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Ecological Controls on Density, Diversity and Community Structure of Polar Megabenthos

By

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ABSTRACT

Polar deep water environments are poorly studied. This thesis investigates fundamental questions as to the nature of controlling factors on megabenthic communities as well as the diversity, densities and distributions of organisms present.

The deep (1000-1660m) Faroe-Shetland Channel harbours an Arctic fauna owing to cold deep-water intrusions from the Norwegian Sea. Despite the relatively low species richness of the megabenthos, variation in faunal composition with depth is apparent. Two distinct communities were identified in the north and south of the channel. Epibenthic megafauna in the south are dominantly filter feeders and in the north deposit feeders. Megabenthic diversity and density decreased to the northeast of the channel. *Lebensspuren* number and area increase northwards in the Channel. The increase in bioturbation and deposit feeder abundance is concurrent with an increase in fine sediment quantity.

The response of a deep, Arctic benthic community to physical disturbance was investigated in the Faroe-Shetland Channel. High levels of physical disturbance, characterised by smothering of the seabed resulted in significant but variable reductions in megafaunal abundance (up to 92.3%). Reductions in diversity, particularly in species richness, were apparent between disturbed ($ES_{(500)}$ = 12.9) and undisturbed areas ($ES_{(500)}$ = 20.6). The implications of selective removal of taxa on ecosystem function and recovery are discussed. Low level disturbance had comparatively little effect on the communities. The effects varied in nature depending on motility and functional group (e.g. motile scavenger abundances were maximal at intermediate distances from disturbance).

Effects of physical factors on the megabenthos of Kangerdlugssuaq Fjord mouth in Arctic Greenland were investigated. Large reductions in faunal density (1881 to 60,132 individuals ha^{-1}) and increases in diversity (H' = 0.93-2.54), through increases in richness ($ES_{(220)}$ = 7.6-18.8) and reductions in dominance (Berger-Parker Index = 0.77-0.38), were found from 270 to 720m depth. Distinct shallow, intermediate and deep communities were identified. Shallower stations had high levels of iceberg disturbance, directly reducing diversity and creating a complex, patchy environment. Responses to disturbance were taxa specific (e.g. mobile suspension feeders aggregate on disturbed areas), but the shallow area has higher densities of suspension feeding epifauna. Deeper areas experience small scale disturbance from deposition of drop stones but its relatively low frequency and magnitude allows increased diversity. Deposit feeding epifaunal and infaunal taxa increase with depth indicated by increased *Lebensspuren*. Density decreases result from decreased food supply with depth.

Benthic megafauna were investigated from the NE Weddell Sea (250 to 500m depth), close to the Fimbul Ice Shelf. Faunal density decreased with depth; diversity was variable but not related to depth. Two distinct communities were found, a shallow community with dense patches of suspension feeders in undisturbed areas and a deep community where these were not present. Disturbance from icebergs was very important in controlling faunal distribution. In shallow waters direct effects of disturbance were observed. In deeper waters habitat changes, caused by past disturbance, controlled faunal distributions. Ice ploughing created a mosaic landscape of fine and coarse sediments. Megafaunal density was highest in coarse sediment and diversity highest in intermediate areas.

Quantitative data on benthic megafaunal abundance and diversity obtained using the same method allowed valid comparisons to be made between these polar areas. Megafaunal abundance was comparable between the Arctic and Antarctic stations, although in both areas abundance decreased with increased depth. Diversity was higher in the Antarctic stations, but species richness and evenness in both areas changed with depth. Iceberg disturbance was found to be very important in structuring megabenthic communities, particularly in the Antarctic.

The results of this study are used to assess the utility of towed camera sleds, remotely operated vehicles and autonomous underwater vehicles as a method for obtaining ecological information in remote environments.

CONTENTS

Chapter 1 – General Introduction

Chapter 2 – Materials and Methods

Chapter 3 – Ecology of the Deep Faroe-Shetland Channel

Chapter 4 – Effects of disturbance on cold-water Faroe-Shetland Channel Communities

Chapter 5 – Ecology of the Kangerdlugssuaq Fjord Mouth, East Greenland

Chapter 6 – Ecology of benthic megafaunal communities in the Fimbul Ice Shelf region, Weddell Sea, Antarctica

Chapter 7 – Conclusions

Biological conclusions

Methodological conclusions

Summary and Conclusions

References

Appendices

Appendix I – Copy of the paper: Laurenson, C., Hudson, I., **Jones, D.**, Priede, I. (2004) Deepwater observations of monkfish, *Lophius piscatorius*, in the Northeastern Atlantic Ocean by means of a remotely operated vehicle. Journal of Fish Biology 65:947-960.
Appendix II – Copy of the paper: **Jones, D.**, McPhail, S., Bett, B., Flewellen, C. and Conquer, M. (2005) Seabed photography from an autonomous Underwater Vehicle. Journal of Marine Science and Environment. C3:29-36

FIGURE AND TABLE LIST

Chapter 1 – General Introduction

Chapter 2 – Materials and Methods

Chapter 3 – Ecology of the Deep Faroe-Shetland Channel

Chapter 4 – Effects of disturbance on cold-water Faroe-Shetland Channel Communities

Chapter 5 – Ecology of the Kangerdlugssuaq Fjord Mouth, East Greenland

Chapter 6 – Ecology of benthic megafaunal communities in the Fimbul Ice Shelf region, Weddell Sea, Antarctica

Chapter 7 – Conclusions

7a: Biological conclusions

7b: Methodological conclusions

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CHAPTER 1: INTRODUCTION AND LITERATURE REVIEW

HISTORY OF DEEP-SEA POLAR EXPLORATION

A large number of expeditions have visited the polar regions (Dell 1972) and despite their remote nature, these areas have played an important part in the history of deep-sea biology. In the early days of deep-sea investigation scattered biological observations were all that were recorded. In the Arctic Ocean the first record of deep-sea fauna was in 1818 when the British explorer John Ross collected a specimen of the basket-star *Astrophyton* on a sounding line at 1600m, whilst searching for the North-West Passage (Menzies et al. 1973; Tyler 1980). In the Southern Ocean, Sir James Clark Ross and J. D. Hooker made the first collections of benthic organisms in 1839-43, with a dredge from the voyages of the '*Erebus*' and '*Terror*' in depths up to 1800m (Dell 1972).

The first structured sampling of deep Arctic water was carried out by Charles Wyville Thomson in the cold Norwegian Sea deep water of the Faroe-Shetland channel using HMS '*Lightning*' and '*Porcupine*'. Inspired by fauna collected from the deep Norwegian fjords by W and G. O. Sars, Thomson discovered abundant fauna in deep waters which provided evidence against Forbes' previously accepted azoic zone below 300 fathoms (550m) (Thomson 1873). Thomson's collections still provide some of the best information on the fauna of the Faroe-Shetland Channel.

The subsequent voyage of HMS '*Challenger'* from 1872-1876 was carried out to consolidate and extend the work of the '*Lightning'* and '*Porcupine'*. As well as laying the foundation for our current knowledge of life in the deep sea, this expedition provided the first substantial benthic samples taken in Antarctic waters (Murray and Hjort 1912).

This first discovery phase continued during the first half of the 20th century primarily for the purpose of completing the inventory of the world oceans fauna. The history of benthic research is relatively well known (Gage and Tyler 1991; Deacon 1997) and has been frequently summarized for the Antarctic (Dell 1972; Fogg 1992; Vinogradova 1997) although less so for the Arctic (Paul and Menzies 1974; Curtis 1975).

THE DEEP OCEAN ENVIRONMENT

Topography

The deep ocean is generally accepted to start at the edge of the continental shelf (the shelf break; Figure 1.1) this is typically around 200m deep although may reach depths of 500m in the Antarctic (Gage and Tyler 1991). Seaward of the shelf break is the continental slope, on which a marked increase in the downward gradient of the seabed occurs. Typically, on passive margins, at the base of the continental slope, slope-derived sediment forms a thick layer, known as the continental rise (Gage and Tyler 1991). By a depth of around 4000m the seabed has leveled off to give a wide expanse of relatively flat abyssal plain which extends gently from 4 to 6 km in depth and globally covers 278,000,000km^2 (Heezen and

Hollister 1971). If the abyssal plain is bordered by an active margin, where oceanic crust is being subducted under an adjacent continent, trenches can occur which can extend to depths of greater than 11km. Throughout the deep sea there are highly heterogeneous topographical features ranging in scale from animal burrows and mounds through to seamounts and ridges. With such high physical diversity and wide area it is perhaps not surprising that the ocean floor offers more niches than all terrestrial habitats together (Rice et al. 1991).

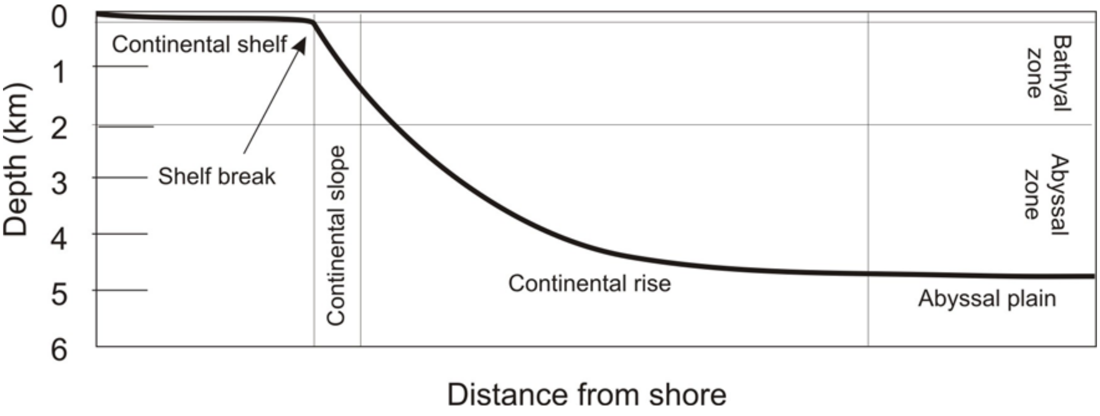


Figure 1.1: Diagrammatic cross section of the ocean showing the major physiographic features and major depth zones. The sublittoral zone (0-200m) is not labeled. Redrawn from Gage and Tyler (1991).

Circulation and temperature

As the deep-sea environment predominantly occurs below the permanent thermocline temperatures typically vary from –1 to 4°C (Svedrup et al. 1942) although temperatures in the Antarctic reach –1.9°C. Most of the deep-sea bed is bathed in water masses formed in either the Antarctic or in the Greenland/Norwegian Seas of the Arctic Ocean. In these areas the surface water becomes dense enough to sink as a result of cooling or, to a lesser extent, becoming more saline from ice formation. This water then sinks to its density level where it spreads out. The very deepest waters are formed in the cold surface layers close to the coast of Antarctica, especially in the Weddell Sea where the winter-cooled surface water is exceptionally cold (-1.9°C) (Gage and Tyler 1991). Salinity is one of the most constant features of the deep-sea bed (>34.7 in the Atlantic) but is unlikely to have any ecological consequences for the deep-sea benthic fauna (Tyler 1995).

Sea ice is a vitally important factor in the formation of deep waters. When seawater freezes to form sea ice, it leaves behind cold, dense salty waters. In some areas this water flushes the cavity beneath ice shelves, where it undergoes further transformations (Nicholls 1997) and eventually contributes the formation of bottom waters, driving deep convection in the oceans (Foldvik et al. 1985; Zwally et al. 1985; Emery and Meincke 1986).

The main global ecological significance of these deep water masses is that they are well oxygenated, the supply of oxygen in the deep waters is sufficient to maintain the surficial sediments of the worlds oceans in an oxidized state (Gage and Tyler 1991). For the benthic communities of Antarctica the advection of surface primary production entrained in density driven water mass sinking would seem to be a very important source of nutrition with varying flux driving changes in standing stock and diversity (Dayton and Oliver 1977; Barry 1988; Barry and Dayton 1988).

The deep benthic environment

The physical properties of the deep-sea environment exhibit a very narrow range below the permanent thermocline except for hydrostatic pressure, current velocity and in some cases substratum. The increase in hydrostatic pressure with depth in the world's oceans is the longest continuous environmental gradient in existence (Gage and Tyler 1991). Pressure increases linearly by 1 atmosphere per 10m increase in depth (Thistle 2001).

Deep-sea currents may originate from two forces: thermohaline and tidal. Thermohaline currents, from the global oceanic circulation driven by polar formation of deep waters, generally cause steady currents towards the equator and can have velocities of up to $1ms^{-1}$ (Tyler 1995). Superimposed on the flow generated by the thermohaline circulation are tidal currents with a typical velocity of $<0.1ms^{-1}$, these currents are particularly well known in the deep NE Atlantic. As well as steady currents more sporadic benthic storms can occur, formed from eddies of major currents, their current velocities can often dramatically exceed mean levels causing scouring of sediment on the seabed (Tyler 1995) and changes in infauna (Thistle and Sherman 1985).

The seabed of the deep ocean environment is predominantly composed of soft, fine sediment derived from pelagic biogenic skeletal material (Tyler 1995). Exposed hard rock is relatively uncommon in the deep sea, being found on the steep continental slopes, seamounts and along the mid-oceanic ridge. Coarser sediments of a terrigenous origin are found on the continental slopes and rises, transported there by turbidity currents and sediment slumps (Gage and Tyler 1991; Weaver et al. 2000). Rafted sediments from melting icebergs also contribute to the coarse sediment fraction (Andrews et al. 1997). The effects of these factors on diversity and abundance of megafauna are reviewed later.

DEEP-SEA COMMUNITY MEASURES

Faunal density in the deep sea

Faunal density refers to the number of organisms per unit area at the moment of sampling. The assessment of megafaunal density requires quantitative data on faunal abundance. Quantitative data on megabenthic density are much more scarce than for smaller deep-sea fauna. Although caught in large trawls, megafaunal organisms are too rare to be collected in classic quantitative samplers such as box cores. Seabed photographs and manned submersible observations have allowed quantitative estimates to be made of the larger epifauna (Grassle et al. 1975; Haedrich and Rowe 1977; Ohta 1983; Lampitt et al. 1986). These estimates ignore the potentially important contribution to density of the motile scavenging megafauna and by the megafaunal burrowers, that are occasionally taken by box corers (Gage 1977); although attempts have been made to estimate their density from the large burrow and faecal traces visible in seabed photographs (Mauviel et al. 1987). Macrofaunal density has been shown to decrease with depth (Rowe et al. 1982; Rowe 1983). Lampitt et al. (1986) show a similar trend for megafauna.

