Further west, the same study sampled the Hatton-Rockall Basin at 1100 m. Within this shallower site, the hexactinellid sponges (*P. carpenteri*) and ceriantharian anemones (Cnidaria: species unspecified) were the most abundant, with mobile crustaceans such as *Munida tenuimana* relatively common amongst the sessile megafauna (Hughes & Gage 2004). The sessile suspension feeders accounted for 92 % of the total megafaunal biomass at this depth, characterised by high abundance of the sponge *P. carpenteri* which is similar to other communities dominated by *P. carpenteri* in the north-east Atlantic (Lampitt *et al.* 1986; Duineveld *et al.* 1997). Seabed photography also revealed subtle traces of biological activity on the fine sediment (typically called Lebensspuren) which are mainly formed by animals burrowing, feeding or moving, traces can also be seen from animals resting on the sediment (Gage & Tyler 1991). At 1100 m, 74 % of seabed photographs recorded traces of Lebensspuren among the sessile suspension feeding species, in the form of circular openings, burrows and polychaete tubes. In contrast, the station at 1920 m showed fewer traces (30 % of photographs) probably as a result of sediment smoothing by high current flow (Hughes & Gage 2004).

The megafaunal community in the SEA 7 area follows the same general trends in standing stock that occur throughout the north-east Atlantic in response to increasing depth (Lampitt *et al.* 1986; Duineveld *et al.* 1997). The BENBO study sites show an exponential decrease in standing stock biomass with depth, from 2.155 g C_{org} m^{-2} at 1100 m to 0.323 g C_{org} m^{-2} at 1920 m and 0.033 g C_{org} m^{-2} at 3580 m (Hughes & Gage 2004). Although, it is not as linear as the relationship with biomass, faunal abundance also decreases with depth, especially between 1100 m and 1920 m. Samples collected from 1100 m, have much higher densities of individuals and taxa (40230 ind. ha^{-1}, 15 taxa) than at deeper sites of 1920 m (5470 ind. ha^{-1}, 8 taxa) or 3580 m (7540 ind. ha^{-1}, 8 taxa) (Hughes & Gage 2004). These differences may be the result of increased along-slope current activity at the shallower depth, as the biomass of suspension feeders is sometimes closely associated with near-bed flow speed (Flach et al. 1998), or critical slopes where sediment can become resuspended by currents or internal waves (Rice *et al.* 1990; White 2003).

To summarise, the composition of the megafaunal communities of the SEA 7 area are representative of the regional north-east Atlantic Ocean, similar to those observed within the nearby Porcupine Seabight and Porcupine Abyssal Plain (Lampitt *et al.* 1986; Duineveld *et al.* 1997; Hughes & Gage 2004). There are some variations, with some species restricted to different depth ranges than would be expected, which are most likely caused by local-scale variability in disturbance. Within the SEA 7 area, the strongest factors which may affect local species composition are topographically influenced hydrodynamic processes that can alter currents, resuspend sediment and organic matter and also change sedimentary processes throughout the area. In general, studies that have undertaken quantified sampling of the megafauna for the SEA 7 area show strong similarities with depth trends observed throughout the north-east Atlantic of decreasing diversity, abundance and biomass.

Macrofauna

In the north-east Atlantic, macrofaunal communities are usually composed of polychaetes (bristle worms), small-bodied peracarid crustacean orders such as Cumacea, Tanaidacea, Amphipoda and Isopoda, molluscs such as Gastropoda, Bivalvia, and Scaphopoda and other worm groups such as the Nemertea, Sipuncula, Pogonophora, Priapulida, Echiura and Enteropneusta. Other fauna, which are not large enough to constitute the megafauna and are described as the macrofauna are species of Porifera, pycnogonids, brachiopods, epifaunal entoprocts, ophiuroids, porcellanasterid asteroids, apodous holothurians and small tunicates (Gage & Tyler 1991).

Broad-scale patterns

Throughout the world's oceans, samples of macrofauna are consistently dominated by a few abundant species, usually from the class Polychaeta (Gage 2004). In samples collected from the north-west Atlantic, the 10 most abundant species accounted for 42 % of the total number of individuals, with a spionid polychaete (*Aurospio dibranchiata*) being the most abundant, accounting for 7 - 9 % of all the individuals collected (Grassle & Maciolek 1992). The dominance of polychaetes is reflected from sites within the north-east Atlantic as well, with many studies reporting that polychaetes account for up to 70 % of all fauna collected, with communities often dominated by a few families such as Cirratulidae, Spionidae and Opheliidae (Flach & Heip 1996; Flach *et al.* 1998; Glover *et al.* 2001; Hughes & Gage 2004).

Peracarid crustaceans are the second most abundant fauna, which have a relatively low diversity in the north-east Atlantic compared to other oceans such as the Mediterranean Sea. Generally only one or two species such as *Munnopsurus atlanticus* and *Ilyarachna longicomis* account for *ca*. 50 % of the total abundance (Cartes et al. 2001). The third most abundant group are bivalves, which account for *ca*. 10 % of the macrofaunal abundance in the north-east Atlantic, and are dominated numerically by species such as *Yoldiella jeffreysi, Y. curta, Y. fibula* and *Malletia abyssorum* (Allen & Sanders 1996).

Other, less abundant macrofauna include the Bryozoa which are usually sessile, active suspension feeders. In the north-east Atlantic, some large forms such as *Kinetoskias cyathus* and *Levinsella magma* exist (Marshall 1979), but the majority are small, fragile and are rarely collected intact (Hughes 2001).

Local-scale patterns

Sampling of the continental shelf within the SEA 7 area supports the broad-scale picture of dominance seen by the polychaetes. The community on the Hebrides Slope is composed principally of polychaetes, crustaceans and molluscs (Jones et al. 1998). The polychaetes accounted for *ca*. 53 % of individual specimens and *ca*. 43 % of all species collected, with the Amphinomidae and Glyceridae the most abundant polychaete families sampled at each station. Crustaceans accounted for *ca*. 20 % of individuals and *ca*. 34 % of species, and the molluscs for *ca*. 10 % of individuals and *ca*. 12 % of species. Proportions varied somewhat at stations from different depths, but the same ratio was retained, with polychaetes always the most abundant followed by crustaceans and then molluscs (Jones *et al.* 1998; Gage *et al.* 2000). Total biomass decreased linearly with increasing depth, falling within the established pattern for the continental margin worldwide (Rowe 1983) and from the eastern Atlantic margin south of Ireland (Flach & Heip 1996). The abundance of the population did deviate somewhat from the expected depth related trend, with polychaete abundance increasing by *ca*. 50 % between 1100 and 1300 m, potentially as a result of local hydrodynamic conditions and disturbance (Jones et al. 1998).

These patterns were reflected at the BENBO study sites in the Rockall Trough and Hatton-Rockall Basin. At all sites, polychaetes were the most abundant group, accounting for 55 - 58 % of the total number of individuals and for 57 - 79 % of the biomass (Hughes & Gage 2004), a figure reflected elsewhere in the Rockall Trough (see Gage 1979). Dominant polychaete species at one locality were often absent or insignificant at another, with only members of the Ampharetidae family accounting for > 5 % of biomass at all three BENBO sites. In the Hatton Basin, small errant polychaetes (e.g. Hesionidae, Glyceridae, Amphinomidae, Nephtyidae) numerically dominated the fauna (69 % of total individuals), but some of the following families *e.g.* Capitellidae, Chaetopteridae, Lumbrineridae, Polynoidae, Ampharetidae contained much larger individuals that dominated the overall biomass. On the Feni Ridge, surface deposit and interface (species which can alternate between suspension and deposit feeding, Duaer et al. 1984) feeders (e.g. Ampharetidae, Onuphidae, Cirratulidae) dominated the fauna (77 % of total individuals). These distinct community differences within the Polychaeta are most likely as a result of local hydrodynamic regime and food supply to the benthos (Gage et al. 2000).

Macrofaunal diversity shows strong links with sediment particle size in the north-west Atlantic between depths of 250 m to *ca*. 3000 m (Etter & Grassle 1992). Variable sediment composition may provide available habitat for species which are attached or otherwise associated with large sediment particles to be included along with those normally found in finer sediments (Jones et al. 1998). On the Hebrides Slope, analysis of bryozoans indicated, that although, they do not comprise a significant proportion of abundance or biomass of the sediment dominated community (Jones *et al.* 1998; Gage *et al.* 2000), they may contribute to the overall diversity of the area and are important on hard substrata such as pebbles and cobbles (Hughes 2001). On the upper Hebrides Slope (569 - 855 m) the substratum is often rich in coarser sediment with finer granulation downslope, which may provide attachment substrate for sessile organisms (Roberts et al. 2000). The species found on the slope are in accord with the known distribution of bryozoans within the north-east Atlantic, including *Diplosolen obelia*, *Entalophoroecia deflexa* and *Onocousoecia dilatans* common in shallower samples between 569 and 665 m and *Disporella hispida*, *Escharella octodentata* and *Celleporina pygmaea* most common in deeper samples between 740 and 810 m, with *Tubicellepora boreale* the more common in the deepest sample at 1278 m (Hughes 2001).

In the north-east Atlantic, the Darwin Mounds are a potentially unique series of coral topped sediment mounds and contains a macrofaunal community that appears to be taxonomically distinct from the majority of other sites within the north-east Atlantic

(Henry & Roberts 2004). However, some consistencies have been recorded at other sites such as the Wyville Thomson Ridge and the Faeroes Plateau, with the most common groups encountered being polychaetes, bryozoans and brachiopods. The coarser sediments and pebbles found at the Darwin Mounds, Wyville Thomson Ridge and Faeroes Plateau form suitable habitat for species such as the bryozoan *Bicellarina alderi*, the tube building polychaete *Serpula vermicularis* and the brachiopod *Platidia anomiodies* which were always found encrusting on pebbles and small boulders (Henry & Roberts 2004). The increased habitat heterogeneity created by the calcareous skeleton of *Lophelia pertusa* further contributed to the diversity of the fauna collected. For example, several species such as *Porella laevis, Stegopoma plicatile* and *Eunice norvegica* occurred > 75 % of the time with *Lophelia* and were absent from neighbouring sites such as the Wyville Thomson Ridge and Faeroes Plateau (Henry & Roberts 2004).

The macrofauna of the north-east Atlantic show strong relationships with depth (Paterson *et al.* 1994; Paterson & Lambshead 1995; Flach *et al.* 2002), latitude (Rex et al. 1997), hydrodynamic disturbance (Levin et al. 2001) and organic matter input (Thurston *et al.* 1994; Hughes & Gage 2004). In comparing several sites throughout the Atlantic Ocean, Flach et al (2002) found that macrofaunal density in the north-east Atlantic decreased linearly with depth, following an established pattern that fits well with models from the north-west Atlantic (Jumars & Gallagher 1982). On the Hebrides Slope the diversity of polychaete communities demonstrates a parabolic distribution in response to depth, peaking at 1400 - 1500 m (Paterson & Lambshead 1995; Gage *et al.* 2000), indicating that strong physical processes, such as along-slope currents may affect the macrofauna at this depth (Gage et al. 2000). Standing stock patterns observed in the north-east Atlantic are most likely related to the carbon deposition flux (Flach et al. 2002), whereas community structure and vertical distribution may be more influenced by the current flow regime, food quality and the predictability of the food supply (Flach et al. 2002).

Meiofauna

The metazoan meiofaunal communities of the North Atlantic Ocean are dominated numerically by the Nematoda (roundworms) and the Harpacticoida (copepods). Other phyla that form a lesser proportion of the meiofauna include the Ostracoda (seed or mussel shrimp), and some rarer phyla such as Kinorhyncha (spiny crown worms), Tardigrada (water bears) and Loricifera (brush heads). After the nematodes and harpacticoid copepods, the third most abundant component of the metazoan meiofauna are juvenile individuals of the Polychaeta and Mollusca which form a temporary component of the meiofauna, before they grow large enough to be described as macrofauna (Pfannkuche 1985; Gage & Tyler 1991; Vincx *et al.* 1994).

Broad-scale patterns

The nematodes are the most numerically dominant metazoan meiofauna, often accounting for 80 - 95 % of the total meiofauna (Pfannkuche 1985; Vincx *et al.* 1994; Vanaverbeke *et al.* 1997). The next major component harpacticoids, usually accounts for 2 - 3 % of the meiofauna in the abyssal zone (Rutgers van der Loeff & Lavaleye 1986), but can range between 3 - 35 % of total individuals depending on depth and local site conditions (Hicks & Coull 1983; Vincx *et al.* 1994). The nematode communities of the north-east Atlantic are numerically dominated by several genera including, , *Sabatieria* spp. on the shelf and upper slopes and *Acantholaimus* spp. on the lower slopes. *Monhystera* spp. and *Daptonema* spp. are dominant from the shelf to the lower slopes (Dinet & Vivier 1979; Vanreusel *et al.* 1992; Soetaert & Heip 1995; Vanaverbeke *et al.* 1997). Some genera including *Microlaimus* spp., *Sabatieria* spp., *Molgolaimus* spp., *Richtersia* spp. and *Halalaimus* spp. ahave a wide distribution but are less abundant throughout the north-east Atlantic (Dinet & Vivier 1979; Vanreusel *et al.* 1992; Vanaverbeke *et al.* 1997; Van Gaever *et al.* 2004).

The protozoan meiofauna consist mainly of the Foraminifera, which are an often overlooked component of the meiofauna, with much research focusing on the metazoans (Thiel 1983; Tietjen 1992; Vincx *et al.* 1994). Foraminifera often account for up to 50 %

of all meiofauna retrieved in samples from the north-east Atlantic (Gooday 1986; Gooday & Lambshead 1989; Pfannkuche 1993). These Foraminifera communities are dominated numerically by members of the suborder Allogromiina, which can account for between *ca*. 5 - 15 % of all foraminiferans (Gooday 1986) and include species common to the north-east Atlantic, such as *Alabaminella weddellensis* and *Nonionella iridea* which are strongly associated with phytodetrital input and other species which are more ubiquitous including, *Angulogerina pauperata*, *Casidulina teretis*, *Gavelinopsis lobatulus*, *Reophax scorpiurus*, *Bulimina mexicana*, *Pseudononion* sp. and *Lagenammina* sp. (Gooday & Hughes 2002).

The majority of meiofauna are infaunal, living buried within the sediment (Gage & Tyler 1991). Some species rest on the surface and feed almost exclusively within the sediment-water interface and on deposited organic matter (Gooday & Lambshead 1989). The meiofauna in the north-east Atlantic are most abundant in the uppermost centimetre of sediment (0 - 1 cm), which contains, on average, 43 % of the total meiofauna extracted from a sediment depth of five centimetres (1 - 2 cm = 24 %; 2 - 3 cm = 16 %; 3 - 4 cm = 11 %; 4 - 5 cm = 6 %; Vincx et al. 1994). The distribution of groups within the sediment are relatively homogenous throughout the vertical profile, in the upper centimetre copepods and nauplii and Foraminifera being proportionally the most abundant, with 66 % and 59 % of their total abundance respectively, nematodes were less abundant with 41 % of their total abundance at this depth. As the depth of the vertical profile increased, the abundance of each group decreased with little deviation from the general meiofaunal pattern (Pfannkuche 1985; Vincx *et al.* 1994). These vertical patterns appear to be related to the distribution of organic matter, in the north-east Atlantic, the highest concentrations of organic matter is usually found in the top centimetre, decreasing as the sediment profile increases. However, there may be some variation in concentration within the vertical profile as a result of bioturbation and the action of macrofauna (Pfannkuche 1985).

Metazoan meiofauna in the north-east Atlantic show a general tendency towards decreasing abundance with increasing water depth (Thiel 1983; Tietjen 1992; Figs. 4 and

6 in Vincx *et al.* 1994; Vanaverbeke *et al.* 1997), with the lowest densities (maximum: 600 ind. 10 cm^{-2}) typically recorded at abyssal depths (Vincx et al. 1994) and the highest (maximum: 2000 ind. 10 cm^{-2}) in shallower waters of less than 1000 m (Vincx et al. 1994). This general pattern in response to depth is also recorded in the biomass of the metazoan meiofauna, which decreases with increasing depth (Soltwedel 2000). Shallow depths (700 m) have biomass values of *ca*. 400 - 500 mgC m^{-2} compared to *ca*. 200 mgC m^{-2} found at depths of 2500 m (Tietjen 1992). Along with changes in standing stock, the species composition can also vary with depth (Table 2). In comparing the major groups (nematodes, copepods and nauplii and juvenile polychaetes), the relative abundance of nematodes generally increases with depth and the proportion of other groups decrease (Table 2, Vincx et al. 1994). These depth trends are less consistent than for the larger size classes, as meiofauna tend to be highly variable on local spatial scales and show a strong response to phytodetrital input to the seafloor. The meiofauna, especially the Foraminifera respond rapidly to this input (Gooday 1988; Gooday & Turley 1990; Pfannkuche 1993), which may cause local abundance and biomass to deviate from regional trends, but has yet to be observed in many oceanic regions (Pfannkuche 1993; Gooday *et al.* 1996). Some comparisons may be drawn with regard to reduced meiofaunal biomass in the western Atlantic compared to the eastern Atlantic which may relate to higher surface productivity on the eastern margins (Soltwedel 2000).

Table 2: Relative abundance of the main meiofaunal groups at different depths in the north-east Atlantic (Vincx et al. 1994).

	% Abundance	
	<1000m	>5000 m
Nematodes	75.1	96.5
Copepods and nauplii	11.2	2.2
Polychaetes	3.2	0.2

Local-scale patterns

Although broad sampling has been undertaken within the north-east Atlantic, the meiofaunal communities of the SEA 7 area remain comparatively less well studied than elsewhere within the region. Samples from the BENBO sites followed the general trend of decreasing biomass and abundance with depth (Hughes & Gage 2004), however, expected abundance was lower than predicted by Soltwedel (2000) for the north-east Atlantic. This may be as a result of lower organic matter and bacterial production at the BENBO sites compared to the rest of the north-east Atlantic, but no significant relationships were found (Hughes & Gage 2004). Meiofaunal composition was numerically dominated by nematodes which comprised 89 - 94 % of the total meiofauna at all sites (Hughes & Gage 2004), within the expected values of 80 - 99 % for nematodes in the north-east Atlantic (Pfannkuche 1985; Vincx *et al.* 1994; Vanaverbeke *et al.* 1997). Meiofaunal samples collected at the BENBO sites fit the general vertical profile within the sediment at 1100 m and 1920 m during June - July. However, a distinct seasonal difference was found during April - May, when the uppermost centimetre contained less meiofauna than the deeper sediments (Hughes & Gage 2004). The site at 3580 m, showed less clear seasonal differences, with the vertical profile being similar between the different time periods. At this depth, 70 % of all meiofauna was found in the uppermost centimetre of sediment (Hughes & Gage 2004).