Species diversity in the deep sea

The diversity of deep-sea benthic fauna is very high, particularly for macro and meiobenthic invertebrates, where a square metre of bathyal or abyssal sediment may contain 250 species (Smith et al. 1998; Levin et al. 2001; Stuart et al. 2003). Such species richness persists to larger scales, with an epibenthic sledge towed for 1-2km across the continental slope often capturing >300 species of mega and macrobenthos (e.g. Hessler and Sanders 1967). Deep-sea sediments have been estimated globally to contain between 500,000 and 10 million macrobenthic species alone (Grassle and Maciolek 1992; May 1992; Poore and Wilson 1993). While these estimates are very crude, they highlight the fact that the deep-sea floor harbours a substantial, as yet poorly studied, fraction of the Earth’s species pool (Smith et al. 1998).

Since the discovery of high species diversity in the deep-sea benthos (Hessler and Sanders 1967) much has been learned about local (Grassle and Maciolek 1992) and regional patterns of diversity (Sanders 1968; Etter and Grassle 1992; Levin et al. 2001). The elucidation of large scale patterns in species diversity has been more of a challenge in deep-sea research (Rex et al. 1997) with most studies concentrating on changes with latitude (Rex et al. 1993; Rex et al. 2000) and depth (Rex 1973; Pineda and Caswell 1998). Typically a poleward decrease in diversity is observed in the northern hemisphere, however in the southern hemisphere a more complex pattern of interregional variation exists (Rex et al. 1993), part of this complexity is driven by high diversity in the Argentine Basin and Antarctica (Arntz et al. 1994).

The possible processes driving high deep-sea species diversity are still unknown, although Grassle (1991) gave four major potential factors: 1) large scale environmental stability, 2) patchy food resources, 3) localized autochthonous disturbances and 4) few large-scale barriers to dispersal.

The explanations for the mechanisms maintaining high species diversity are still the subject of much speculation. Potential mechanisms have been divided into equilibrium and non-equilibrium hypotheses (Connell 1978). Equilibrium of species composition is usually defined as follows: (i) if perturbed away from the existing state (equilibrium point) the species composition would return to it; (ii) without further perturbations, it persists in the existing state (Connell 1978). In equilibrium hypotheses: the species composition of communities is usually in a state of equilibrium; after a disturbance it recovers to that state. High diversity is then maintained without continual changes in species composition. For example, at equilibrium, each species is competitively superior in exploiting a particular subdivision of the habitat (niche diversification). In the non-equilibrium hypotheses: the species composition of communities is seldom in equilibrium. High diversity is maintained only when the species composition is continually changing. Connell (1978) investigated several equilibrium and non-equilibrium hypotheses in coral reefs and concluded that the non-equilibrium "intermediate disturbance hypothesis" was most applicable, although he acknowledged that all hypotheses tested may act in different situations. The intermediate disturbance hypothesis states that intermediate levels of disturbance maximize species diversity. At low disturbance, species diversity is reduced because of competitive exclusion between species; with a slightly increased level or frequency of disturbance competition is relaxed, resulting in an increased diversity, and at still higher or more frequent levels of disturbance species start to become eliminated by stress and local extinctions lead to a fall in diversity.

The intermediate disturbance hypothesis (Connell 1978) continues to be important in explaining the effects of ecological disturbance (Collins et al. 1995; Hiura 1995; Dial and Roughgarden 1998). However, the intermediate disturbance hypothesis has been criticized as being too simplistic to account for the structure of communities (McGuinness 1987). It is also dependent on a tradeoff between colonization and competitive ability that may not be realistic for assemblages of motile species (McCabe and Gotelli 2000), such as many deep-water megafaunal assemblages (Kaufmann and Smith 1997). Finally the intermediate disturbance hypothesis assumes disturbance affects only competing species at a single trophic level. In deep-water megafaunal assemblages this assumption may be more valid than for macrofauna. Huston's dynamic equilibrium model (Huston 1979) offers a broader range of predictions than the intermediate disturbance hypothesis. The dynamic equilibrium model predicts that the location of the diversity peak depends on the rate of population growth and competitive displacement in the community. Huston's (1979) dynamic-equilibrium model states that population growth rates determine the rate at which communities approach competitive equilibrium, where superior competitors will exclude inferior species and thereby decrease diversity. Disturbance, either biotic or abiotic, interrupts a community's approach to competitive equilibrium, reducing exclusion and promoting coexistence. Both disturbance (Thistle 1988; Vale and Rex 1988; Gage 1997;

Thistle and Levin 1998) and competition (Rex et al. 1988) are known to affect deep-sea communities (Stuart et al. 2003). It is not well known how these processes vary with depth or other physical or biological controlling factors.

The stability-time hypothesis (Sanders 1968) has been used to explain high deep-sea species diversity. This states that as the gradient of physical stress increases in a biological community there is a transition from predominantly biologically accommodated communities to predominantly physically controlled communities. In the deep sea where generally constant conditions exist, physical conditions are not critical in controlling the success or failure of a species. With time biological stress increases and interspecific interactions result in stable, equilibrium, complex and buffered assemblages with a large number of stenotopic species. In more physically-controlled environments fewer species can adapt to the conditions and so diversity is lower. This hypothesis was used to explain the increased diversity of polychaetes with depth found by Sanders (1968) and has been used to explain other patterns of diversity by Gage (1972). However this hypothesis has been criticized, on empirical and theoretical grounds (Gray 1974; Abele and Walters 1979a; Abele and Walters 1979b) and contradicted (Thistle 1983b).

Dayton and Hessler (1972) present the Disturbance theory, this states that the maintenance of high species diversity in the deep sea is more a result of continued biological disturbance than of highly specialized competitive niche diversification. They theorize that the dominance of deposit feeders prevents smaller animal populations from competitive exclusion and allows high overlap in the utilization of food resources. They explain the high numbers of deep-sea species by accumulation over time as a result of speciation and immigration. This may help to explain lower diversity patters observed in the deep-sea benthos of younger and isolated basins such as the Arctic Ocean.

It appears that, by themselves, none of these hypotheses are adequate to explain all deep-sea diversity patterns, and that the observed patterns are the result of many factors interacting simultaneously, but with certain factors having more influence at different scales, in certain areas, at certain depths or at certain times (Nybakken 1993). These factors include microhabitat diversification owing to a heterogeneous environment, energy input, competition, predation and rate of disturbance. More quantitative samples from a wider area of the deep sea may help understand the issue of diversity and find the forces that structure the organization of communities.

PHYSICAL CONTROLS ON DEEP-WATER COMMUNITIES

Benthic distribution and community features, such as composition, diversity and standing stock, are known to be influenced by a complex of abiotic and biotic factors (Dayton 1984). A wide variety of parameters have been discussed in this context such as water depth, habitat heterogeneity, seafloor properties, bottom water hydrography, food availability as well as inter and intraspecific competition and disturbance caused by predation or burrowing activities (Gray 1981). The relative importance of these benthic community determinants strongly depends on the spatial scale considered (Levin 1992). Seabed attributes are most commonly suggested to be major control factors (Snelgrove and

Butman 1994), but recently the quality, quantity and temporal pattern of food supplies have been recognized as equally important in affecting the benthos (Dayton and Oliver 1977; Graf 1992; Thurston et al. 1994). Changes in physical factors have long been shown to be integral in governing ecosystem structure (e.g. Connell 1972).

Depth

Depth is often seen as the greatest environmental gradient on earth and its effects have been shown to be very important in structuring marine ecosystems (Gage and Tyler 1991). Organisms are broadly constrained by depth as a result of their physiological tolerance to pressure. Pressure is invoked as the cause of the decrease in diversity at higher taxon level as depth increases. Many higher taxa, such as decapod crustaceans, anemones and echinoids, do not occur below 6000m, whereas other taxa, especially holothurians and polychaetes, appear to show an increased abundance below this level (Tyler 1995). While depth sets lethal limits, the bathymetric zone in which species are abundant may be narrowed by other local factors (Rowe 1983; Billett 1991; Howell et al. 2002).

Qualitative (Rex 1981) and quantitative (Etter and Grassle 1992) sampling studies indicated that diversity-depth patterns in the deep sea are unimodal with a peak at intermediate depths and depressed diversity at the upper bathyal and abyssal depths (Levin et al. 2001). These studies are predominantly pertaining to the North Atlantic, these unimodal patterns do not appear to be universal (Rex et al. 1997; Stuart et al. 2003), and where they do occur in other basins have been attributed to varied environmental gradients

(Paterson and Lambshead 1995; Cosson-Sarradin et al. 1998). A variety of oceanographic conditions at specific depths interrupt and modify bathymetric diversity trends (Gage 1997; Levin and Gage 1998; Vetter and Dayton 1998).

Habitat

Habitat is highly significant in governing distribution of fauna in the deep sea (Levin et al. 2001) with changes in habitat type directly influencing fauna. Numerous studies have shown that the structure and composition of soft-sediment communities are related to sediment characteristics (Sanders 1968; Rhoads 1974; Gray 1981), but the explanations for these relationships are varied and remain controversial (Snelgrove and Butman 1994).

On the northwest Atlantic slope, spatiotemporal variation in species diversity is correlated with the heterogeneity of sediment grain size across a wide variety of spatial scales (Etter and Grassle 1992). Where sediment grain size is more varied, more species coexist (Levin et al. 2001). It seems likely that species partition sediment with respect to size. There is abundant evidence that deposit feeders selectively ingest sediments of particular size classes (Wheatcroft and Jumars 1987; Self and Jumars 1988)

Reductions in habitat heterogeneity has been shown to be strongly correlated with reduced diversity in the deep sea (Levin et al. 2001), although this does not imply causality as the activities of more diverse communities may increase sediment heterogeneity.

Food supply

The deep sea lacks *in situ* primary production (Levin et al. 2001), apart from relatively small areas of chemosynthetic production at vents and seeps (Van Dover 2000). Most material sinks from surface production in the euphotic zone as particles. The availability of food to the benthos is generally negatively correlated with depth of water through which the food sinks (Suess 1980; Berger et al. 1988; Herguera 1992). Energy availability in deep-sea benthic habitats is positively correlated with: sediment community respiration (Berelson et al. 1997), rate of organic carbon burial within the sediment (Jahnke 1996), benthic biomass and abundance (Cosson et al. 1997) and overlying primary productivity (Lampitt and Antia 1997).

Food supply or particulate organic matter (POM) flux is important in regulating the number of species (Levin et al. 2001). Diversity will be low at low food levels because there are insufficient resources to support viable populations of many species conversely diversity will increase with food supply as more species can maintain viable populations. Diversity has been found to decline at high food levels, although this process is not well understood but may reflect a decrease in habitat heterogeneity, differential population responses leading to increased dominance by a few species (Rosenzweig and Abramsky 1993; Waide et al. 1999) and increased physiological stress owing to oxygen limitation or sulphide toxicity (Levin et al. 2001). As these increases in food supply are often seasonal, diversity decline may also reflect increased extinction rates of more specialized forms as a result of competitive exclusion (Rex 1976). At upper bathyal depths, diversity might be depressed by seasonality of nutrient input causing fluctuations in prey populations, and limiting the ability of predators to diversify by specialization in diet (Stuart et al. 2003).

Spatial gradients in productivity are widely believed to influence species diversity (Waide et al. 1999). Diversity within a functional group increases with productivity as increased availability of resources allows more species to coexist within the group, particularly as increased resources allow species to reduce their niche breadth (Rosenzweig and Abramsky 1993).

Currents

Deep-sea currents have been shown to have an effect on the benthic fauna (Rowe and Menzies 1969; Lampitt et al. 1983). The effects of currents are among the agents of disturbance that can modify the structure and composition of benthic faunas (Hall 1994).

Currents can modify diversity both locally and regionally, although the mechanisms are not well understood (Levin et al. 2001). The effects can be either positive or negative, and may be linked to faunal size with greater effects on larger fauna (Thistle 1983a; Thistle and Levin 1998). Impacts result from direct impacts (e.g. carrying away of fauna) and predominantly indirect impacts, such as: enhanced food supply, entrainment of propagules and changing sediment heterogeneity (Thistle and Levin 1998). Given the large areas of seafloor swept by erosive currents (e.g. Faroe-Shetland Channel) the impacts of hydrodynamics on regional scale deep-sea diversity and biogeography may be considerable (Levin et al. 2001)

Disturbance

The effects of physical disturbance in soft sediment environments, such as the deep sea, have been typically manifested as the partial or complete defaunation of disturbed patches through physical smothering, overturning and direct mortality. In addition numerous additional effects of disturbance on sediment properties have been found, such as its stability and bed roughness (Hall et al. 1994). Changes to sediment topography as a result of disturbances can alter near bed hydrodynamics (Thrush et al. 1992) and may therefore affect the deposition of particles, such as organic matter and benthic invertebrate larvae (Dernie et al. 2003). The increase in suspended particulate loading as a result of disturbance may lead to clogging of filter feeding apparatus of some organisms (Sharma et al. 2001). On the positive side, redistribution of nutrient-rich subsurface layers could have lead to an increase in population size over time (Raghukumar et al. 2001; Sharma et al. 2001).

In addition to physical disturbance, biological disturbances have been found to be important in the deep sea, often as a result of foraging by predators (Thrush et al. 1991), bioturbation (Turnewitsch et al. 2000; Lohrer et al. 2004), deposit feeding (Ginger et al. 2001) and other biotic interactions that have caused changes to habitat properties such as sediment stability, permeability and biological communities (Jones and Jago 1993; Thrush et al. 1996).

Habitat type may have an important effect on the impact of disturbance on marine communities. In studies of disturbance by trawling in shallow water, recovery was quickest in areas of coarse sediment (Thrush et al. 1995) but more stable areas recovered slowly (Tuck et al. 1998). Measured rates of recovery for mobile species from fishing disturbance were largely as a result of immigration, since what is known of life histories of benthic species (Brey 1999) suggested that population regeneration would not occur on this time scale.

Natural disturbance is widely recognised as an important determinant of the occurrence and abundance of species (Dayton 1971; Pickett and White 1985; Huston 1994; Paine et al. 1998; Sousa 2001). The effects of disturbance on diversity have been an important area of research since the formulation of the intermediate disturbance hypothesis (Connell 1978).

Increasing levels of environmental stress, particularly through disturbance, have historically been considered to decrease diversity through decreasing species richness and decreasing evenness (i.e. increasing dominance). This interpretation may, however, be an over-simplification of the situation. Subsequent theories on the influence of disturbance or stress on diversity have suggested that it is at immediate levels of disturbance that diversity is highest (Connell 1978; Huston 1979). Therefore, depending on the starting point of the community in relation to existing stress levels, increasing levels of stress (or disturbance) may either result in an increase or decrease in diversity. It is difficult to say at what point on this continuum the community under investigation exists, or what value of diversity one might expect at a site without any stress. Concurrent with theory, empirical observation (e.g. Widdicombe and Austen 1998) suggests that diversity may be either increased or decreased with increasing disturbance. Changes in diversity are best assessed by comparisons between stations along a spatial stress gradient or with historical data (Clarke and Warwick 2001). In reality it is often found that diversity does not behave consistently or predictably in response to environmental stress. Diversity is commonly thought of as an indicator of ecosystem health or wellbeing, however the exact relationship of diversity to ecosystem functioning is as yet unknown and is the subject of much recent research (Loreau et al. 2001; Loreau et al. 2002; Naeem 2002).

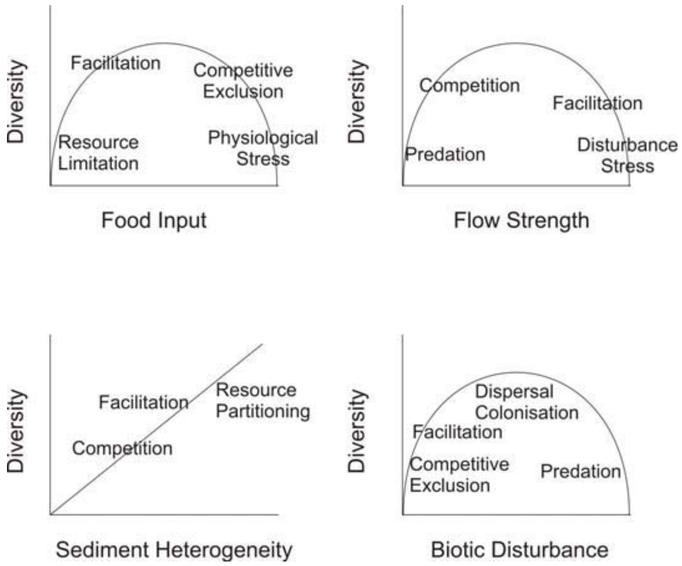


Figure 1.2: Patterns of diversity change along environmental gradients in the deep sea shown with biotic interactions hypothesized to be responsible for generating diversity patterns. Productivity, Flow, Sediment heterogeneity and biotic disturbance. Redrawn from Levin et al (2001).

MEASURING DIVERSITY

Species diversity

Species diversity is a critical concept in ecology. From the early days of biology the study of spatial and temporal variations in diversity has remained a central theme in ecology. Much debate surrounds the measurement of diversity (Magurran 1991) and while it may appear to be a simple concept, diversity is difficult to define. This is because diversity consists of two components, the variety (species richness) and the relative abundance (evenness) of species.

Species Richness

Species richness is the simplest way to describe community and regional diversity (Magurran 2003), it is defined as the number of species in a community (McIntosh 1967). The presence of more species may increase functional diversity of the community, allowing a more complete exploitation of available niche space, and thus increasing resource use and biomass production (Loreau et al. 2002). Quantifying species richness is important, not only for comparison amongst sites, but also for addressing the saturation of local communities colonised from regional source pools (Cornell 1999). In the marine environment particularly, with limited barriers to dispersal, the saturation of communities is likely driven by small-scale changes in physical and biological factors amongst communities.

Evenness

Evenness is a measure of the relative contribution of each species to the total biomass or number of individuals (Wilsey and Potvin 2000). As evenness of species in a community increases diversity becomes greater. The degree to which abundances are evenly divided among the species of a given community is a basic property of any biological community (Ricotta 2004). A greater evenness may be biologically equivalent to having more species, since a species that is present in small numbers or has small individuals is unlikely to contribute much to ecosystem function either directly or through species interactions (Grime 1998; Mulder et al. 2004).

Measuring species richness

In spite of the importance of species richness, ecologists have not always appreciated the effects of abundance and sampling effort on richness measures and comparisons (Gotelli and Colwell 2001). Although species richness is a natural measure of biodiversity, it is difficult to measure properly; this is because as more individuals are sampled, more species will be recorded (Bunge and Fitzpatrick 1993). This sampling curve rises rapidly at first, then much more slowly in subsequent samples as increasingly rare taxa are added (Gotelli and Colwell 2001). It is rarely possible to sample every species in a community and hence elucidate true measures of species richness, for this reason richness has to be approximated from sampling. There is dichotomy in both the protocols for species assessment and the methods for determining species richness from these.

There are two approaches to species assessment used to gather information on species richness: individual-based and sample-based assessment (Gotelli and Colwell 2001).

- In individual-based assessment a random sample of some number of individuals is taken from a study site, with the species identity recorded sequentially of one individual after another. Unreplicated mass samples such as deep-sea dredge samples are an example of individual-based assessment commonly used in deep-water ecology.
- In sample-based assessment, the number and identity of all individuals in a known sub-area (quadrat) is assessed. Total number of species is accumulated as additional quadrats are censused. Quantitative underwater photographic studies can use sample-based assessments of species richness.

If sample-based data are available either individual- or sample-based approaches could be used, but it is generally preferable to use the sample-based approach, to account for natural levels of sample heterogeneity (patchiness in the data). For patchy distributions, individual-based rarefaction inevitably overestimates the number of taxa that would have been found in an area (Colwell and Coddlington 1994).

In addition to the differences in species assessment there is a further dichotomy in species richness measures. This distinguishes accumulation from rarefaction-based species abundance curves (Colwell et al. 2004). Both of which can be either individual-based or sample-based, although in the case of sample-based curves, the x axis should be rescaled to individuals as datasets may differ systematically in the number of individuals per sample (Gotelli and Colwell 2001).

- Accumulation curves record the total number of taxa revealed, during the process of data collection, as individuals or sample units are added to the pool of all previously collected individuals or samples.
- Rarefaction curves are produced by repeatedly re-sampling a pool of N individuals (or samples), at random without replacement, plotting the average number of species represented by 1, 2,…N individuals or samples. Thus rarefaction generates the expected number of species ($ES_{(n)}$) in a small collection of n individuals drawn at random from the large pool of N individuals.

Rarefaction and accumulation curves are often confused owing to shared variables. Accumulation curves, in effect, move from left to right, as they are further extended by additional sampling. In contrast rarefaction curves move from right to left, as the complete community is increasingly sampled. Because the entire rarefaction curve depends upon every individual or sample in the pool at the accumulation curve’s right hand end, each individual or sample is equally likely to be included in the mean richness value for any level of re-sampling along the rarefaction curve (Gotelli and Colwell 2001). Rarefaction curves have been used for a long time in deep-water biology (Sanders 1968) although the original expression was incorrect (Hurlbert 1971) the principle was sound. Accumulation curves are becoming increasingly widespread (Colwell et al. 2004) and avoid some of the shortcomings of rarefaction.

Species density (e.g. the number of species per m^2) is a commonly used measure of species richness, especially favoured by botanists (Kershaw and Looney 1985). However, it gets little attention in marine ecology. Species density depends on both species richness and on the mean density of individuals (disregarding species), consequently the ordering of communities may differ when ranked by species richness vs. species density (McCabe and Gotelli 2000; Gotelli and Colwell 2001). Although it sounds paradoxical, the ratio of richness to area is not a valid measure of species density, because the number of species increases non-linearly with area. Instead, species density is valid only when compared with the appropriate taxon sampling curves.

In some well-sampled communities species abundance curves may approach asymptotical values; in these cases species richness curves can be extrapolated, only with extreme caution, to give asymptotical values and hence measures of true species richness (Colwell et al. 2004). In deep-water studies this is generally inappropriate (Rex et al. 2000) as deep water communities are often characterised by large numbers of species at very low abundances. This coupled with the difficulties of sampling in deep-waters means that in very few cases species abundance curves will be sufficient for meaningful extrapolation. If accumulation curves fail to reach an asymptote, with appropriate scaling the curves themselves can often be compared. It is important to note, however, that if sample sizes are not sufficient, rarefaction will not distinguish between different richness patterns, because all rarefaction curves tend to converge at low abundances (Tipper 1979).

Disentangling metrics of species diversity in gradients of abundance

Testing hypotheses in community ecology, even with experimental data, can be difficult as a result of subtle ambiguities in the definition of richness as well as the interrelated effects of abundance on metrics. It is important to decide if assemblages should be compared on the basis of area sampled (species density) or number of individuals sampled (species richness). Species density is a natural choice as it follows the practice of using standardized samples of equivalent area or sampling effort. However, more abundant samples tend to have more species, so differences in species density among samples of differing abundance must be viewed as potential sampling artifacts unless a rarefaction technique provides evidence to the contrary (McCabe and Gotelli 2000).

It is particularly important, therefore in studies of physical disturbance, where disturbance gradients have been shown to reduce abundance directly (Connell 1979; Sousa 1985; McCabe and Gotelli 2000), to ensure that the effects of these abundance gradients are not driving changes in diversity measures. In community studies, number of individuals sampled and the number of species in a sample are positively related (Gotelli and Graves 1996). Because disturbance lowers total abundance, it is expected that there will be fewer species per unit area in disturbed areas. Many studies, particularly in freshwater ecosystems use only species density to quantify diversity (McCabe and Gotelli 2000). In addition it is important to investigate species richness (using a rarefaction technique or similar), as expected species richness is free from this bias. The diversity measure used must be free of influence from total abundance. In a study of disturbance of stream macroinvertebrates to disturbance McCabe and Gotelli (2000) found decreasing species density with disturbance but increasing species richness.

Measuring evenness

Evenness can be measured in a number of ways. Perhaps the most common method uses the ratio of observed diversity to maximal diversity; as the maximum diversity that could possibly occur is found in a situation where all species are equally abundant (Pielou 1969). The evenness component of diversity is expressed as the rate at which the species abundance curve approaches the asymptote. Curves generated from samples numerically dominated by few species show a less steep rate of climb than those in which abundances are move evenly spread amongst the species (Gage and Tyler 1991).

Combined diversity measures

Indices based on the proportional abundances of species provide an alternative and commonly used approach to the measurement of diversity. These univariate indices are often termed heterogeneity indices as they take into account both evenness and species richness (Magurran 1991). As no assumptions are made about the shape of the underlying species abundance distribution these indices have been referred to as non-parametric (Southward 1978). The non-parametric indices fall into two categories, those derived from information theory and the dominance indices.

Information theory indices are among the most widely used, the most common being the Shannon-Wiener index. These indices are based on the rationale that diversity, or information, in a natural system can be measured in a similar way to the information contained in a code or message (Magurran 1991). It has a number of important assumptions: all individuals are randomly sampled, the population is infinitely large and all species in the community are represented. Of these the last one is perhaps the most important source of error in ecological studies. It is important that care is taken in the use or interpretation of information theory indices (Magurran 1991).

The second group of non-parametric measures are referred to as species dominance measures since they are weighted towards the abundances of the commonest species rather than providing a measure of species richness (Magurran 1991). The Simpson's index is one of the best know of these indices (Simpson 1949).

There are a wide variety of univariate diversity indices in use, of these, there are two main groups of index, type I and II. Type I indices place most weight on the rarer species in a sample, the most extreme example of which is S, the number of species found. Type II indices place most weight on the common species in a sample, the proportional dominance of the most abundant species (Berger-Parker Index) is the extreme type but Simpson's index also falls into this category. Diversity indices should be selected that cover the spectrum between Type I and II indices so that patterns in both rare and common taxa can be elucidated.

Measurement of diversity between habitats

Species diversity is commonly regarded as being synonymous with ecological diversity. However, species diversity is not the only variety of ecological diversity. Species diversity, commonly referred to as alpha diversity, refers to the number and proportion of species in a given sampling unit. Another type of diversity is also important, β diversity or differentiation diversity. The term β diversity was coined by Whittaker (1960; 1977) and it is essentially the same as MacArthur's (1965) between habitat diversity. β diversity is a measure of how different (or similar) a range of habitats or samples are in terms of the variety (and sometimes the abundances) of species found in them (Magurran 1991). β diversity is often said to be the degree to which the species composition of samples, habitats or communities differ (Southward 1978). This is commonly approached by investigating how species diversity changes along a gradient (Wilson and Mohler 1983). β diversity can be measured with univariate indices (e.g. Whittakers β_w), the more commonly used approach is to investigate the degree of similarity or association of sites or samples using standard ecological techniques of classification and ordination (Southward 1978; Pielou 1984; Magurran 1991).

In looking at whole community patterns, it is important to look at patterns in all species abundance and compare these across sites. Community data are usually highly multivariate (large numbers of species, each subject to high statistical noise) and need to be analysed together in order to elicit the important biological signal and its relation to the environment. Multivariate methods are characterised by the fact that they base their comparisons of two or more samples on the extent to which these samples share particular species, at comparable levels of abundance. Either explicitly or implicitly, all multivariate techniques are founded on such similarity coefficients, calculated between every pair of samples. These then facilitate a classification or clustering of samples into groups that are mutually similar, or an ordination plot in which, for example, samples are mapped (usually in two or three dimensions) in such a way that the distances between pairs of samples reflect the relative dissimilarity of species composition (Clarke and Warwick 2001). These techniques are widely used throughout marine ecology, with a proven track record in interpretation of a wide range of marine community data (Clarke 1993; Piepenburg et al. 1997b; Underwood and Chapman 1998). Multivariate techniques for community analysis evaluate species-dependent attributes of community structure. Univariate methods tend to be species independent (Clarke and Warwick 2001).

In an evaluation of both univariate and multivariate methods of data analysis from a broad range of studies on various components of the marine biota from a variety of localities Clarke and Warwick (2001) came to a number of conclusions. The similarity in community structure between sites or times based on their univariate attributes is different from their clustering in multivariate analysis, furthermore the species-dependent multivariate method is much more sensitive than the species-independent methods in discriminating between sites or times. In examples where more than one component of the fauna has been studied, univariate methods may give different results for different components, whereas multivariate methods tend to give the same results (Clarke and Warwick 2001). The sensitive multivariate methods are most suitable for detecting change in communities between sites and although these changes can be correlated with environmental variables, only univariate methods explicitly indicate whether changes are deleterious. There is some evidence that the variability of community composition among samples is increased with disturbance (Warwick and Clarke 1993), this is best assessed by multivariate community analyses such as Multi Dimensional Scaling (MDS).

MEGAFAUNA

The benthic community is typically separated into different size classes, micro- meio- and macrobenthos, these empirically separated size classes seem to correspond to distinct peaks in size-class spectra (Warwick 1984) and biomass (Schwinghamer 1981) for the total benthic community. Furthermore, these peaks seem to correspond to functionally disparate groupings (Gage and Tyler 1991).