On the Darwin Mounds, nematodes and copepods (including nauplii) dominate the metazoan meiofaunal taxa with abundances accounting for 94.8 % and 3.7 % of the total collected fauna (Van Gaever et al. 2004), similar to the BENBO sites (Hughes & Gage 2004) and the north-east Atlantic (Vincx et al. 1994). Sampling of the mounds was undertaken over a narrow depth range from 904 - 960 m. Here, the meiofaunal diversity was high, with species from 15 different phyla collected, and a total of 155 different species of nematodes (Van Gaever et al. 2004). In total, a mean of 765 ± 99 individuals 10 cm^{-2}, were collected from the mounds, which are similar to other sites in the north-east Atlantic (Vincx et al. 1994), and more abundant than at similar depths such as from the 1100 m BENBO site (271 ind. 10 cm^{-2}, Hughes & Gage 2004).

The foraminiferan communities in the SEA 7 area have been less well-studied than those of the neighbouring Porcupine Seabight. Only a few surveys have collected high quality samples, using standardised methodologies that are comparable (Hughes & Gooday 2004). The Foraminifera collected from the Darwin Mounds are generally representative of the north-east Atlantic (Murray 1991; Hughes & Gooday 2004), especially the species *Nonionella iridea* and *Eponides pusillus* which are abundant at the Darwin Mounds, the BENBO site at 1950 m (Gooday & Hughes 2002; Hughes & Gooday 2004) and outside the SEA 7 area in the Porcupine Seabight (Gooday 1986). The abundance of Foraminifera collected ranged from 352 and 2238 ind. 10 cm^{-3} at the Darwin Mounds at 946 - 958 m depth, with the number of species ranging from 63 to 153 (Hughes & Gooday 2004). These values are comparable to other studies, such as the BENBO site at 1950 m with abundances between 830 and 2379 ind. 10 cm^{-3} and the Porcupine Seabight with abundances between 1246 and 2324 ind. 10 cm^{-3} at depths of 1320 - 1361 m (Gooday 1986; Gooday & Lambshead 1989).

In summary, the meiofaunal communities of the SEA 7 area are generally representative of the wider north-east Atlantic. Communities are dominated by very high proportions of nematodes, often accounting for 89 - 95 % of the metazoan meiofauna, with the remaining meiofauna usually comprising harpacticoid copepods and bivalves. The often overlooked protozoan meiofauna are mainly Foraminifera, and may sometimes constitute similar, if not greater abundances as the metazoans. The meiofaunal communities of the SEA 7 area also follow established trends in depth and vertical sediment profiles, but with local variation arising from phytodetritus input and local hydrodynamic regime, which may indicate a community variable in composition, diversity and abundance within the larger SEA 7 area.

Trends in benthic communities

Miniaturisation

Within the benthic community, the established convention of describing species in discrete size categories is purely artificial. Species belonging to the mega, macro and meiobenthos are not discrete singular groups and may interact in a variety of different ways. One of the major hypotheses presented to explain changes in the benthic communities of the deep-sea, is a trend for increasing miniaturisation with depth both in the overall community and also within individuals (Thiel 1975). In shallower seas, large bodied megafauna and macrofauna are thought to be sustainable by highly abundant food sources (Lampitt et al. 1986), whereas in deeper waters the food supply becomes a limiting factor with smaller bodied macrofauna and meiofauna increasing in abundance and biomass (Thiel 1975; Jensen 1988).

Table 3: The relative size structure of the biomass benthic communities for some benthic communities within the north-east Atlantic Ocean. Biomass is recorded as $gC_{org}\ m^{-2}$ for BENBO, OMEX and Bay of Biscay and by $gAFDW\ m^{-2}$ for BIOTRANS. (Data sources: BIOTRANS; Christiansen & Thiel 1992; Bay of Biscay; Mahaut *et al.* 1995; OMEX; Heip *et al.* 2001; BENBO; Hughes & Gage 2004).

Depth	% Megafauna	% Macrofauna	% Meiofauna	Source
1034	5.8	92.6	1.7	OMEX
1100	60.7	38	1.3	BENBO
1425	24.6	69.2	6.3	OMEX
1920	41.5	49.4	9.2	BENBO
2100	50.8	40	9.2	Bay of Biscay
2182	19.1	73	7.9	OMEX
3580	28	61.5	10.5	BENBO
3670	22.7	68.8	8.5	OMEX
4460	8.7	85.5	5.8	OMEX
4550	52	23.4	24.6	BIOTRANS

In the north-east Atlantic, there is some support for this generalisation (Pfannkuche 1985; Vanreusel 1995; Pfannkuche & Soltwedel 1998; Flach *et al.* 1999). However, many studies have not recorded data for multiple size classes within a single sampling effort. The BENBO study largely supports the trend towards smaller individuals, especially at the size class level, with the megafauna becoming a smaller component of the benthos at increasing depths (Table 3: BENBO, 1100, 1920 and 3580 m), and increasing proportions of the macrofauna and meiofauna in samples from deeper waters (Hughes & Gage 2004). However, in comparing studies from the north-east Atlantic which have conducted similar sampling methodologies at different depths, do not reveal any significant trends with megafauna or macrofauna, but there is an almost significant linear increase in the proportion of meiofauna with increasing water depth (model I regression; $r^2 = 0.356$, $p = 0.053$). The trend towards miniaturisation can reverse, e.g. some studies have identified gigantic individuals that occur at abyssal depths >3500 m (Birstein 1957; Wolff 1962), but these gigantic individuals are against a general trend for decreased body size in response to depth (Thiel 1975).

Hydrodynamics

At both a local and a regional scale, the hydrodynamic regime is a strong factor acting upon the benthic community, having both positive and negative effects (Gage 1997). Strong hydrodynamic disturbance may be a limiting factor for sediment dwelling macrofauna and small-bodied epifauna, which are particularly vulnerable to sediment erosion (Gage & Tyler 1991). The High Energy Benthic Boundary Experiment (HEBBLE) was conducted in the north-west Atlantic and intensively studied the effects of strong hydrodynamic regime on benthic communities. The HEBBLE site occurs at *ca.* 4800 m (an abyssal depth which would usually be relatively stable) and is characterised by the occurrence of benthic storms, which occur several times per year and persist for a few days to a few weeks (Gage & Tyler 1991; Gage 1997). Flow velocity during storms often exceeded 20 cm s^{-1} and occasionally was recorded exceeding 70 cm s^{-1}, the flow velocity during non-storm periods was less than 10 cm s^{-1} (Richardson *et al.* 1981; Weatherly & Kelley 1985). This level of disturbance scours the seabed of sediment and post-storm this material is deposited as a layer < 0.5 - 12.5 cm thick (Weatherly & Kelley 1985). As a result, the fauna of the HEBBLE site are significantly affected by these events. Epifaunal harpacticoid copepods (Thistle 1988), isopods (Thistle & Wilson 1987) and tanaids (Reidenauer & Thistle 1985) are all less abundant than in control sites, as are large epifauna, most likely a result of being swept away by the storm currents (Thistle & Wilson 1987). The dominant infaunal taxa at control sites, nematodes and harpacticoid copepods were less abundant, whereas species of polychaetes, bivalves, tanaids and isopods, which are characteristic of disturbed sites were more abundant (Thistle et al. 1991).

The SEA 7 area is much less prone to the intense periodic disturbance recorded at the HEBBLE site. However, the ecological effects of such disturbance may be observed even in lower flow environments. The complex and irregular topography of the banks and seamounts in the SEA 7 area can alter and amplify the hydrodynamic regime, creating areas with sediment scour and smoothed, current-lineated bed features (Lonsdale & Hollister 1979; Howe & Humphery 1995; Roberts *et al.* 2000). Disturbance from storm driven currents may also occur periodically, such as those recorded next to the Hebrides Terrance Seamount with several low frequency events when current speeds exceeded 50 - 60 cm s^{-1} (MacDougall & Edelsten 1987). The amount of sampling conducted in the SEA 7 area is much higher than in the HEBBLE site, and over a broader area, however, some generalisations about the effects of hydrodynamics can be inferred by comparing the two areas. The significant occurrence of strong periodic disturbance in the HEBBLE site creates an area which supports an abundant community of polychaetes, which are numerically dominated by a few species. In the SEA 7 area, relatively consistent levels of disturbance has a comparatively lesser abundant polychaete community that is more diverse and with much lower community dominance (Gage 1997). Consistent disturbance, in the form of moderate flow speeds appears to increase the diversity of the community, potentially by improving conditions for deposit feeders (MacDougall & Edelsten 1987; Gage 1997) and suspension feeders (Genin et al. 1986). Some sites within the SEA 7 area are often devoid of relatively fragile species such as xenophyophores and hexactinellid sponges potentially due to a strong hydrodynamic regime, instead the community may be characterised by infaunal species or larger epifauna such as brittle stars, which are usually indicative of disturbed areas (e.g. Jones et al. 1998).