The megafauna, defined as organisms large enough (typically >1cm) to be identified in photographs (Grassle et al. 1975), are an important constituent of many deep-sea benthic communities despite being often less numerous and diverse that their meio- and macrofaunal counterparts (Lauerman et al. 1996). There is evidence that megafaunal organisms form a functional component distinct from the macro- and meiofauna (Lampitt et al. 1986). Megafauna can contribute significantly to deep-sea benthic biomass (Sibuet and Lawrence 1981; Christiansen and Thiel 1992), energy reserves (Walker et al. 1987) and organic matter recycling (Smith 1992; Smith et al. 1993). They are more important in benthic habitats than their comparatively low abundances imply, especially in food limited systems such as the polar seas and the deep sea (Haedrich and Rowe 1977; Lampitt et al. 1986; Romero-Wetzel and Gerlach 1991; Smith et al. 1993; Thurston et al. 1994; Piepenburg et al. 1995; Piepenburg and Schmid 1997). Motile species of epibenthic megafauna have caused the dispersal of large food falls and significant vertical and horizontal sediment mixing (Smith 1985; Smith et al. 1993). Megafaunal species may be important components in the overall energy budget of the deep sea (Lauerman et al. 1996), a quantitative understanding of their abundances and spatial patterns is necessary in order to assess their contribution to energy flow through these systems (Smith 1992; Lauerman et al. 1996).

Benthic megafaunal diversity in the deep sea is high, however three main groups are typical representatives of this size class; these are the arthropods, echinoderms and fish. Crustaceans are common in the deep sea contributing 30-50% of the fauna in the abyssal Atlantic area (Nybakken 1993). Also particularly common in abyssal areas are echinoderms, especially holothurians and ophiuroids. Asteroids, crinoids and echinoids are also present but generally not in abundance. Fish presence is probably high although not well know, the estimation of scavenging fish abundance from the deployment of baited cameras to the sea floor (Rowe et al. 1986; Priede and Merrett 1998; Witte 1999) will help in determining abundance. Other representative fauna of the deep sea include sponges, particularly hexactinellids (glass sponges) that are rarely found in shallow water and Cnidaria, almost entirely represented by anthozoans, pennatulids and gorgonians. Polychaetes are very common in the deep sea but are typically not well represented in photographic studies.

The reasons why certain habitats harbour a high number or organisms while others support a very limited number is the subject of much discussion (Sanders 1968). Various theories have been proposed for the differences in abundance and distribution of benthic organisms but the most commonly are physical habitat preference (Grassle et al. 1975; Genin et al. 1992; Sharma and Rao 1992; Pogrebov et al. 1994; Piepenburg et al. 1997a; Gutt and Starmans 1998; Gutt et al. 1999; Starmans et al. 1999; Piepenburg et al. 2001), especially depth and substratum, food (Tyler and Zibrowius 1992; Thurston et al. 1994; Bett et al. 2001; Billett et al. 2001) or a combination of these factors (Lauerman et al. 1996) are cited as the main factors driving megabenthic distribution.

Megafaunal organisms are important in the biological mixing of sediments with foraging and feeding by deposit feeders being the dominant mode of benthic sediment particle displacement (Turnewitsch et al. 2000). The term *Lebensspuren* (German, life traces) describes the physical manifestations of benthic animals in sediments, these are also called traces (Gage and Tyler 1991). Throughout the history of deep-sea photography the prevalence of *Lebensspuren*, rather than the benthic animals themselves has been noted (Ewing et al. 1967; Heezen and Hollister 1971; Bett et al. 1995). It has been estimated from seabed photographs that roughly 7% of the sediment surface on the continental slope is visibly disturbed by traces and about half this value in the abyss (Laughton 1963). This estimate is based on photographs covering a square metre or more. Gage and Tyler (1991) show that at the microscale an even more dynamic landscape exists, indicating almost continuous disturbance.

DEEP-SEA SAMPLING

Traditional methods

Qualitative ecological information has been obtained for megabenthos in the polar seas, as elsewhere, by the traditional use of trawling and dredging techniques (e.g. Galeron et al. 1992). However, as a result of the relative inaccessibility of these environments there are few quantitative data with sufficient spatial and temporal coverage to yield a meaningful description of community structure (Lauerman et al. 1996). In particular the quantification of megabenthos has proven difficult as, depending on the species, they may be sparsely distributed, fragile or highly mobile.

Barthel and Gutt (1992) state that although dredge hauls in deeper water normally provide the material necessary for species identification, organic substance determination and coarse dominance and abundance information much valuable biological information is lost that could be obtained from underwater photographs such as habitat preference, association with other (especially motile) fauna and small and medium scale patchiness. Hedgpeth (1971) shows that a combination of the two approaches results in a better appreciation of the true situation.

A number of previous, mostly deep-sea studies have shown that biomass and abundance calculations for macro- and megafauna based on phototransects yield much higher values than those based on trawls and dredges (McIntyre 1956; Aldred et al. 1979; Ohta 1983).

Photography

History of use

The first photographs taken of the benthic environment were of the sunlit Mediterranean seabed in 1893 (Boutan 1893), after which followed an explosion in the use of underwater photography in shallow seas, opening up this environment to a wider public (e.g. Cousteau and Dugan 1963). Deep-sea photography started in the 1940s at the Woods Hole Oceanographic Institution by a group led by Maurice Ewing (Ewing et al. 1946; Ewing et al. 1967). The cameras developed by this group photographed the sea floor when triggered by contact with the bottom (Thorndike 1959). Schenck and Kendall (1954) discuss underwater photography in these early days and provide a bibliography of the older literature.

Whilst there were many good deep-sea photographs available between the 1950s and early 1970s few biologists studied them, often as no corresponding samples of animals were taken, making identification difficult (Fell 1967). However, there were a few notable exceptions who carried out detailed investigations using seabed photography during this period (Vevers 1951; Fell 1962; Clark 1963; Marshall and Bourne 1964; Hersey 1967; Heezen and Hollister 1971). After this, photography became established as an important tool for the study of the deep-sea environment (Grassle et al. 1975; Rowe et al. 1986; Smith et al. 1993; Thurston et al. 1994; Lampitt et al. 2001).

Photographic techniques

The development of photographic techniques has enabled quantitative data to be obtained on the spatial and temporal abundances and distribution of megabenthic fauna. On a smaller scale from surveys taken by free-fall cameras ‘bounced’ along the seabed (Gage and Tyler 1991) or deployed on the seabed for long periods, taking photographs at regular intervals e.g. ‘Bathysnap’ (Lampitt and Burnham 1983). On a larger scale photographic surveys have been made by towed camera sleds which may be towed over the sediment (e.g. Rice et al. 1982; Cailliet et al. 1999) or using acoustic telemetry, fly at a set altitude e.g. Wide Angle Survey Photography (WASP) system (Bett 2001); manned submersibles (Grassle et al. 1975); Remotely Operated Vehicles (ROV) (Starmans et al. 1999) and with the development of Autonomous Underwater Vehicles (AUV) e.g. Autosub (Babb 1993) previously inaccessible environments can be sampled.

Photographic techniques as tools for ecological assessment

Freefall cameras

Freefall camera systems were the first photographic tools for deep-water ecological assessment (Hersey 1967; Heezen and Hollister 1971). They have been used extensively in the deep sea (Menzies et al. 1973; Rowe and Sibuet 1983; George et al. 1985) with the more recent models typically depicting a small area of seabed and allowing identification of organisms down to 1mm (e.g. Piepenburg and Schmid 1997). They provide a quantitative quadrat type sample although the area covered, even by systems bounced along the seabed is typically very small. These camera systems have been important in the study of all deep-sea environments (Hersey 1967; Heezen and Hollister 1971; Menzies et al. 1973; Langton and Uzmann 1989; Gutt and Starmans 1998; Gutt et al. 1999). Freefall cameras have also been used to get the first impressions of life under ice shelves (Lipps et al. 1979; Dayton and Kooyman 1985) although these studies are based on very few often unclear photographs. These systems, equipped with high resolution 70mm cameras have been used extensively in the polar regions to increase the information available on these important megafaunal communities (Piepenburg and Schmid 1996b; Piepenburg and Schmid 1997; Gutt and Starmans 1998; Gutt and Starmans 2001; Piepenburg et al. 2001).

Time-lapse cameras

Time-lapse cameras, typically deployed on benthic landers provide a quantitative photographic sample of a small area of benthos over a typically long time period (Bett 2003). Previously unknown important temporal variations in megabenthic abundance have been discovered using this method, for example using the SOC 'Bathysnap' time-lapse camera Bett et al. (2001) reported a radical change in the abundance and activity of megabenthos on the Porcupine Abyssal Plain, northeast Atlantic.

Towed cameras

Towed camera systems provide a quantitative picture of a relatively large area of the benthic environment and can be used for transect type biological studies (Rice et al. 1982; Holme and McIntyre 1984; Wakefield and Smithey 1989; Hecker 1990; Christiansen and Thiel 1992). They typically lack the resolution of the freefall cameras although good results have been obtained from sledge type cameras. Towed camera platforms are used particularly for geological studies (Kleinrock et al. 1992) and were instrumental in the location of hydrothermal vents (Lonsdale 1977b; Lonsdale 1977a), biological studies are less common. Most studies concentrate on the distribution and abundance of megafaunal organisms for example in the abyssal northeast Pacific (Lauerman et al. 1996), towed camera platforms have also been used to investigate Lebensspuren on the sea floor (Bett et al. 1995).

Submersibles

Manned submersibles have been used extensively for the study of deep-sea benthic fauna. Many of these studies have included some photographic sampling of the benthos along the submersible track. Grassle et al (1975), in one of the most comprehensive submersible photographic studies, investigated the pattern of distribution of benthic megafauna along the well-studied Gay Head-Bermuda transect and provides detailed descriptions of the highly variable megafauna and their distribution patterns.

ROVs

Remotely Operated Vehicles are becoming increasingly used in deep-sea research and industry. All are equipped with video systems and often still cameras that can be used in ecological studies of the seafloor. Real time control of the vehicle allows different survey strategies to be employed (Barry and Baxter 1992), verification of species and observations of behaviour (e.g. Hudson and Wigham 2003) to occur. Several polar studies have used ROVs in a similar way to a towed camera platform to investigate megabenthic diversity (Starmans et al. 1999; Gutt and Starmans 2003). An increasing number of biological studies are using ROVs to undertake structured megabenthic survey (Barry and Baxter 1992; Starmans et al. 1999; Gutt and Starmans 2003; Jonsson et al. 2004) and investigations into polar megabenthos (Hamada et al. 1986; Barthel et al. 1991; Stein et al. 2005).

AUVs

Several Autonomous Underwater Vehicles have been fitted with camera systems although the technology is not fully developed for imaging, the potential of AUVs for biological survey is great. AUVs will be able to cover large distances and conduct detailed biological surveys in the open ocean as well as in habitats that were previously inaccessible such as the benthic environment under ice.

Video

Video has been used as an important tool for the study of deep-sea megabenthos (George et al. 1985; Christiansen 1993; Starmans et al. 1999; Starmans and Gutt 2002; Gutt and Starmans 2003). It is used more widely in shallow water, particularly in the study of benthic communities on coral reefs (Leonard and Clark 1993; Carleton and Done 1995; Aronson and Swanson 1997) as it allows a wide swathe of benthos to be recorded quickly and by operators with limited identification skills (Ninio et al. 2003). Despite the continuous coverage of video it has an inherently lower resolution than photographs (Carleton and Done 1995). It is often combined with photography in the deep sea to provide a combination of detail and areal coverage (Bett 2001) or to direct the camera to the most suitable location.

Limitations of photography

Although photography can be a very important tool for the study of megabenthos in the deep sea it is worth bearing in mind that it has inherent problems. Photographs only show the epibenthic megafauna, burrowing forms are not seen or at least undersampled. Estimates of burrowing megafaunal abundance from *Lebensspuren* (e.g. Ewing and Davis 1967) makes many unfulfilled assumptions and may be misleading (Owen et al. 1967; Holme and McIntyre 1984). Photographic samples of motile fauna are also likely to be poor estimates as many will undertake behavioural responses to the camera system and may be repelled from or attracted to it (Herring et al. 1999). Species identification is also a problem especially in photographs of poor resolution. The solution adopted by many workers is to take concurrent trawl samples (e.g. Piepenburg and Schmid 1997).

Work in the Polar Regions using deep-sea photography

Photographs of the Antarctic sea floor were first published by Bullivant (1959) showing massive sponge formations on the Ross Sea floor. At a similar time Hunkins et al. (1960) published biological observations based on the first photographs of the deep Arctic Ocean floor. Early deep-water polar photographic megafaunal studies have been reviewed by Menzies (1962). Since then there have been several megafauna community studies in polar shelf areas using underwater photography (Simmons and Landrum 1973; Brunchhausen et al. 1984; Christiansen 1993; Pogrebov et al. 1994; Piepenburg and Schmid 1997; Gutt and Starmans 1998; Starmans et al. 1999; Sejr et al. 2000; Starmans and Gutt 2002; Barry et al. 2003). Elements of the ecology of several specific groups of polar megafauna have been investigated using photography, including Antarctic octocorals (Orejas et al. 2002), Antarctic shrimps (Gutt et al. 1991), Antarctic notothenioid fish (Ekau and Gutt 1991; Gutt and Ekau 1996; Gutt 2002), Arctic fish (Stein et al. 2005), Antarctic holothurians (Gutt 1988), Antarctic sponge associations (Barthel et al. 1991; Barthel 1992; Barthel and Gutt 1992) as well as the traces (*Lebensspuren*) that animals create on the seafloor (Hunkins et al. 1960; Kitchell et al. 1978; Kitchell and Clark 1979). Photography has also been used to investigate the effects of physical and biological factors on the polar benthos, for example, Antarctic epibiotic relationships (Gutt and Schickan 1998) and the impact of iceberg scouring on polar benthos (Gutt et al. 1996; Gutt and Piepenburg 2003; Teixido et al. 2004).

SITES OF INTEREST

The polar environment

The Antarctic and Arctic regions are both sited over the geographical poles, hence are subject to extreme seasonal variation in solar radiation; both are cold, receive relatively little precipitation and are dominated by ice. Despite this the differences between the regions are considerable, the Arctic is predominantly a landlocked basin allowing only a limited exchange of water with adjacent oceans and receiving an enormous amount of freshwater and sediment. The Antarctic is a single landmass isolated on all sides by deep oceans. The two areas are also very different in their tectonic and evolutionary history (Clarke 1996).