Temporal trends

Temporal variation in deep-sea benthic communities can arise from both predictable and seemingly random disturbances or inputs (Gooday 2002). Broad-scale disturbances such as sediment slides and turbidity currents (Masson et al. 1996), the development of seeps and vents (Van Dover 2000), benthic storms (Thistle et al. 1991), periodic resuspension and downslope transport of shelf sediments that originate from fluvial sources (Gehlen et al. 1997), may not occur with any temporal regularity but may re-occur episodically in a similar geographic location. Other disturbances occur with regularity and may have consistent temporal effects on the benthic community, sources such as large food falls (Smith 1986; Smith *et al.* 1989) and faecal deposits from migrating pelagic animals (Graf 1989; Pfannkuche & Lochte 1993) occur over small spatial scales and may appear random but these often occur in areas along annual migration routes (Tyler 1988). Large-scale oceanic phenomena such as the El Niño (Arntz et al. 1991), variation in current energy (Tyler 1988; Arntz *et al.* 1991), diurnal tidal cycles (Lampitt *et al.* 1983; Lampitt & Paterson 1988), input of detritus from coastal sources (Tyler 1988, 1996) and phytodetrital input from near surface waters (Gooday 2002) are much more predictable and many species may respond to these cues (Tyler 1988; Gooday 2002).

The shortest temporal trigger is diurnal tidal variation. Evidence for ecological responses to this trigger in the deep sea is sparse, but physical manifestations often occur as flood currents (Tyler 1988) and reversals in flow direction (Lonsdale & Hollister 1979). Benthic organisms may use tidal variations to assist in locomotion (Gould & McKee 1973; Lonsdale & Hollister 1979), general flow supplying food and resuspending organic matter (Duineveld et al. 2004) or as a cue for synchronised spawning (Lampitt & Burnham 1983). In the north-east Atlantic, cycles in oceanic currents may also occur on seasonal time-scales (Duineveld et al. 2004). Cues from increased eddy kinetic energy during these seasonal variations may influence spawning in some organisms, such as the

Echinodermata (Guennegan & Rannou 1979; Dickson *et al.* 1982). The most significant source of seasonal variation that affects the benthic community may be from the input of phytodetrital matter from surface productivity (see reviews by Tyler *et al.* 1982; Beaulieu 2002; Gooday 2002). Until relatively recently, the deep-sea environment was considered to be buffered from seasonality by the overlying water column (Gooday 2002), however, research programmes in the late 1970s and early 1980s have shown strong seasonal input of organic matter to the seafloor (reviewed in Tyler 1988), with modern studies in the late 1990s and early 2000s recording the effect of organic input on the benthic organisms on the seafloor (reviewed in Gooday 2002).

In the north-east Atlantic the majority of phytodetrital deposits usually reach the seafloor during the spring and early summer and disappears during the course of the summer (Tyler 1988), delivering an estimated 2 - 4 % of spring-bloom surface production to the seafloor (Gooday 2002). This phytodetritus usually consists of fresh phytoplankton and a high proportion of diatoms from the spring bloom as well as other biogenic particles (Lampitt 1985; Turley *et al.* 1995), other detrital deposits that fall during the course of the summer are predominantly gelatinous and includes coccospheres and coccolithophores (Billett et al. 1983). These deposits of phytodetritus are important sources of labile organic matter, but the quantity of matter can vary widely as a result of biologically-mediated transformation during the descent to the seafloor (De Wilde *et al.* 1998; Bett *et al.* 2001; Gooday 2002).

Community responses to a pulse of phytodetrital input have been observed in the different size classes with limited success. The most obvious response is an increase in biomass and activity in protozoans and bacteria within days of the arrival of organic matter (Graf 1989; Soltwedel 1997). This is demonstrated by the response of Foraminifera at the BIOTRANS site (north-east Atlantic), where the abundance increased from 40 % in March and May to 60 % after the deposition of phytodetritus in July (Pfannkuche 1992, 1993). The responses of the metazoan meiofauna are often less clear and harder to detect (Soltwedel 2000), for example, after a phytodetritus input at the BENGAL site (4842 - 4844 m) in the Porcupine Abyssal Plain, juvenile opheliid polychaetes increased in abundance but the overall community abundance did not change (Galeron et al. 2001). Within the north-east Atlantic one of the most dramatic temporal changes was observed at the BENGAL site. Using time-lapse photography from 1991 - 1994 and 1997 - 2000, Bett et al. (2001) recorded significant changes in megafaunal composition. From 1991-1994 the abundance of epibenthic megafauna such as ophiuroids, principally *Ophicoten hastatum* and the holothurian species *Amperima rosea* were low. The total megafaunal density of *ca*. 71.6 ha^{-1} was dominated by larger bodied holothurians. In contrast, photographs from 1997 - 2000 recorded a decrease in the abundance of phytodetritus and increases in the total megafauna (Figure 10). In particular, the abundance of ophiuroids increased 10-fold and *A. rosea* by 1500-fold. This has become widely known as the "*Amperima event*".

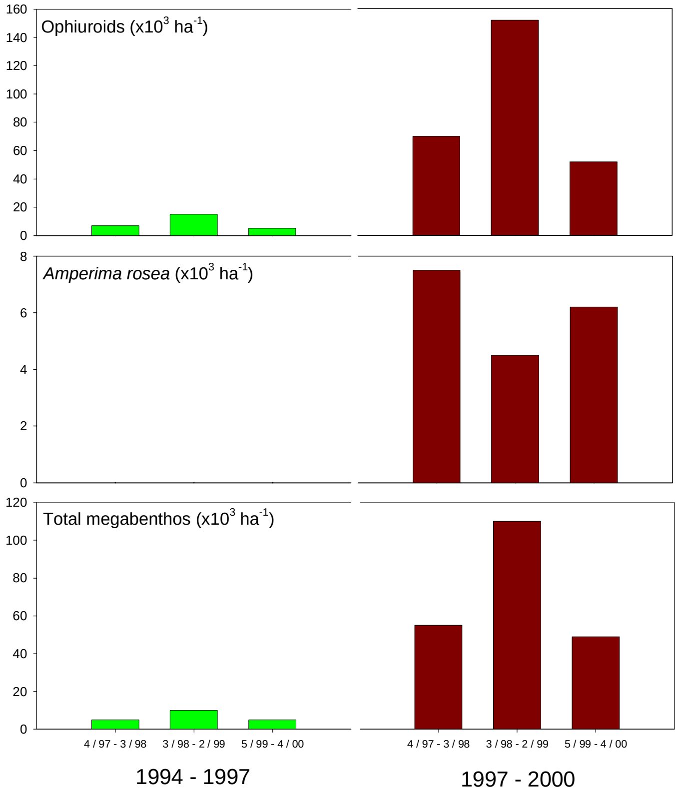

Figure 10: Temporal variations in megabenthos abundance, activity and the occurrence of phytodetritus at the BENGAL site, (re-drawn from: Bett et al. 2001).

Within the SEA 7 area, the BENBO sites were sampled in May 1998 and July 1998, before and after the main seasonal phytodetrital input (Hughes & Gage 2004). The sites at 1100 m and 3580 m did not show a significant response in community composition or standing stock between the two months, however, the site at 1920 m had the largest phytodetrital input of all depths (Black 2001) which resulted in a 2.7-fold increase in metazoan meiofaunal abundance (Hughes & Gage 2004).

Seasonality may not always be most obvious in the abundance, biomass or composition of communities. Reproductive activity and spawning of many deep-sea organisms often occurs continually throughout the year (Tyler 1986). However, some species do exhibit pronounced seasonality in reproduction (Tyler 1988). In the Rockall Trough, a significantly higher proportion of some female isopod species brood during the winter (25 %) compared with the summer (7 %) and the timing of vitellogenesis appears to coincide with the deposition of phytodetritus during the summer (Harrison 1988). Several bivalve species also exhibit a cycle of ovarian growth, with the species *Ledella pustulosa* and *Yoldiella jeffreysi* having small oocytes in late January and February, which reach a maximum size in December to early January (Lightfoot et al. 1979). However, data on the reproduction of thirteen species from the Pacific Ocean show the vast majority of species reproduce continually throughout the year, with only two species exhibiting any seasonality, the brachiopod *Frieleia halli*, which spawns between January and April, and the scaphapod *Cadulus californicus* which spawns between July and October (Rokop 1974). This pattern is likely to be reflected in the reproductive activity of the majority of organisms in the SEA 7 area.

The Echinodermata have received the most attention in deep-sea reproductive studies (Tyler 1988). In the north-west Atlantic seasonal reproduction has been observed in *Ophiura ljungmani* and *Ophiomusium lymani* (Schoener 1968). The reproductive biology of *O. lymani* is not seasonal (Rokop 1974), but the age structure of *O. lymani* populations in the north Atlantic suggests there are seasonal variations in recruitment (Schoener 1968; Gage 1982). The reproductive biology of *O. ljungmani* has been well studied within the north-east Atlantic, showing a distinct seasonal reproductive cycle with oogenesis occurring in March and April (active vitellogenesis during summer) with spawning in January to April (Tyler & Gage 1979; Tyler & Gage 1980; Tyler *et al.* 1982; Tyler 1986). The dispersal of some echinoderm larvae also exhibits seasonality. For example, the larvae of the ophiuroid *Ophiocten gracilis* are regularly found in plankton samples during the spring in the north Atlantic (Geiger 1963), with recruitment occurring during late spring and summer (Gage & Tyler 1981). The asteroid *Plutonaster bifrons* shows a similar pattern; gametogenesis is initiated in the spring, maximum vitellogenesis occurs in summer and autumn, with spawning occurring between March and June (Tyler & Pain 1982). The urchin *Echinus affinis* in the north-east Atlantic shows seasonality in its life cycle. Gametogenesis is initiated in November, followed by oocyte proliferation in spring, vitellogenesis in summer, and spawning between January and March. Two generations of oocytes can therefore occur within the ovary (Tyler & Gage 1984; Tyler 1986). A similar cycle can also occur in *E. alexandri* and *E. acutus* var. *norvegicus* (Tyler & Gage 1984).