ARCTIC

Arctic bathymetry

The Arctic Ocean (Figure 1.3) surrounds the North Pole and is bordered by Europe, Siberia, Alaska, Canada and Greenland. It is essentially a landlocked ocean, with limited exchange with the Atlantic and Pacific through shallow sills. The Arctic basin is divided by the Lomonosov Ridge (with a crest depth of between 850 and 1200m) into two major basins, the Amerasian and Eurasian Basin. The Amerasian Basin is bounded by the East Siberian, Chukchi and Beaufort Seas and the Canadian Arctic Islands, and is subdivided by the Alpha Cordillera (crest depth around 1000m) into two basins, the large Canada Basin and the smaller but deeper Makarov Basin (Paul and Menzies 1974). The Eurasian Basin is divided by the Nansen-Gakkel Ridge which separates the very deep Fram (or Amundsen) Basin from the Nansen Basin (Clarke 2003).

Arctic benthic environment

The study of Arctic deep-sea sediments has been limited as a result of sampling difficulties. The limited data available are predominantly from samples taken beneath drifting ice stations almost exclusively west of the Lomonosov Ridge (Clarke 2003). From the presence of larger grain sediments in photos (Clarke 2003) and geophysical investigation (Dowdeswell et al. 1997) of the Arctic deep sea, ice rafting of material would appear to be important. The importance of ice rafting is currently unquantified, but the content of ice rafted material in sediments of the Arctic abyssal plain has been put at 60-70% (Darby et al. 1989). Unlike the Antarctic, there is a significant contribution to the sediments of the Arctic from riverine sediments. These are carried into the Arctic Ocean predominantly during the summer continental melting period. There is evidence that turbidity currents are important in transporting sediments from the continental shelves on to the deep basins (Clarke 2003).

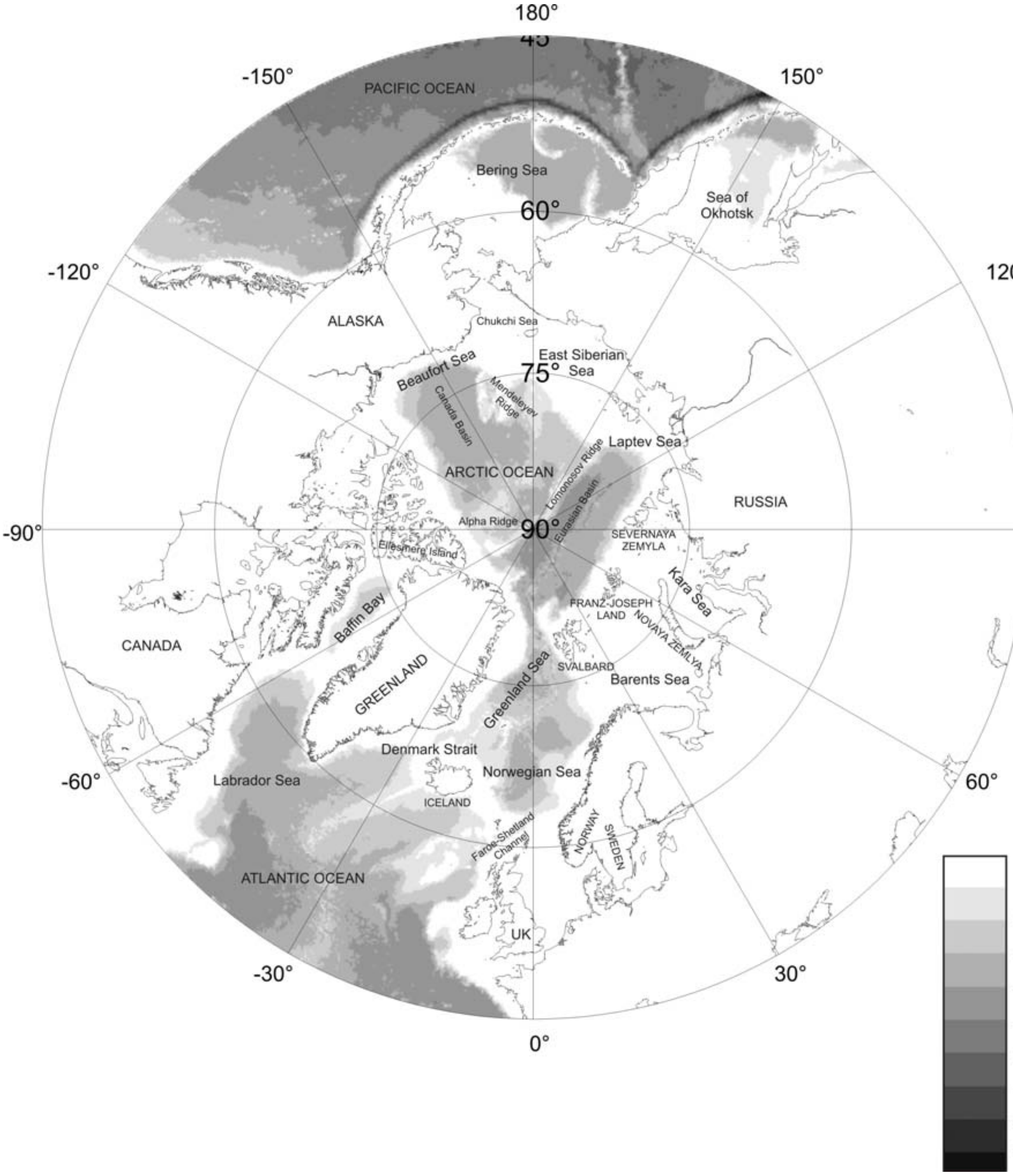


Figure 1.3: Map showing the bathymetry of the Arctic and adjacent oceans (45° N - 90°N).

Arctic primary production

The perennial ice-cover of the Arctic Basin, and the freshwater lens at the surface together reduce primary productivity in the water column and also make it difficult to measure (Clarke 2003). In a thorough survey of primary production in the Arctic Ocean, Andersen (1989) gave estimates of annual water column productivity varying from <5 g C m^{-2} y^{-1} beneath ice to 15 g C m^{-2} y^{-1} in the central Arctic Basin. Longhurst (1998) gives monthly estimates of surface productivity from satellite data ranging from 3 to 80 gC m^{-2} month^{-1}.

Arctic seawater characteristics

Analysis of temperature, salinity and stability of the water column are used to separate the water in the central Arctic Ocean into three basic water masses (Sater 1969). The bottom water from about 900m to the bottom is characterised by almost constant salinity (34.93 to 34.99), nearly uniform temperature (-0.3 to –0.4°C) and dissolved oxygen values between 6.0 to 6.5 ml/l (Paul and Menzies 1974). Circulation of the bottom water is virtually unknown although it is thought that significant but slow currents exist to the bottom (Coachman and Aagaard 1974).

Arctic ice

In contrast to the Antarctic, where variation in sea ice cover is around 75-80%, in the Arctic the variation is substantially less at about 20-25%. Thus while Antarctic multiyear ice is relatively rare and thin (1-2m thick), in the Arctic most of the ice remains for several seasons and becomes quite thick (2-4m) (Foster 1984). Multi year ice covers much of the Arctic basin, of the 6.2×10^{6} km^2 of permanent ice cover, most is multi-year ice (Gloersen et al. 1992). Around the margins the ice grows and melts seasonally, with significant quantities carried into the North Atlantic on the East Greenland Current. Passive microwave data from satellites indicate that the area of seasonal ice in the Arctic Basin averages 0.88×10^6 km^2 (Clarke 2003). Icebergs are common (Dowdeswell and Forsberg 1992; Dowdeswell et al. 1992), formed from the numerous glaciers that feed into the basin and as a result are generally smaller than the Antarctic icebergs which typically break off the ice sheet. Icebergs are produced at a rate of approximately 280 cubic km per year in the Arctic and 1,800 cubic km in the Antarctic (Orheim 1985).

ANTARCTIC

Antarctic bathymetry

The bathymetry of the Southern Ocean (figure 1.4) reveals three deep basins that surround Antarctica: the Atlantic-Indian Basin, the Southern Indian Basin and the South-east Pacific Basin. These basins are partially bounded on the north by the Scotia Ridge and the Atlantic-Indian ridge, the South-east Indian Ridge and the Pacific-Antarctic Ridge respectively. These ridges and the Kerguelen Plateau tend to prevent the free flow of bottom waters and may also deflect the surface currents. The Drake Passage between South America and the Antarctic peninsula is the major constriction to the circulation around

Antarctica and has an important influence on the oceanic circulation (Foster 1984). The continental shelves around Antarctica are unusual, compared to other continents, in being deep, typically as much as 800m in places. This is primarily the result of the isostatic depression of the continent as a whole resulting from the mass of the polar ice cap (Clarke 1996). Although the continental shelf around Antarctica is generally narrow (Dell 1972), in the Weddell and Ross Seas there are very broad shelves with depths ranging from 400-500m. These deep shelves may have resulted from isostatic adjustment of Antarctica to its massive icecap and from scouring by the Filchner Ice Shelf in the Weddell Sea and the Ross Ice Shelf in the Ross Sea, where their extent was much further north in the past. This results in a near shore circulation that can be expected to be quite different from that at lower latitudes (Foster 1984).

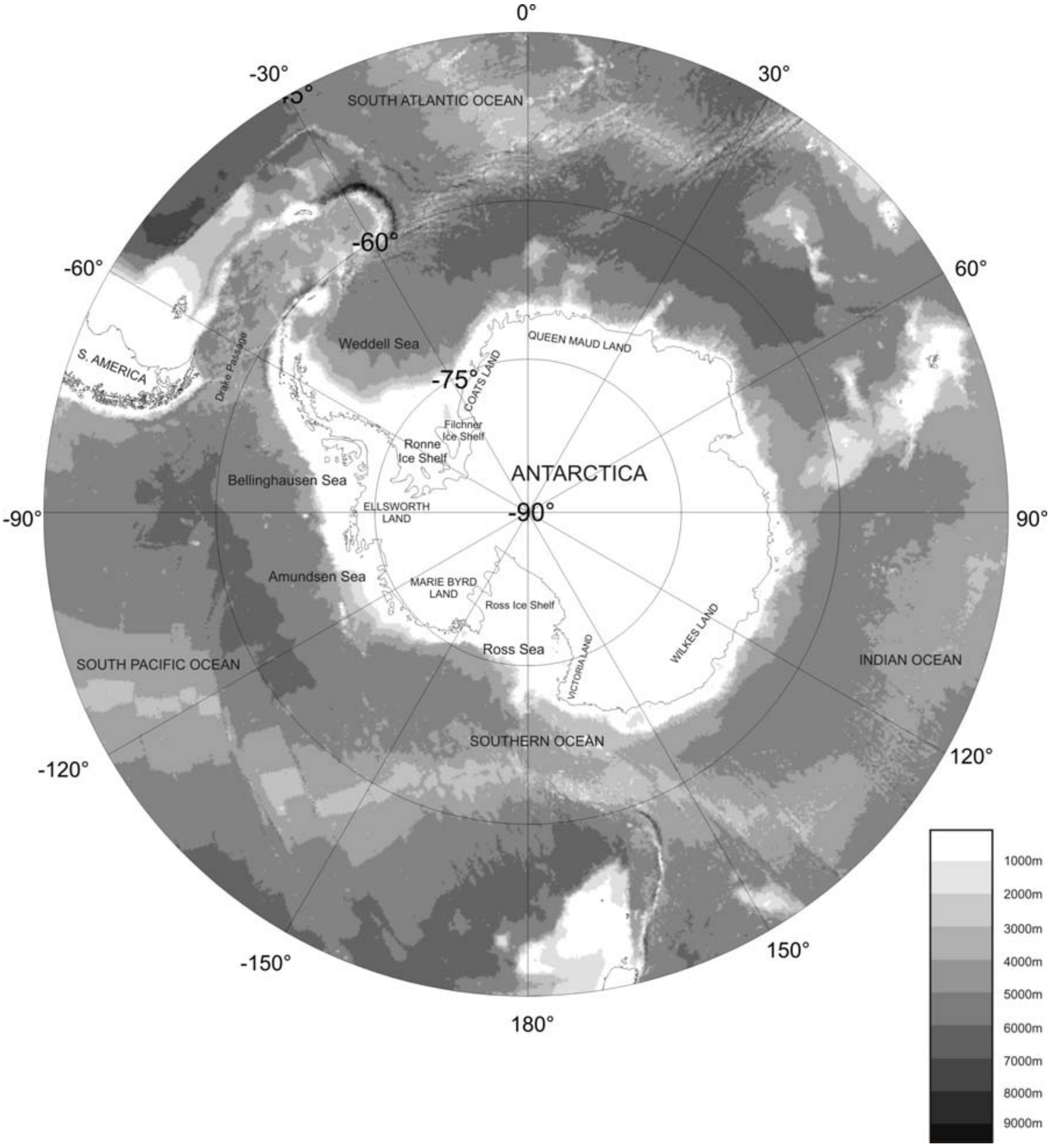


Figure 1.4: Map showing the bathymetry around Antarctica (45° N - 90°N).

Antarctic benthic environment

The sediments found close to the Antarctic continent contain an abundant silt fraction comprised of rock flour with coarse, poorly sorted debris, and containing little calcite or biogenic material. These glacial marine sediments form a wide circumpolar band around Antarctica, which can be divided, into four roughly concentric zones, distinguished on textural grounds, with a decrease in the amount of coarse material with increasing distance from the continent. The northernmost limit of these glacial marine sediments is related to the surface 0°C isotherm, which influences the rate of iceberg melting (Clarke 1996). Icebergs are the major route for ice-rafted sediment transport in Antarctica, transporting 0.5×10^9 tons per year (Knox 1994). This is unlike the Arctic where sea ice is more important for moving terrigenous material. This is not the case in Antarctica, as the extensive development of ice-shelves essentially precludes the capture of sediments by sea ice. Ice shelves also greatly reduce the importance of riverine and aeolian (wind-driven) input into the marine system of the Antarctic compared to the Arctic (Clarke 1996).

Most of the Southern Ocean overlies the abyssal plain (Clarke 1996). The abyssal plains around Antarctica, like those of elsewhere, are composed primarily of soft sediments. However, they differ from those of elsewhere in two ways: the surface waters are of low temperature resulting in siliceous rather than more typical carbonate sediments, and there is a strong influence of glacial processes (Clarke 1996). Large ice rafted boulders (drop stones) are important in providing isolated patches of hard substratum on the otherwise soft abyssal plain of the Southern Ocean. The concentration of these drop stones is thought to decline with distance from the ice front and their distribution will influence the colonisation dynamics of some encrusting taxa in the Southern Ocean. Little is known on either the distribution or fauna of these drop stones (Arntz et al. 1994; Clarke 1996).

Primary production is highly seasonal, with a major input in spring and a smaller one in the autumn (Picken 1985) This is in line with most biological activity in the water column where most activity is restricted to a short period in spring and summer which starts with the melting of the pack ice. Related sedimentation of organic matter to the seafloor reflects this situation, with available data suggesting a strong vertical flux after the primary production phase (Arntz et al. 1992). The vertical flux of organic matter from surface waters links benthic habitats to processes in the overlying water column. Local hydrography is critical to this benthic-pelagic coupling. There have been few studies of the hydrography of direct relevance to benthic habitats in Antarctica (Clarke 1996).

In the Antarctic benthic environment there are low but stable temperatures, both the mean annual temperature and the extent of annual variation are supposed to increase from the Antarctic continent out towards the Antarctic Convergence (Clarke 1988). In McMurdo Sound, as an extreme example (Arntz et al. 1994), the annual temperature range, at 585m depth, is ±0.07°C around an average of 1.89°C (Picken 1985). Although water temperatures on the shelf do not show pronounced seasonal variations, at greater depths oscillations are common in the bottom water, for example in the Weddell Sea temperatures oscillate between –1.8°C and +0.4°C. This is owing to deep, warm water regularly advancing into the shelf areas (Arntz et al. 1992).

In the Antarctic deep sea there are low fluctuations in salinity (Arntz et al. 1994). The normal range in the benthic realm is 34.6-34.9 (Lipps and Hickman 1982). There are exceptions in shallow water owing to melt water inflow, tides and currents, which can cause substantial variations in salinity (Arntz et al. 1994).

Antarctic primary production

Longhurst (1998) gives monthly estimates of surface productivity from satellite data as ranging from 1 – 60 gC m^{-2} $month^{-1}$ for the Austral Polar Province located within the Antarctic Divergence (~65°S) although for several months this region is ice covered.

Antarctic ice

Although the general distribution of the sea ice in the Southern Ocean has been known for some time (Foster 1984), modern satellite imagery has provided continuous year round observation of the detailed changes that take place on the pack ice (e.g. Murphy et al. 1995). Antarctic ice does not grow and decay in a simple north-south progression and regression (figure 1.2). It proceeds irregularly especially in the areas of the Ross and Weddell Sea regions. In the Weddell Sea the pattern of growth and decay is strongly influenced by both oceanic and atmospheric circulation. In the north, the extension of the ice edge is a result of ice from the western Weddell Sea being carried around to the east. The rapid decay of ice in the south-east is caused by warmer water entering the region

(Foster 1984). The Antarctic sea ice shows a rapid growth in the austral spring and more rapid decay in early austral summer. There is a 75-80% variation in the area of sea ice cover from a maximum in August-October to a minimum in February-March although it is thought that the variation in sea ice mass will be larger (Foster 1984). In the Ross and Weddell sea the ice sheets which extrude from the continent float on the ocean forming the extensive Ross, Filchner and Ronne Ice Shelves (Foster 1984).

The movement of icebergs is one of the most important factors influencing the ecology of many shallow water polar benthic communities (Gutt et al. 1996; Conlan et al. 1998; Peck et al. 1999; Gutt and Starmans 2001). Although the majority of effects are in shallow waters Antarctic tabular icebergs can impact on the seabed at depths ≤ 600m (Gutt and Starmans 2001).

The importance of sea ice which is obvious for life in the water column and for seasonal changes in phytoplankton (Spindler 1990) is generally hypothesized for the benthos underneath (e.g. Picken 1985) but has rarely been measured quantitatively (Dayton 1990). Arnaud and Hain (1992) found highest values of benthic species richness in the Weddell Sea near the ice-shell edge and from the rise of the shelf to some 800 m on the slope although the opposite trend was observed for biomass.

FAROE SHETLAND CHANNEL (FSC)

FSC bathymetry

The Faroe-Shetland Channel is a deep basin separating the Faroese plateau from the Scottish continental shelf (Figure 1.5); it narrows southward from about 190 km wide at 62° 30' N to 90 km wide at 60° N. It is bounded to the south by the complex of the Wyville Thomson Ridge (approx. 450m deep) and the Faroe Bank. At its northern entrance (1500-2000m deep), it is connected to the Norwegian Sea (Turrell et al. 1999). In the southwest the Faroe-Shetland Channel along with the Faroe Bank Channel connect the deep Norwegian Basin to the Icelandic Basin. These channels and others allow the cold, subzero temperature, Norwegian Sea Deep Water to enter the Atlantic (Bett 2001).

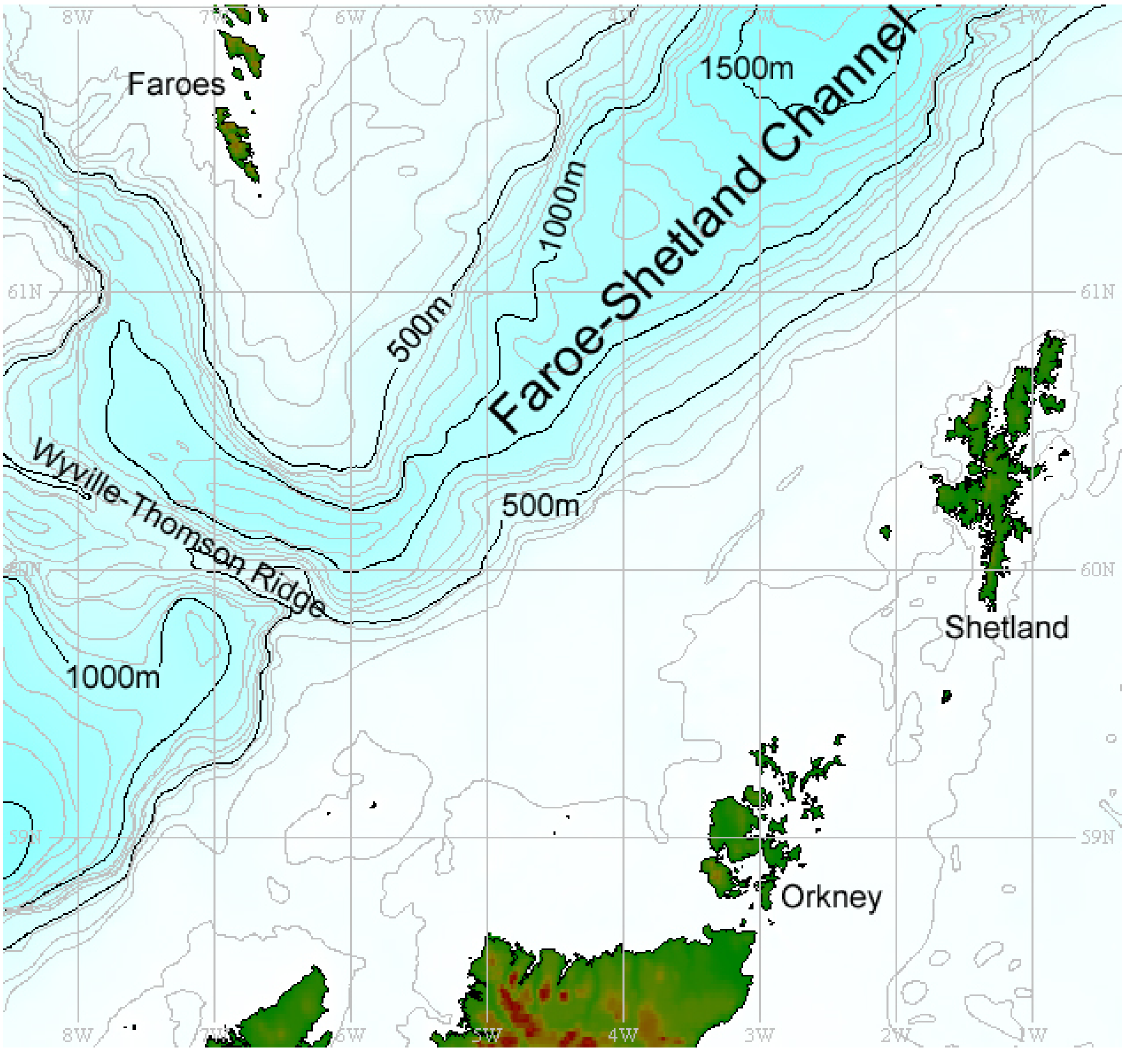


Figure 1.5: Bathymetry of the Faroe-Shetland Channel.

FSC hydrographic regime

The hydrographic regime of the Faroe-Shetland Channel is complex with warm North Atlantic waters overlying the cold water flows from the Norwegian Sea (Turrell et al. 1999; Bett 2001). The surface waters (0-400m), are warm (>8°C) North Atlantic Water, these overlay cold (-2 to 5.5°C) Arctic Intermediate Water (400-600m), Norwegian Sea

Arctic Intermediate Water (-0.5 to 0.5°C in 600-800m) and Faroe Shetland Channel Bottom Water (approx. -1°C and below 800m). It has recently been shown that contrary to previous beliefs, there is a marked decadal variation in the properties of these water masses (Turrell et al. 1999). The temperature regime of the eastern Faroe-Shetland channel shows a very distinctive drop in temperature with depth (figure 1.4).

Short scale fluctuations in the depths of isotherms occur in the Faroe-Shetland Channel, these internal tides are wave-like oscillations of isotherms within the channel. The deep water thermocline (between water of 6 and <0°C) at 550m depth in the southeastern part of the channel can vary in depth by more than 40m during a tidal cycle (Sherwin 1995). The internal wave propagates northeastwards along the channel at speeds of 0.6ms^{-1} and can cause strong currents to the benthic environment which have been observed by submarine (Sherwin 1995) and very rapid large changes in temperature. These internal tides cause the transition zone of the benthos between the cold arctic bottom water and the more normal temperature water to become extended.

Currents in the upper water mass of the Faroe Shetland Channel are typically 30 to 60 cm s^{-1} towards the northeast, and in the lower water mass 10 to 20 cm s^{-1} towards the southwest (Saunders 1990). Sediment bedforms observed on the upper slope allow estimates of currents in the range 40 to >75 cm s $^{-1}$ (Kenyon 1986).

Longhurst (1998) gives monthly estimates of surface productivity from satellite data as ranging from 1 – 65 gC m^{-2} month^{-1} for the Atlantic Subarctic Province. Ship-board measurements of primary production revealed rates of 1.2 - 3.8 gC m^{-2} day^{-1} although these were associated with spring bloom conditions (Riegman and Kraay 2001).

FSC benthic environment

Using deep towed (TOBI) and sidescan sonar Masson et al. (2000) investigated the seabed of the Faroe Shetland Channel. Bett (2001) divided their findings into five main sediment type bands:

- Outer continental shelf (120-200m), having a variable cover of sand overlying a gravel substratum.
- Iceberg ploughmark zone (<200-500m), ploughmarks dominate this zone although few now have any topographic relief
- ‘Sediment wave’ zone (approx. 500-850m), a relatively featureless zone with long wavelength sediment waves.
- Ultra-low backscatter zone (approx. 500-850m), an unusual zone of extremely low backscatter that appears to correspond to a sandy contourite sheet.
- Faroe-Shetland Channel floor (>1000m), a relatively featureless mud, muddy sand and gravel zone with a general decrease in grain size to the northwest.

In general the sediment type varies with depth, grading from coarse sands on the shelf edge to finer sediments on the floor of the Faroe-Shetland Channel (Bett 2001).

POLAR MEGABENTHOS

Arctic megabenthos

Photographic analyses of the deeper water Arctic megabenthos are relatively sparse although there have been some studies in the deep Norwegian fjords (Christiansen 1993), the waters off northeast Greenland (Starmans 1997; Starmans et al. 1999; Starmans and Gutt 2002), the waters around Svalbard (Piepenburg et al. 1996) as well as the Arctic north Atlantic (Piepenburg et al. 2001) and some shallower water studies in the Barents Sea shelf and the high Arctic Laptev Sea (Piepenburg et al. 1995; Piepenburg and Schmid 1996a; Piepenburg and Schmid 1997).

Species richness and biodiversity

Curtis (1975) shows a higher relative importance of deposit feeding organisms in the Arctic shelf seas than in other marine areas at comparable depths and sediment type. This is illustrated by the higher proportions of deposit-feeding taxa within the polychaetes and bivalves typically found at higher latitudes (Rasmussen 1973). On the other hand the most abundant species found by Paul and Menzies (1974) in the high Arctic deep sea were sessile suspension feeders which was expected in oligotrophic regions characterized by low sedimentation rates and small quantities of deposited organic material. The distribution of shelf megafauna off northeast Greenland could be explained by water depth alone, but also similarly with a combination of water depth and latitude (Starmans et al. 1999). This megabenthic gradient from suspension feeder dominated assemblages to those with higher numbers of detritus feeders has also been shown in the Antarctic although there is a less pronounced depth zonation on the high Antarctic shelf compared to the Arctic (Gutt and Starmans 1998; Starmans et al. 1999).

Species diversity for the high Arctic was found to be low (H′ = 0.44 - 1.66) by Paul and Menzies (1974) suggesting that the Arctic ecosystem is young (Margalef 1968). A particular reduction in Arctic epifaunal species diversity was found by Thorson (1957) compared to warmer seas. Using evidence from a number of sources, Curtis (1975) shows the largest number of species are found in areas of mixing between cold polar and non-polar waters, such as occurs around the Faroe Shetland Channel (Bett 2001; Narayanaswamy et al. 2005).

Distribution and zonation

Many of the benthic invertebrates occurring in the northern seas are not limited to Arctic or sub-Arctic habitats, but may also be found in adjacent parts of the North Atlantic and North Pacific. While some species are circumpolar in distribution, others are global. There are several exclusively Arctic or sub-Arctic species, but these do not form the majority of any taxonomic category (Curtis 1975).

Analysis of the benthic species distribution by Starmans et al. (1999) revealed a conspicuous depth zonation in the fauna off northeast Greenland. Similar bathymetric zonation patterns in the same area have been reported for the megafauna, epifauna and selected species by a number of authors (Piepenburg and Schmid 1996b; Piepenburg et al. 1997b; Starmans et al. 1999). The results of these studies show that deeper stations tend to have high numbers of taxa but low abundances while the shallower stations showed the opposite trend.

Faunal densities and biomass

Using trawls and cores to study the benthic ecology of the high Arctic deep sea, Paul and Menzies (1974) found extremely low biomass values of 0.04gm^{-2} in the Amerasian Basin at depths of 1000-2000m which is comparable to the oligotrophic mid-Pacific at depths of 5000-6000m. In a review, Curtis (1975) shows a sharp decline of biomass with depth in Arctic areas, with deeper areas (>100m) having a biomass of a few tens of grams per m^2. Higher biomass values than this are most frequently encountered on coarser, more rocky substrata in areas of relatively strong current flow, where larger epifaunal organisms dominate the benthos. The relative abundance of various taxonomic groups in different habitats also offers a useful perspective on trophic relationships in the Arctic benthos. Over most of the northern continental shelves ophiuroid echinoderms, polychaetes and occasionally bivalves dominate the offshore benthic biomass (Curtis 1975) although sponges have also been shown to be important in the Norwegian-Greenland sea as well as other parts of the Arctic basin (Barthel and Tendal 1993). The dominance of echinoderms, particularly ophiuroids, in stations off northeast Greenland has been reported in a recent study by Starmans et al. (1999) and agrees with previous studies in Arctic regions (Carey 1991; Piepenburg and von Juterzenka 1994; Piepenburg et al. 1996; Piepenburg and Schmid 1996a; Bluhm et al. 1998).