Habitat modifying species

The complexity of habitat is directly related to species richness and comparisons may be drawn between the canopies of tropical rainforests, the structural complexity of tropical coral reefs and deep-sea communities (Grassle & Maciolek 1992; Gage 1996). In the deep sea, certain species can modify the complexity of the habitat by forming biogenic structures such as reefs, tests or their own body form or if mobile, by manipulating the sediment to form burrows, tracks and feeding depressions (Grassle *et al.* 1975; Jumars & Eckman 1983). These structures may persist for long periods in low energy abyssal environments (Jumars 1975b; Jumars & Eckman 1983) and may serve as valuable microhabitat and macrohabitat, which may serve a range of different functions, such as refuges from predators, mating and nursery grounds and may offer enhanced feeding prospects (Grassle 1989; Levin 1991; Beaulieu 2001).

Sediment heterogeneity

In the abyssal deep sea, traces of life left behind by benthic organisms in the form of feeding tracks, burrows and faecal pellets are obvious in seabed photographs and are known as Lebensspuren (Gage & Tyler 1991) (Figure 11). These features may be important in increasing the complexity of the deep-sea floor, providing refuge, feeding and social grounds. In areas of strong current regime, these traces are often diminished or absent (Lonsdale & Hollister 1979; Tucholke *et al.* 1985), but they are often present in less energetic areas (Swift et al. 1985). Investigations in both shallow and deep-sea areas, as well as laboratory studies have shown infaunal communities to be significantly affected by both inhabited and uninhabited burrows formed by macro and megafauna, both positively by promoting microbial growth and enhancing biological activity (Aller & Yingst 1978; Aller & Aller 1986) and negatively by reducing the suitability of the burrow for other organisms (Dobbs & Guckert 1988). The presence of tubes and tests can also influence microbial activity (Eckman 1984), as well as promoting faunal abundance and species richness (Woodin 1978; Gallagher *et al.* 1983; Hughes & Gooday 2004). Faecal mounds left by megafaunal deposit feeders are rapidly colonised by macrofauna (Smith et al. 1986) and agglutinating Foraminifera (Levin et al. 1991). On a smaller scale, the deep seafloor is not featureless. Bioturbation often increases the complexity of the habitat further promoting increased species richness and abundance.

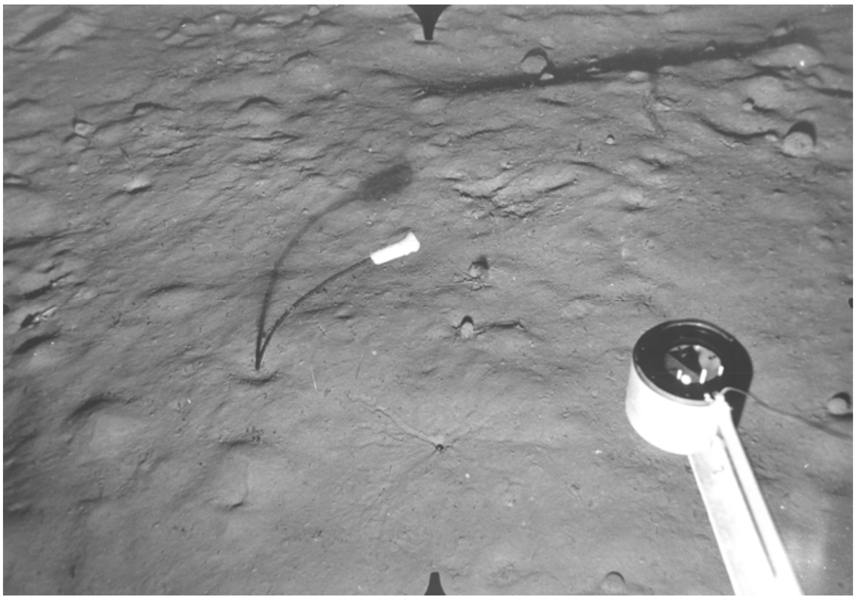

Figure 11: Seabed photograph from the Hebrides Slope (Enterprise Oil block 154/1) at 1295 m. In the foreground there is a stalked glass sponge, *Hyalonema* sp and also traces of Lebensspuren with small ‘volcano’ mounds and the radial marks around the burrow opening in the foreground caused by feeding and burrowing activity of relatively large animals (Gage 2001).

Xenophyophores

Xenophyophores are large protozoans, most accurately described as giant, multinucleated, agglutinated rhizopods which are found exclusively in the deep sea (Gooday & Tendal 2000; Hughes & Gooday 2004) (Figure 12). They agglutinate sediments to form elaborate tests which are often large (> 25 cm), either on or within sediments or on rock surfaces (Tendal 1972). Xenophyophores are found in all the known oceans, with the exception so far of the Arctic, and are best known from bathyal, abyssal and hadal depths near continental or island margins and in tropical waters (Tendal 1972; Levin & Gooday 1992). In the north-east Atlantic, xenophyophores can be a major component of the benthic community, with some species such as *Reticulammina* sp.

attaining densities of several thousand per 100 m^2 (Tendal & Gooday 1981) and *Syringammina fragilissima* attaining densities of 7 - 10 m^{-2} (Roberts *et al.* 2000; Bett 2001).

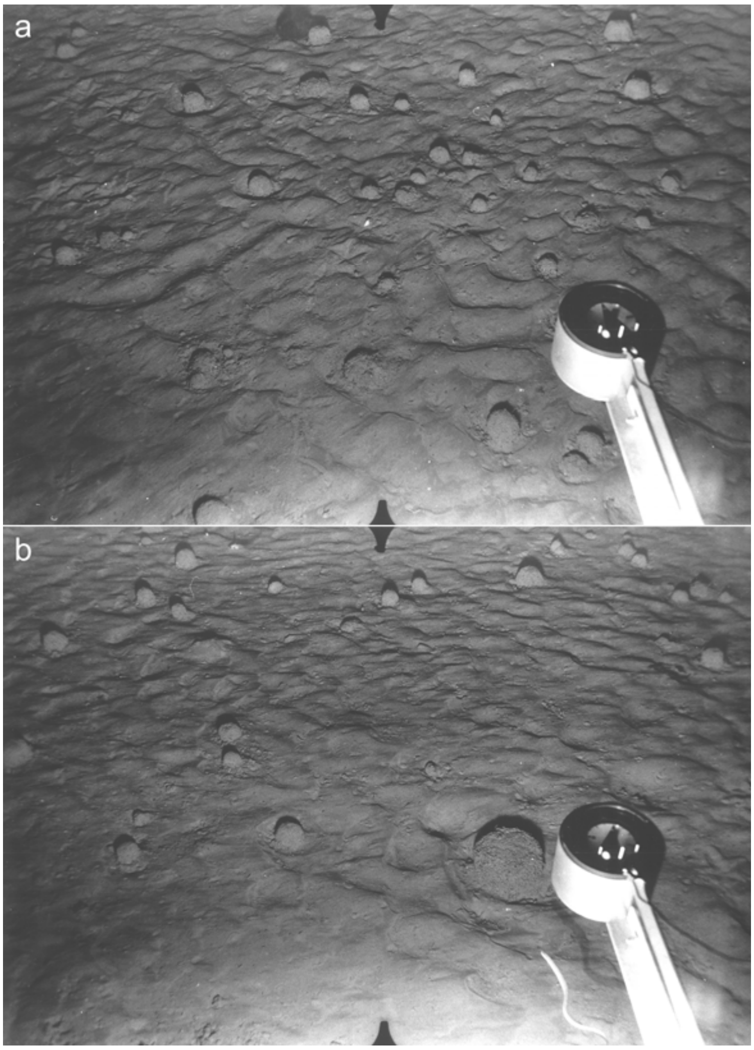

Figure 12: Fields of the xenophyophore *Syringammina fragilissima* photographed at depths of (a) 1108m (b) 900 m on the Hebrides Slope (Enterprise Oil block 154/1), with some current induced bed-forms (Jones *et al.* 1998; Gage 2001).

The presence of xenophyophores appears to significantly increase the abundance of metazoan macrofauna in the immediate area (Levin *et al.* 1986; Levin & Thomas 1988), as well as providing potential habitats for metazoan meiofauna (Gooday 1984) and

Foraminifera (Gooday 1991; Shires *et al.* 1994; Hughes & Gooday 2004). Gooday and Hughes (2004) found links between Foraminifera assemblages and the large xenophyophore *S. fragilissima*. They suggest this species may perform many different roles, such as providing hard substrate for epifaunal species, elevating suspension feeders above the seafloor and increasing food available to deposit feeders resulting from the deposition of fine particles. The tests of xenophyophores may also passively trap larvae, leading to concentrated prey populations which may benefit predators, as well as forming a habitat for mating, reproduction and nursery functions. In a regional context, xenophyophores form an important component of the deep-sea community, forming numerically dominant aggregations in some locations, which can increase habitat heterogeneity promoting increased species abundance and richness (Hughes & Gooday 2004).