Antarctic megabenthos

In the Antarctic deeper water photographic studies of megabenthos have concentrated in the Weddell Sea (Starmans 1997; Gutt and Starmans 1998; Starmans et al. 1999; Starmans and Gutt 2002) with several additional studies concentrating on specific megafaunal groups e.g. fish (Ekau and Gutt 1991; Gutt et al. 1994) and sponges (Barthel and Gutt 1992). The benthos under the Ross Ice Shelf has also had some preliminary photographic studies (Lipps et al. 1979; Dayton and Kooyman 1985). The megabenthos of the Antarctic have been studied in more depth using trawls, again most deeper studies are concentrated in the Weddell Sea (Voss 1988; Hain 1990; Arnaud and Hain 1992; Galeron et al. 1992; Piepenburg et al. 1997b).

It would seem that caution should be exercised in the generalisation of the Antarctic zoobenthos (Clarke and Crame 1989; Gutt 1991; Arntz and Gallardo 1994). Some groups, such as sessile suspension feeders (sponges, bryozoans), motile epibenthos (amphipods) and taxa which cover a wide range in terms of mobility and trophic function (polychaetes) are rich in species; others seem to occupy an intermediate level (bivalves, gastropods, isopods) and some are missing altogether (stomatopods) or restricted to a few representatives (cirripedes and decapods where reptants are totally absent from the high Antarctic) (Arntz and Gallardo 1994). For the species that live in Antarctic waters, Arntz et al. (1997) confirm a high level of endemism in most groups.

Species richness and biodiversity

Using the best estimates for the biodiversity of the Southern Ocean from Arntz et al. (1997) and comparing these with the estimated marine species numbers in the worlds oceans from Winston (1992, table 10.1), reveals that most of the Antarctic higher taxa provide between 3 and 7% of the worldwide marine species number of their respective group. Only pycnogonids and priapulids have much higher values. Three to seven percent is less than the share of the Southern Ocean in the world ocean; the area covered by pack ice in winter alone exceeds 10% of the world ocean surface (Laws 1989). However the data presented by Winston (1992) have been derived from actual knowledge of shelf species, whereas shelf areas of the same depths are relatively scarce in Antarctica under present geological conditions (Arntz et al. 1997). These figures are likely to change in the future with more research into species diversity in the Antarctic.

For the species that live in Antarctic waters, Arntz et al. (1997) confirm a high level of endemism in most groups. Endemicity values of taxa may reflect environmental changes in the past and both duration and degree of isolation from other biogeographic zones. If marked environmental changes such as the advance and retreat of ice shelves coincide with isolation, as is suggested for the Antarctic, allopatric speciation may be favoured, leading to adaptive radiation into groups with many endemic species. Levels of endemism are thus helpful in explaining the great differences in species richness found among Antarctic taxa (Arntz et al. 1997). The ice shelf processes that favour species formation must also have caused extinctions of many species as well. This may be the reason why taxonomic diversity is not higher in most cases (Arntz et al. 1997).

The epifaunal suspension feeder communities found on the Antarctic shelf have been considered rich in species and diverse (Dearborn 1968; Dell 1972) and can be compared, in terms of total species numbers within assemblages, with tropical or subtropical seagrasses (Gambi et al. 1992; Mazella et al. 1993) or even with coral communities (see Gutt 1991), both of which are also three dimensional.

The Antarctic marine system as a whole seems to have a lower percentage of species known to date in most higher taxa than would be expected from its share of the area of the worlds oceans. However, comparison with other marine ecosystems is difficult because of differences in area, environment, sampling and processing and taxonomic knowledge. Comparison with the Arctic Ocean indicates that species numbers of most groups are much higher in Antarctic waters, but many more comparable data are needed to judge whether this also holds generally true for diversity, and whether large-scale latitudinal gradients exist for more than a few groups (Arntz et al. 1997).

Distributions and zonation patterns

The South Polar Sea, like other marine ecosystems, reveals distinct differences between its various subsystems: in shallow water, on the deeper shelf and slope and in the deep sea. These systems do, however, show a surprising number of eurybathic species. The intertidal and upper sublittoral levels are highly impacted by ice. The richest communities, mostly dominated by sessile suspension feeders, are found on the deeper shelf and the upper slope. The deep sea does not appear to be very different from other deep-sea areas of the worlds ocean, although, sampling in that area has been very limited and further sampling may provide new evidence (Arntz et al. 1997).

Faunal densities, biomass and productivity

Densities in most Antarctic benthic communities, excluding those of shallow water, are the same order of magnitude as in similar marine communities in other areas, and are usually much below the numbers that are reached in temperate soft bottoms (Arntz et al. 1997). Only a single infaunal community in McMurdo Sound has been found to have exceptionally high density where densities of between 118712 and 155572 individuals m^{-2} have been reported (Dayton and Oliver 1977). Most other faunal abundances have been found to be 1 to 2 orders of magnitude lower (Muhlenhardt-Siegel 1988; Gerdes et al. 1992).

Densities and biomasses of macrobenthos are traditionally thought to be high in the Antarctic both on hard and soft substrata (White 1984; Clarke and Crame 1989) especially in comparison with the Arctic (Dayton 1990). Antarctic biomass can appear high, such as, in the epifaunal suspension-feeding communities (with an important share of silici- and calcimass) (Arntz et al. 1997), although not reaching the peak values found elsewhere such as in temperate mussel beds (Munch-Petersen and Kristensen 2001) or intertidal clam beds of upwelling regions (Arntz et al. 1987). Biomass seems comparatively low in most high Antarctic infaunal communities (Gerdes et al. 1992). However, Brey and Clarke (1993) state that average Antarctic benthic biomass is higher than that of temperate and sub-tropical communities. The distribution of both biomass and abundance values is highly patchy (Arntz et al. 1997). Biomass (wet wt.) values ranged between 0.12g and 1644.20g m^{-2} in the Weddell Sea (Gerdes et al. 1992) and between 9.06g and 57.13g m^{-2} in the Antarctic Peninsular/Scotia Arc area (Muhlenhardt-Siegel 1988). Antarctic biomass values are higher than those of the Arctic macrobenthos at similar depth (Brey and Clarke 1993).

For individual taxa or species, numbers and biomasses may differ greatly in the Antarctic benthos. Many species occur in particularly low numbers (Arntz and Gallardo 1994). Relatively high densities and biomasses have been reported for amphipods (Jazdzewski et al. 1991), limpets (Picken 1980) and scallops (Berkman 1990). Low mean values, but locally dense patches were seen in caridean shrimps (Gutt et al. 1991), holothurians (Gutt and Piepenburg 1991) and sponges (Barthel and Gutt 1992). Low values have been found for shelled molluscs in the Weddell Sea (Hain 1990), echinoderm predators in McMurdo Sound (Dayton et al. 1974) and the sea urchin *Sterechinus* sp. (Brey and Gutt 1991).

THE FAUNA UNDER ICE

As a result of the temporary extension and calving of icebergs, ice shelves have been shown to suppress the benthic fauna underneath and create unpredictable conditions (Arntz et al. 1994). There was no local primary productivity from algae under the Ross Ice Shelf, but bacterial densities and organic carbon were equivalent to deep-sea values. No benthic infauna was collected, although a motile faunal element, mostly crustaceans and several fish, under the ice shelf was found as much as 430km away from the ice edge, under 420m of ice and in a water depth of about 600m (Lipps et al. 1979; Brunchhausen et al. 1984; Dayton 1990; Arntz et al. 1994). The fish beneath the ice shelf may have fed on the abundant *Orchomene* amphipods (Brunchhausen et al. 1984) whereas a food source for the amphipods was less obvious. Their stomachs contained sediment, bacteria and small crustaceans. It is likely that as scavengers, they are dependent on occasional carcasses that get caught under the ice. This was investigated using baited traps, which have attracted several hundred of them (Stockton 1982).

Benthic life in the vicinity of the Ross ice shelf edge was found to be rich and varied, with species that were common even in areas with annual sea ice (Oliver et al. 1976). Samples taken in the southern Weddell Sea shortly after the calving of three large ice isles in 1988 by Gerdes and Gutt (unpublished) in an area formerly covered by the Filchner ice shelf revealed the existence of motile (amphipods, ophiuroids) and low numbers of sessile elements (tunicates, hydrozoans) (Arntz et al. 1994).

AIMS

The main objective of this study is to investigate the physical controls on polar megabenthic communities. This will be investigated by using deep-water imaging techniques to investigate community structure along physical gradients primarily in depth. In the high polar environments the extent and effects of disturbance effects from ice grounding on the megabenthic communities will be quantified. The effects of disturbance on cold water communities will be explored in more detail by investigating experimentally the outcomes of wide scale smothering of the seabed, as may occur in relation to ice disturbance. The results from this experimental approach will be used to facilitate understanding of processes that may explain observed patterns in the other studies. The effects of other factors will also be investigated where appropriate.

The major topics covered in this study are:

- Ecology of the deep Faroe-Shetland Channel: Arctic communities in a temperate setting.
- Experimental investigation of disturbance in the deep Faroe-Shetland Channel
- Arctic community ecology: patterns in the true Arctic, East Greenland
- Antarctic community ecology: patterns in the Antarctic

Through using a range of imaging techniques it will be possible to draw some conclusions as to the use of various photographic techniques in deep waters.

CHAPTER 2: MATERIALS AND METHODS

DATA COLLECTION

Photographic data were collected using the NOC WASP (Wide Angle Seadbed Photography) system, a Remotely Operated Vehicle (ROV) and the Autosub Autonomous Underwater Vehicle (AUV). Specimens, if obtained, were collected using ROV suction sampling (at Laggan; Chapter 4), Agassiz trawl (Greenland only; Chapter 5) and rock dredge (Greenland and Antarctic; Chapters 5 and 6).

WASP

The National Oceanography Centre (NOC) WASP (Wide-Angle Seabed Photography) system was used throughout this study in its standard configuration. Briefly, WASP (Figure 2.1) is a self-contained, off-bottom, towed camera vehicle that provides still and video footage of the seabed, and is capable of operation to 6,000m water depth on a simple mechanical cable (i.e. conducting or fibre-optic cable not required). As deployed, WASP was fitted with: OSIL Mk7 (stills) camera, OSIL 1200J flash gun, NOC OceanCam6000V (digital video) camera, 2 x 250W DSPL video lamps, 3 x DSPL 24V batteries, Simrad Mesotech 200kHz altimeter, and a NOC acoustic telemetry system (10kHz). Data from the altimeter are telemetered to a shipborne display enabling the operator to make fine adjustments of the amount of cable deployed with the aim of keeping the vehicle at c. 3m above the seabed. The still and video cameras are both automatically activated by the altimeter when the range to the seabed is <10m. For all deployments made during the cruises, the still camera was loaded with 30m of Kodak Vision 250D and the video camera loaded with a 63 minute MiniDV tape.

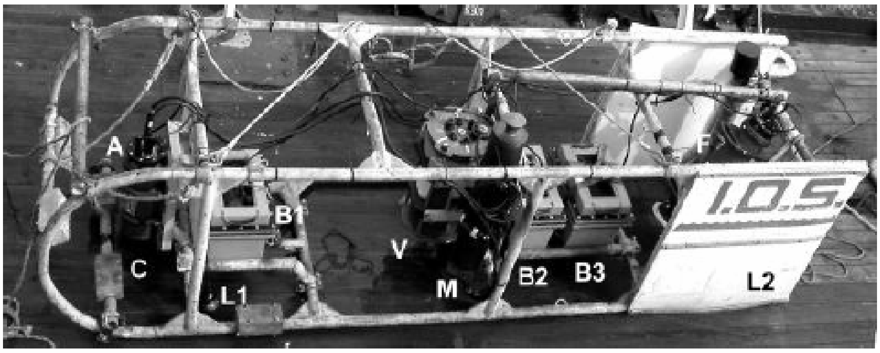


Figure 2.1: The National Oceanography Centre WASP vehicle, showing locations of A-altimeter, C-still camera, L-video lamps, B-batteries, V-video camera, M-monitor (acoustic telemetry) and F-flashgun.

The acoustic telemetry from WASP was received through the ship's hull mounted transducers and monitored with the BAS PES system. It was usually possible to operate WASP at a roughly constant altitude (2.5m ±1m).

REMOTELY OPERATED VEHICLE

Data were collected using an industry-operated work-class Clansman ROV. The Clansman (now re-named Warrior) ROV is 2m long x 1.7m wide x 1.6m high (Figure 2.2), it is powered by 6 thrusters with 90kW of power. It is equipped with 2 manipulator arms, a 5 and 7 function arm. The ROV was equipped with a colour video camera (Remote Ocean Systems) and digital still camera (Kongsberg OE14-208), flash (Kongsberg OE11-242) and Sonar (Tritech). Cameras were mounted on a pan and tilt unit at the front of the ROV (Figure 2.3), which enabled oblique video to be taken. The camera system could be controlled from the surface via a laptop running the Kongsberg Graphic User Interface, this enabled zoom settings, flash output, focus, aperture and exposure to be controlled. Before each transect the video was zoomed out to maximum extent and the camera was set to its most vertical angle (47° below the horizontal). The vehicle had 4 x 500W variable intensity lights positioned for optimal lighting.

Figure 2.2: Clansman ROV returning to *Jack Bates* Rig. ROV is contained within yellow 'garage' used for transport to and from the surface. Note the Tether Management System (TMS) above the ROV. The entire inner yellow cage is lowered to around 50m from the seabed and the ROV launched from the garage using the 250m long yellow tether (coiled on the TMS) to move around.