Sponge beds

Sponge beds may have many of the same effects on the benthic community as xenophyophores. The north-east Atlantic deep sea contains abundant aggregations of the hexactinellid sponge *Pheronema carpenteri* at depths of *ca*. 1000 m to 1300 m (Rice *et al.* 1990; Duineveld *et al.* 1997; Flach *et al.* 1998; Hughes & Gage 2004). The sponge aggregations appear to be directly related to increased abundance and richness of the macrofauna, particularly where there are large deposits of sponge spicules in the immediate area (Rice *et al.* 1990; Bett & Rice 1992). Bett and Rice (1992), discussed the effects of sponges based on generalisations made for agglutinating protozoans (Levin 1991). Dense spicule mats may have several effects on the benthic community, such as providing hard substrate, suitable for colonisation by species such as actinarians, hydroids and bryozoans (Bett & Rice 1992). They also suggest spicule mats and sponge bodies may serve as refuge for prey species, as well as serving to trap particulate matter and phytodetritus. Sponge bodies and high local concentrations of spicules may be used by organisms such as ophiuroids and actinarians to gain elevation, allowing access to potentially higher flow rates above the sediment-water interface (Rice et al. 1990). In the north Pacific, the stalks of some species of hexactinellid sponge form a substrate for epifaunal species to colonise as well as accumulating sediments which polychaete worms and copepods may colonise (Beaulieu 2001).

Cold-water coral reefs

Cold-water coral reefs consisting mainly of the scleractinian coral *Lophelia pertusa* were discovered within the north-east Atlantic in the mid 18th century (Linnaeus 1758), with new discoveries occurring regularly to the present (e.g. Le Danois 1948; Wilson 1979; Zibrowius 1980; Long *et al.* 1999; Rogers 1999; Roberts *et al.* 2003). On a global scale, *L. pertusa* appears to have a cosmopolitan distribution with records from the North Atlantic, South Atlantic, Mediterranean Sea, Gulf of Mexico, Indian Ocean and north-east Pacific (Rogers 1999) (Figure 14). However, the distribution of this cold-water coral species appears to be most prevalent within the north-east Atlantic (Wilson 1979; Rogers 1999), with the region potentially being of global significance (Rogers 1999).

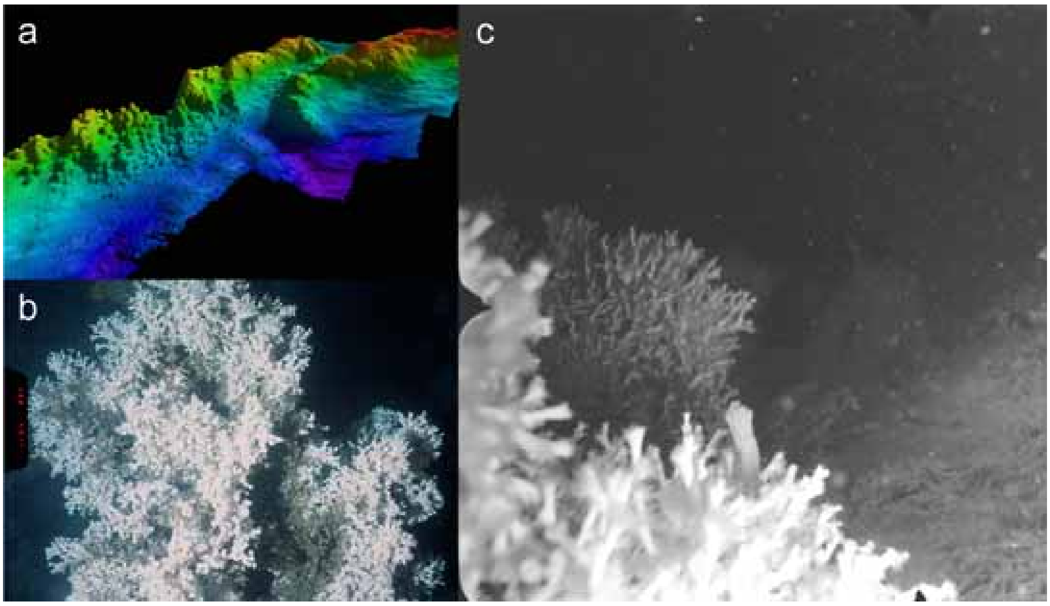

Figure 13: *Lophelia pertusa* colonies recorded in the SEA 7 area. (a) Multibeam echosounder survey showing characteristic mounds formed by *L. pertusa* in the Sea of the Hebrides (Roberts et al. 2005a).(b) Seabed photograph of one of these *L. pertusa* mounds (Roberts et al. 2005a). (c) *L. pertusa* from the Rockall Bank, photograph taken from a submersible at 256 m depth in 1973 (Wilson 1979).

Lophelia pertusa is also closely associated with some mud and carbonate mounds, the surfaces of which are draped with patches of coral. These mounds may form through skeletal growth and sediment infill over thousands of years (De Mol et al. 2002). In the north-east Atlantic many mounds have already been discovered (Freiwald et al. 2004). *Lophelia pertusa* reefs frequently occur on the exposed hard substrate of banks, seamounts and shelves usually between depths of 200-400 m (Rogers 1999), but may occur towards extremes between 39 and > 3000 m (Squires 1959; Rapp & Sneli 1999). In the SEA 7 area *L. pertusa* colonies are distributed sparsely to the west of Shetland, but are more abundant on the south and west flanks of the Rockall Bank (Wilson 1979), Wyville Thomson Ridge, Lousy Bank and Hatton Bank (Roberts et al. 2003) and in the Sea of the Hebrides between the Outer Hebrides and Scottish mainland (Roberts et al. 2005a) (Figure 13a and 13b). During the SEA 7 survey *L. pertusa* was also found in the northern part of the Rockall Bank as well as George Bligh Bank (Narayanaswamy et al. 2006). In recent surveys of the northern Rockall Trough, colonies of *L. pertusa* have been discovered capping mounds, more famously known as the Darwin Mounds at depths of *ca*. 900 - 1000 m. These mounds are up to 75 m in diameter and 5 m high, and host an associated community of sessile suspension feeders that occur in close association with the coral (Masson et al. 2003), such as the xenophyophore *Syringammina fragilissima* at densities of up to 7 m^{-2} (Bett 2001).

Lophelia and other cold-water corals such as *Madrepora oculata* and *Solenosmillia variabilis* create three-dimensional habitats in waters where the seafloor may be relatively featureless (Rogers 1999) (Figure 13). In turn, these corals may provide habitat for a wide variety of different species, including fish (Costello et al. 2005) and invertebrates (Jensen & Frederiksen 1992). Numerous studies have found associations between cold-water corals and abundant associated populations, for example, larger rockfish (*Sebastes* spp.), asteroids (e.g. *Hippasteria heathi*), nudibranchs (e.g. *Tritonia exulsans*) and various suspension feeders including crinoids, basket stars, anemones and sponges which were found to be associated with gorgonian corals (*Primnoa* spp.) in the Gulf of Alaska (Krieger & Wing 2002). On *L. pertusa* reefs, extensive video surveys have revealed numerous fish species such as *Sebastes* sp., *Molva molva*, *Brosme brosme* and *Pollachius virens* among the living coral (Mortensen et al. 1995). Species such as *B. brosme* and *Anarhichas lupus* were found amongst the dead coral framework (Freiwald et al. 2002). Pregnant *Sebastes viviparus* may use the reef as a refuge or as a nursery ground (Fosså et al. 2002).

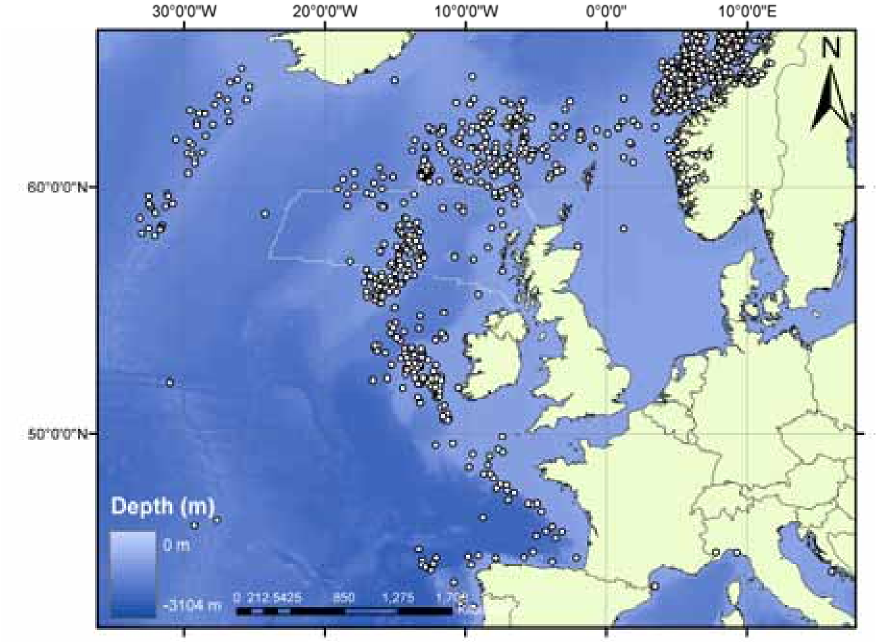

Figure 14: Cold-water coral distribution (*Lophelia pertusa*, *Madrepora oculata* and *Solenosmillia variabilis*) within the SEA 7 area (white box) and the larger north-east Atlantic Ocean (Coral location data from JNCC and J.M. Roberts, SAMS; bathymetry, GEBCO 2001).

As well as fish, diverse invertebrate fauna have been recorded on living reefs, the dead coral framework and the adjacent coral rubble areas. Jensen and Frederiksen (1992) collected 25 blocks of *Lophelia* and found 4,626 individuals belonging to 256 species, a further 42 species were identified amongst coral rubble. Living coral is relatively clear of epifauna, with stinging nematocysts within polyps deterring both predators and settlers (Rogers 1999). Jensen and Frederiksen (1992) found only 1366 individuals from 11.94 kg of live coral compared to 3260 individuals from 6.52 kg of dead coral framework. Individuals from the groups Polychaeta and Gastropoda were twice as abundant in dead coral than in live coral; the Crustacea, Sipuncula, Bivalvia and Nematoda were 4 to 8 times more abundant on dead coral. Individuals of the Ascidiacea, Anthozoa and Echinodermata were 10 times more abundant on dead coral, whereas Brachiopoda were 50 times more frequent on dead than live coral. The most common species found on live coral were the polychaete *Eunice norvegica*, the bivalve *Modiolus modiolus* and a species of nematode (unspecified) (Jensen & Frederiksen 1992).

6. Anthropogenic Activities and Impacts

Scientists' understanding of the biology of the deep sea is still incomplete, but currently, the SEA 7 area represents one of the best-studied deep-sea areas in the world. The area also represents the largest expanse of deep sea within the UK's territorial waters and in turn, may contain vast exploitable resources. Human activities may have significant impacts on the deep sea, both directly and indirectly. The main direct impacts include the disposal of waste directly into the sea, oil and gas drilling and fishing, with the dominant indirect impact being climate change (Glover & Smith 2003). The impact of various anthropogenic activities and the level of disturbance caused by them were summarised by Glover and Smith (2003), with potential impacts for the next 25 years being theoretically assessed (Table 4).

Waste disposal

The disposal of waste into the deep sea has been occurring for many decades, with particular reference to ship sinking, both accidental and deliberate, the dumping of radioactive waste, sewage sludge and dredge spoils from estuaries, waterways and harbours (Glover & Smith 2003). The effects of a ship sinking may create a localised reducing environment (Dando et al. 1992), release chemical pollution and provide a hard substrate for colonisation by a variety of different organisms (Hall 2001). Hard-substrate from ships or oil and gas platforms may create 'artificial reefs' which may increase habitat complexity and in turn, the diversity and abundance of species in the local area (i.e. Gulf of Mexico, Dauterive 2000), but more quantitative research is required into the impact of artificial structures on the seafloor (Tyler 2003). The disposal of radioactive waste into the deep sea is now banned, but occurred throughout the north-east Atlantic between 1949 and 1982, with a total of 220,000 drums of low and intermediate-level radioactive waste dumped by European countries (Thiel 2003). Dumped radioactive waste may impact the surrounding organisms, with measurable levels of radionuclide contamination in anemones, holothurians, asteroids, decapods and fish (Smith et al. 1988).

The sequestration of CO_2 into the deep sea may be a potential solution for reducing the amount of atmospheric CO_2 potentially reducing the effects of global warming. This is already a reality. Direct injection of CO_2 into sub-sea rock substrata occurs in the Sleipner oil and gas field (North Sea), with plans for the direct injection of industry created CO_2 into the deep sea in the near future. However, broad-scale CO_2 sequestration will not occur for several decades (Glover & Smith 2003). The impacts of injecting CO_2 into the deep sea may be both local and regional, if not global. *In situ* experiments showed fish in immediate contact with liquid CO_2 to suffer respiratory stress and loss of consciousness. However, these effects were not observed in fish and benthic organisms several centimetres from the CO_2 source (Brewer *et al.* 1999; Tamburri *et al.* 2000). Direct contact may cause significant respiratory stress in organisms, and prolonged contact may result in mortality (Tamburri *et al.* 2000; Carman *et al.* 2004), with organisms being potentially more affected by respiratory stress than changes in pH (Tamburri et al. 2000). On a larger scale, simulations of the global carbon cycle in response to elevated CO_2 concentrations have shown that large changes may occur in oceanic chemistry, in particular increasing acidification world-wide (Caldeira & Wickett 2003; Orr *et al.* 2005). These changes may lead to decreased levels of aragonite, which is essential for carbonate production on reefs and the shells of planktonic organisms (Orr et al. 2005). Whether these large-scale changes would be amplified by CO_2 sequestration requires further investigation.

Mining

Glover and Smith (2003) predict deep-sea mining may become widespread within the next 25 years, with intense efforts potentially focusing on the mining of polymetallic nodules, sulphides, phosphorites and methane hydrates. The exploitation of these and similar resources is beginning to become commercially viable, as shown by the recent discovery of offshore diamond deposits and the increased efficiency of extraction technology (Wiltshire 2001). The impact of deep-sea mining has been compared to strip mining in terrestrial environments (Jumars 1981), especially with respect to nodule mining, which may utilise a tracked collector vehicle that strips up to 5 cm of surface sediment, removing nodules and discarding the surplus sediment to the rear (Oebius et al. 2001). The majority of surface macrofauna and megafauna, along with any infauna in the top 5 cm of sediment would be killed instantly, with large areas to the rear of the mining vehicle smothered with re-deposited surface sediment (Jumars 1981; Oebius *et al.* 2001). The potential impacts of seabed mining may be devastating both in the short and long term (Jumars 1981; Glover & Smith 2003), and may require extensive environmental impact assessment.

Table 4: Summary of anthropogenic environmental forcing factors on the deep-sea floor (reproduced from Glover and Smith, 2003).

Human forcing factor	Temporal scale of activity	Knowledge of Impact/Severity/Spatial scale	Estimated importance in 2025
Past impacts			
Dumping of oil/gas structures	Isolated incidents (now banned)	good/low/regional	low
Radioactive waste disposal	1950s-1990s	good/low/local	low
Lost nuclear reactors	1960s onwards	good/low/local	low
Dumping of munitions	1945-1976 (now banned)	poor/low/local	low
Present impacts			
Deep-sea fisheries	1950s onwards	good/high/regional	high (unsustainable)
Collateral damage by trawling	1950s onwards	good/high/regional	high
Deep-sea oil and gas drilling	1990s onwards	poor/moderate/basin	moderate
Dumping of by-catch causing food falls	1900s onwards	poor/moderate/basin	moderate
Research and bio-prospecting at vents	1960s onward	good/low/local	very low
Underwater noise	1960s onward	poor/low?/local	probably low for benthos
Future impacts			
Polymetallic nodule mining	10-20yr timescale	poor/very high/regional basin	high
CO_2 sequestration	10-30 yr timescale	poor/very high/local-regional	high
Dumping of sewage sludge	5-10yr timescale	good/moderate/local-regional	moderate
Dumping of dredge spoil	5-10yr timescale	poor/low/local	moderate
Climate change	50-100 yr timescale	poor/very high/basin-global	low
Manganese crust mining	unknown	poor/high/local	low
Polymetallic sulphide mining	unknown	poor/high/local	low
Methane hydrate extraction	unknown	poor/moderate/regional	low

Oil and Gas Developments

The effects of oil and gas exploitation and prospecting on the benthic community have been heavily researched in the shallower waters surrounding the North Atlantic Ocean (Davies & Kingston 1992; Kingston 1992). In recent years, existing oil reserves have begun to run out, increasing the commercial viability of exploiting deep and ultra-deep reserves in the north-east Atlantic (UKOOA 1998). To date, over 200 wells have been drilled along the Atlantic Margin region (AFEN 2000), and this number is expected to increase. The environmental impacts of these activities include the construction and presence of the foundations of oil platforms, excess drill cuttings and drilling muds, and discharges of oil and other chemicals (Glover & Smith 2003).

Drill cuttings accumulate around oil platforms. In the North Sea, the single largest cutting pile is 66,816 m^3 of material, with estimates for the total area of 1.3×10^6 m^3. The area of material in the Norwegian sector is estimated to be 6.5×10^5 m^3 (Bell *et al.* 1998; Bell *et al.* 2000). The physical smothering of these accumulations affects the benthic community most strongly in the immediate area, but the effects may be observed within a zone extending in some areas as far as 6 km from the piles (Olsgard & Gray 1995). Benthic communities within the immediate area are often of low diversity and usually dominated in abundance and biomass by a few opportunistic species (Gray 1989). Further away, diversity remains low with detectable changes in the composition of the community (Olsgard & Gray 1995). Drill cuttings can also cause localised organic enrichment, chemical contamination by hydrocarbons, heavy metals and sulphides close to the platform which have further effects on the benthic community and may persist for several years even after cessation of drill cutting discharges (Olsgard & Gray 1995). Reports from the North Sea have shown the effects of drill cutting discharges to persist for longer and with significant localised environmental impacts in deeper waters with low current flow, compared to shallower, higher energy areas which allow biodegradation to occur (UKOOA 2002), an effect which is likely to be observed in the deep waters within the SEA 7 area.

Once oil platforms have reached the end of their operational life, decommissioning may cause further damage to the benthic community, either from dumping of the structure or the disturbance caused during the removal. The key case study for the decommissioning of oil platforms was the storage platform Brent Spar in the mid 1990s (Anon. 1994a, b; Gage & Gordon 1995). Since then, defunct oil and gas platforms have been retrieved and scrapped on land, reducing the impact of decommissioning such structures. During the decommissioning of the Brent Spar, unexpected occurrences of the cold-water coral *Lophelia pertusa* were discovered on the physical infrastructure (Bell & Smith 1999). Further reports of coral growth have been made throughout the North Sea (Bell & Smith 1999; Roberts 2002; Gass & Roberts in press). This suggests some taxa may not be as sensitive to oil discharges as previously suggested (Bell & Smith 1999; Roberts 2002; Gass & Roberts in press).

Fishing

The effect of fishing on deep-sea benthic organisms is largely restricted to collateral damage caused by long-line and trawl fishing gear. Highly destructive effects on the benthic community and seafloor have been recorded in shallow waters (Jones 1992; Jennings & Kaiser 1998; Gõni 2000) and it is likely that the effects are similar in the deep sea (Gage et al. 2005). In the deep sea, linear marks on the seafloor are being discovered with increasing regularity in sonar and photographic surveys in the north-east Atlantic (Roberts *et al.* 2000; Hall-Spencer *et al.* 2002; Gage *et al.* 2005; Wheeler *et al.* 2005) (Figure 15). The intensity of trawling in the SEA 7 area is unclear, but from studies conducted on the Hebrides slope off Scotland, trawling marks are clearly visible in 2 - 12 % (Roberts et al. 2000) and 5 - 47 % of seabed photographs (Lamont & Gage 1998). Side-scan sonar surveys have also recorded trawling marks on the Darwin Mounds at 900 m depth (Wheeler et al. 2005).

The damage caused by trawling can have lasting effects on the benthic community. Perhaps the most heavily impacted group are the epifauna which can be physically damaged, dislodged and removed by the trawl (Gage et al. 2005). Boulders are observed throughout the continental shelves of the north-east Atlantic and often host a wide variety of sessile fauna. Trawls can uproot and dislodge boulders, causing damage to sessile organisms which are unable to move (Freese et al. 1999). Recurring trawls are also likely to limit the recovery of epifauna on boulders due to reoccurring damage (Pitcher et al. 2000). Perhaps the best publicised impacts of trawling on epifauna have been those on cold-water corals, such as gorgonians and scleractinians (Hall-Spencer et al. 2002). Corals have been labelled as flag-ship species for conservation agencies as a result of their vulnerability to destructive damage from trawling. Cold-water coral reefs have been discovered throughout the north-east Atlantic (Wilson 1979), with continual discovery of new areas, such as the Darwin Mounds (Masson et al. 2003). Hall-Spencer et al (2002) observed widespread damage to coral reefs caused by the trawls of commercial fishing vessels on the shelf edges of Ireland and Norway. The passage of the trawl may increase mortality of the coral by crushing, burying or wounding corals, increasing susceptibility to infection and epifaunal recruitment which may eventually smother corals (Fosså et al. 2002). The destruction of the coral reduces the three-dimensional structure to rubble, decreasing the complexity of the habitat with potential impacts on the associated community composition (Koslow *et al.* 2001; Fosså *et al.* 2002).

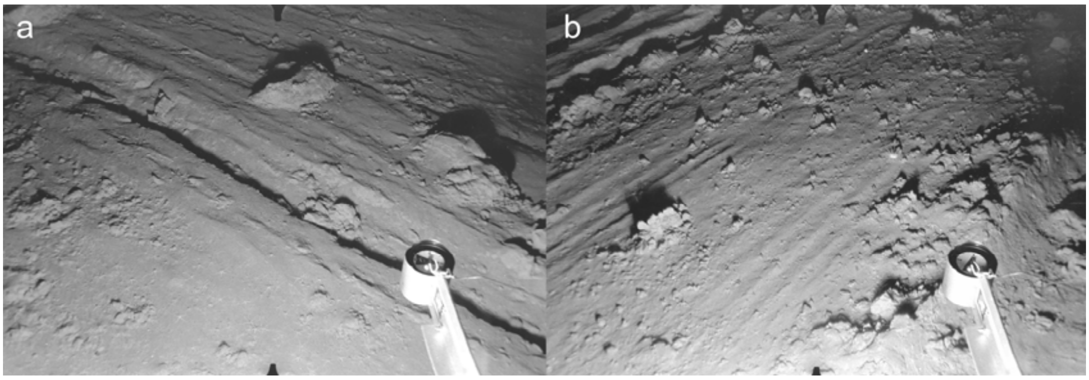

Figure 15: Photographs showing trawl marks at 885 m depth from the Hebrides Slope in 1988. (a) The muddy sediment is marked by the passage of a trawl that has produced a trench about 25 cm wide and 8 cm deep. (b) A series of trenches produced by a trawl and clods of sediment scattered on the bed, presumably in the wake of the trawl (Roberts et al. 2000).

To some extent the infauna may be buffered from the impacts of trawling by being buried within the sediment. However, the small scale heterogeneity observed on the muds serves to increase the diversity and abundance of the fauna (Jumars 1975a, 1976) and any disturbance may potentially homogenise this complexity leading to lower diversity and abundance (Gage et al. 2005). The infaunal community may have some resilience to the effects of trawling, with observations of trawl marks showing biogenic structuring within the trawl scar which must have occurred after trawling (Gage et al. 2005). Studies from shallow water show larger infauna such as large bivalve molluscs (Rumohr & Krost 1991; Gage *et al.* 2005), mobile epifauna (Rumohr & Krost 1991) and some sessile epifauna (Kaiser et al. 2000) to be damaged and even removed by trawling (Pitcher et al. 2000).

7. Recent discoveries, forthcoming research, associated problems and gaps in knowledge

The SEA 7 area has been intensively studied compared to most of the deep ocean, but recent research has continued to reveal new findings. In the Sea of the Hebrides, a new inshore coral reef complex consisting of *Lophelia pertusa* was recently rediscovered and mapped using the latest multibeam echosounder technology (Roberts et al. 2005a). The recent SEA 7 cruises have reinforced many existing datasets by supporting previous findings at particular sites, as well as revealing a diverse benthic community on many of the banks and seamounts in the area that had not previously been recorded (Narayanaswamy et al. 2006). During SEA 7, two separate cruises were undertaken in 2005, sampling a total of 86 stations, collecting 2071 still images and over 54 hours of video from these areas (Narayanaswamy et al. 2006).

On the Hebrides Slope (*ca*. 650 - 2200 m) observations largely supported existing datasets (Gage 1986; Gage *et al.* 2000), with some areas showing evidence of hydrodynamic activity at shallower stations with a relatively low megafaunal density and diversity. The most frequently seen species were the echinoid *Echinus acutus* and the ophiuroid *Ophiomusium lymani*, different to the communities described by Jones et al (1998) and Roberts et al (2000) with the ophiuroid *Opiocten gracilis* and octocoral *Acanella arbuscula* were observed in seabed photographs taken in 1998. Moving to the west, the relatively understudied Anton Dohrn Seamount showed evidence of strong hydrodynamic activity on the flanks and plateau (Narayanaswamy et al. 2006) supporting earlier work conducted in the 1970s (Roberts et al. 1974). There were no discoveries of large sessile epifauna such as gorgonians, corals or massive sponges. Instead, the sessile community was mainly composed of brachiopods (probably *Dallina septigera*) and barnacles (probably *Bathylasma hirsutum*), whereas the mobile megafauna were mainly composed of echinoderms such as the echinoids *Calveriosoma* cf. *fenestratum* and *Cidaris cidaris* (Narayanaswamy et al. 2006).

The Rockall Bank was the most intensively sampled area, with a total 44 stations and over 25 hours of video data collected. These samples showed the bank to consist of different sedimentary regions, with the south-east mainly composed of fine muddy sand, with the echinoid *E. acutus* the most common mobile megafauna. The eastern flank of the bank has extensive areas of exposed bedrock showing evidence of strong sediment scour (Narayanaswamy et al. 2006). To the west and north-west of the bank, several areas of live coral reef framework were recorded composed of *L. pertusa* and *M. oculata* as reported from submersible observations from 1970s (Wilson 1979). The Hatton and George Bligh Banks have been less studied than the Rockall Bank and Trough. However, both these areas have extensive live and dead coral framework comprised of *L. pertusa* and *M. oculata*, with a diverse associated community, including the cnidarian *Phelliactis* sp., the antipatharian coral *Stichopathes* sp. and many hydroids / bryozoans and mobile epifauna such as crustaceans and ophiuroids (Narayanaswamy et al. 2006).

The SEA 7 samples have provided some of the first visual inspections of some areas, showing some highly diverse communities. The available data from the study show parallels with previous work undertaken in the SEA 7 area, especially reinforcing evidence of the strong hydrodynamic regime in the area. However, there are some differences, especially with respect to the relatively well-studied Hebrides Slope. Here, the SEA 7 surveys showed the community to be dominated by different species compared to previous work in the area, which may be indicative of local variation most likely caused by hydrodynamic disturbance. It is clear that more research needs to be conducted within the SEA 7 area, especially with respect to the interaction of species with physical variables. Studying the deep sea is inherently difficult and costly, which makes replicate sampling difficult to execute but this is a limitation that needs to be addressed. Large scale habitat mapping and photograph / video transects are one way to characterise these communities, but reveal little in quantitative biomass and abundance data.

In conclusion, the deep sea is much less understood than terrestrial and coastal systems and unless biologists begin to address problems with non-replication of samples will continue to lag behind. Trying to address this deficiency is difficult and potentially timeconsuming, mainly due to the inherent difficulties in sampling and visualising in deep water. In the future, the best data may be collected from collaborative research efforts utilising sonar, visual surveys, *in situ* observations and quantitative sampling. These multi-disciplinary cruises are happening as biologists begin to recognise the need to investigate as many aspects of the deep sea as possible.

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