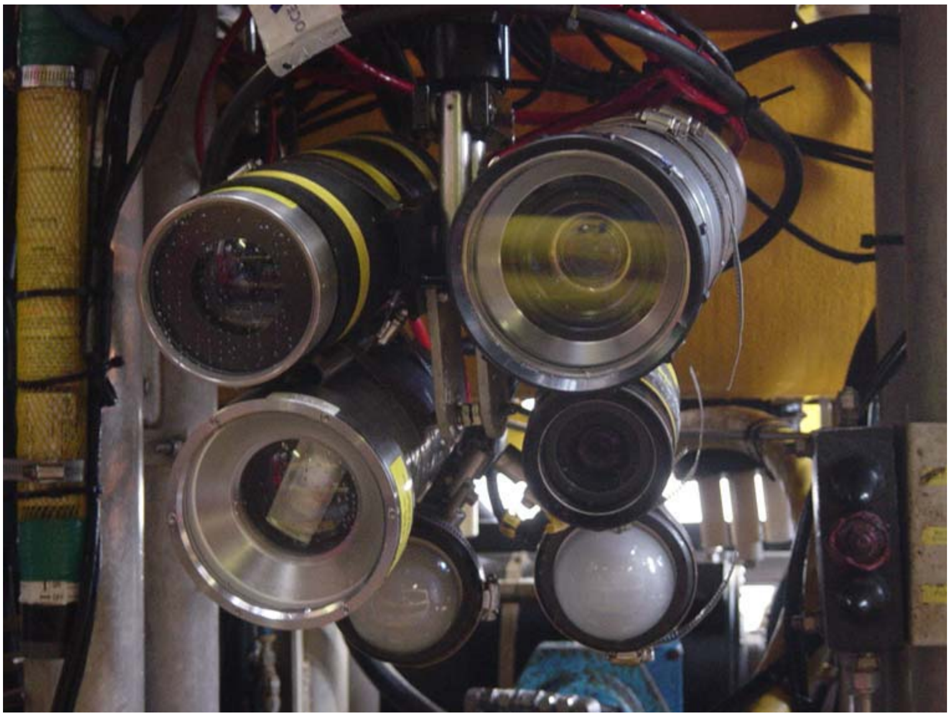


Figure 2.3: Camera package on Clansman 2. (Top Left) SIT system (Top Right) OE14-208 Stills, (Bottom Left) Still Flash Unit, (Bottom Right) Pan – Tilt Colour Video.

AUTOSUB VEHICLE

The Autosub2 AUV is 6.7 m long, 0.9m maximum diameter and has a 3.6 m^3 form displacement. The vehicle (Figure 2.4) splits into three sections: rear, central and front:

The *central section* comprises seven, 3 m long carbon fibre reinforced plastic (CFRP) pressure vessels, with interstitial spaces filled with syntactic foam. Four of the tubes housed the battery system, (3900 “D type” primary Manganese Alkaline cells, total weight = 540 kg) which provided up to 60 kW hr of energy (depending upon usage rate and temperature). The three other tubes house control and sensor electronics. The CFRP pressure vessels limited the safe operating depth of Autosub2 to 1600m.

The *rear section* is mainly free-flooding with some extra buoyancy (syntactic foam). It houses essential sub-systems, (eg navigation, control actuation and propulsion systems) and scientific sensors (eg digital camera, upward looking 300kHz RDI Acoustic Doppler Current Profiler (ADCP) and multibeam receiver).

The navigation housing consists of a 150kHz RDI ADCP and Ixsea PHINS fibre optic gyro based inertial navigation system (INS). For best accuracy, the navigation system needs bottom locked velocity data aiding from the ADCP, requiring a range to the seabed of less than 500m. With bottom tracked aiding, operational results with Autosub2 demonstrated accuracy of better than 0.1% of distance travelled, even at high latitudes (as high as 80 degrees north), where INS systems are generally less accurate. This is of vital importance in under-ice operations, where Autosub may need to return to a small area of clear water after a long run under sea-ice or ice shelf. A single brushless direct drive (no gearbox) d.c. motor and five bladed propeller propels the vehicle with a speed range of 1 to 2 m/s. A rear mounted rudder and sternplane provides control in yaw, pitch and depth.

The *front section* of Autosub2 is free-flooding and houses other essential sub-systems (eg forward looking collision sensor and emergency abort system) and science sensors (eg the Conductivity Temperature Depth (CTD) system and the multibeam transmitter). The control system for Autosub was based upon a distributed, networked control architecture. One of the major advantages of such a modular approach is that new sensors can be integrated into the system with relative ease.

Three small hydrophones on the base of the nose section, act as receivers for the homing system which guides the Autosub back to the mother ship. This facility is particularly useful when the Autosub is operated under mobile sea-ice and it is not possible to predict in advance where there might be an opening in the ice cover suitable for Autosub recovery. The homing system was used to effect safe recovery of Autosub in several of the missions during the AUI campaign in August 2004.

The Autosub camera system was a Starlight SXV-H9, a black and white CCD imager. The imager used a Sony ICX285AL Exview HAD CCD with square pixels size of 6.45x6.45µm and an imaging area of 1392 x 1040 pixels. The camera was fitted with a 25 mm focal length cine lens, which with the water/air interface magnification factor of 1.33, gave a field size of 2.7 m by 2.0 m with Autosub flying at 10 m altitude (pixel resolution on the seafloor of 2 mm square). The camera was installed pointing vertically downwards in the tail section of Autosub within a 150 mm diameter, 400 mm long aluminium housing, with a plane glass window.

A Minolta 3600HS zoom flash was selected, modified with a fixed zoom setting of 85 mm (for a 35 mm camera). The flash was mounted in a 100mm diameter enclosure, with a glass window and installed in the nose section of Autosub, angled back at 27 degrees to match the 10m flying altitude.

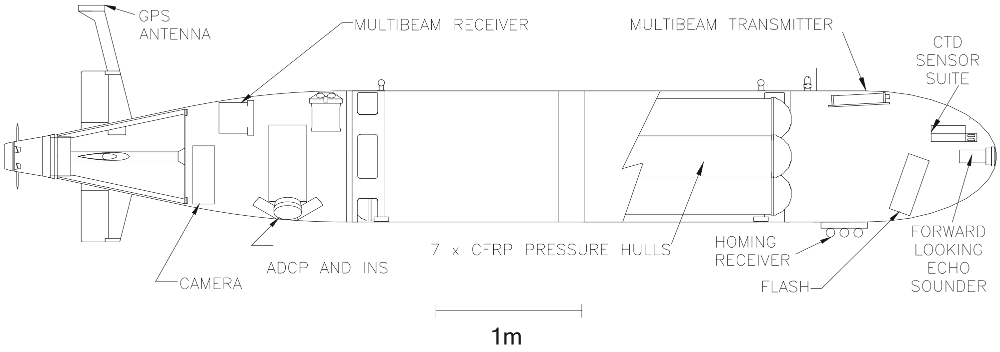


Figure 2.4: Autosub2 schematic. The camera is mounted vertically in the tail section and the flash gun is mounted in the nose section, angled back at 27 degrees to the vertical (optimum for a flying altitude of 10m). Diagram from Autosub Operation Team.

COLLECTION DEVICES

ROV SUCTION SAMPLER

Samples from the ROV were collected by ROV suction sampler (Figure 2.5). This used a Venturi driven Zip pump with mesh bag (mesh size 0.5mm) connected to the back of a 10cm diameter hose with the collecting end controlled by 5 function manipulator. The device could be switched to pump water in or out from the surface.

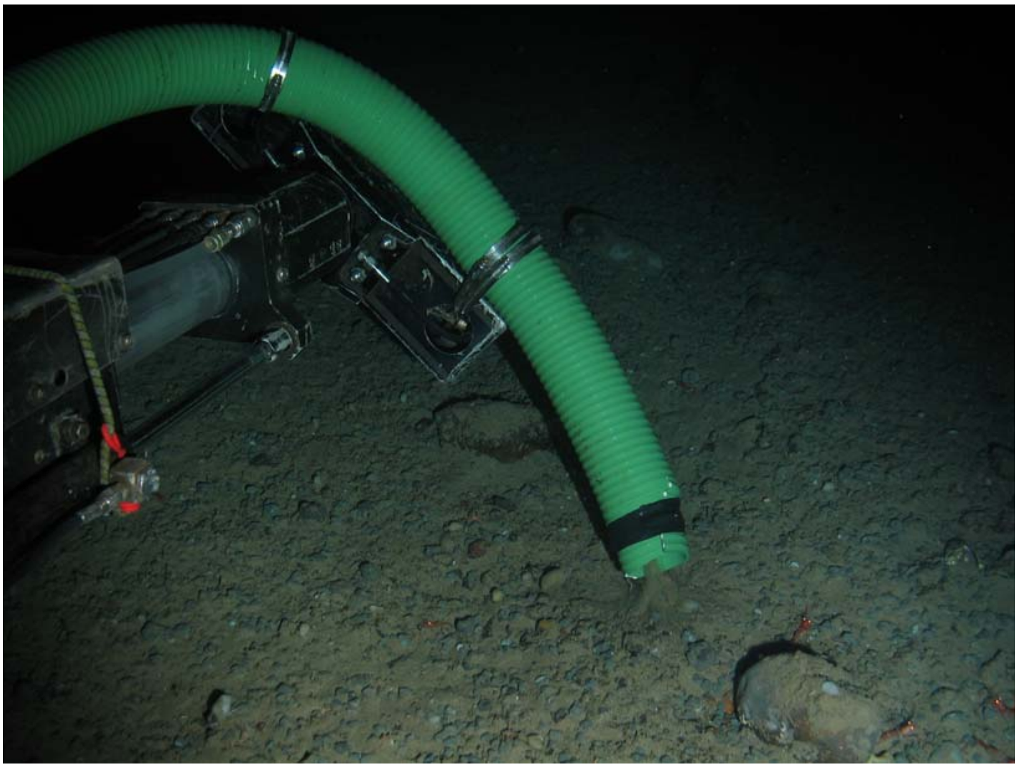


Figure 2.5: ROV suction sampling undertaken at 600m in the Faroe-Shetland Channel. Venturi pump provides the suction, samples collected in 5mm mesh bag via 10cm diameter hose.

AGASSIZ TRAWL

An Agassiz trawl (Figure 2.6) was supplied from the UK National Marine Equipment Pool (NOC). The trawl was rigged and fished in a conventional manner.

Figure 2.6: The UK National Marine Equipment Pool (NOC) Agassiz trawl.

ROCK DREDGE

A rock dredge was supplied from the UK National Marine Equipment Pool (NOC). It was conventionally rigged (i.e. with dredge bucket; Figure 2.7a). For some deployments (stn 56510#1 and 11#1) the dredge bucket was removed and six un-stranded hemp rope "tangles" added to the bucket chains (see Figure 2.7b).

Figure 2.7: The UK National Marine Equipment Pool (NOC) rock dredge: (a) conventionally rigged with dredge bucket, (b) dredge bucket replaced with hemp tangles.

IMAGE ANALYSIS

The methods for image analysis are outlined in the methods section of each chapter. Although the general technique is the same for analysis of photographs, specific environmental conditions required the use of different approaches to successfully characterise the ecology of each area.

CHAPTER 3: ECOLOGY OF THE DEEP FAROE-SHETLAND CHANNEL

INTRODUCTION

The Faroe-Shetland Channel is a deep basin separating the Faroe Plateau from the Scottish continental shelf (Figure 3.1), it narrows southward from about 190 km wide at 62° 30' N to 90 km wide at 60° N. It is bounded to the south by the complex of the Wyville Thomson Ridge (approx. 450m deep) and the Faroe Bank. At its northern entrance (1500-2000m deep), it is connected to the Norwegian Sea (Turrell et al. 1999). In the southwest the Faroe-Shetland Channel, via the Faroe Bank Channel, connects the deep Norwegian Basin to the Icelandic Basin. These channels, and others, allow subzero temperature Norwegian Sea Deep Water to enter the Atlantic Ocean (Ellett and Roberts 1973; Bett 2001).

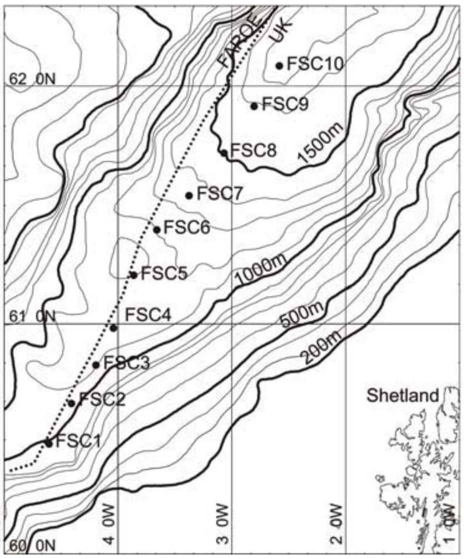


Figure 3.1: Study sites and bathymetry of the Faroe-Shetland Channel

The hydrographic regime of the Faroe-Shetland Channel is complex with warm North Atlantic waters overlying cold water flows from the Norwegian Sea (Turrell et al. 1999). The surface waters (0-400m) are warm (>8°C) North Atlantic Water, these overlie cold (2 to 5.5°C) Arctic Intermediate Water (400-600m), Norwegian Sea Arctic Intermediate Water (-0.5 to 0.5°C in 600-800m) and Faroe-Shetland Channel Bottom Water (c. -1°C and below 800m). The boundary between the warm and cold waters is dynamic and may occur variously between 400 and 600m depth (Bett 2001). It has recently been shown that there is a marked decadal variation in the distribution, extent and salinities of these water masses (Turrell et al. 1999).

Using deep towed side scan sonar (TOBI) supported with seabed observations and samples, Masson (2001) investigated the seabed of the deep Faroe-Shetland Channel floor (>1000m) and found it to be a relatively featureless mud, muddy sand and gravel zone with a general decrease in grain size to the northwest.

Photography is increasingly used to investigate the fauna of deep-sea environments (Smith et al. 1993; Priede and Merrett 1998; Lampitt et al. 2001; Solan et al. 2002), however, in the Faroe-Shetland Channel, only preliminary descriptions of the megafauna have been carried out using this technique (Bett 2001). Towed camera platforms allow the megabenthos of large areas of seabed to be studied quantitatively without disturbing the environment under study. Along with the geology of an area (Masson 2001), megafaunal species richness and standing stock are commonly assessed from photographs (Fell 1967; Bohnsack 1979; Gutt and Starmans 1998; Gutt et al. 1999). In addition, analysis of *Lebensspuren* (Ewing and Davis 1967; Kitchell et al. 1978; Gage and Tyler 1991; Bett et al. 1995), faunal size and associated biomass inferences (Christiansen and Thiel 1992; Piepenburg and Schmid 1997) can also provide valuable ecological information. Photographs can provide an undisturbed view of the benthos over a wide area allowing the description of large-scale faunal spatial pattern in the deep sea (Solan et al. 2002).

The fauna of the deep Faroe-Shetland Channel was first sampled in 1868 by Charles Wyville Thomson onboard HMS '*Lightning*' and '*Porcupine*' (Thomson 1873). Since these pioneering cruises this area has been largely ignored, but recent expansion of oil and gas exploration has prompted a large scale environmental survey in this area (Bett 2001). The benthic megafauna of the channel axis is largely unknown except from the early studies, most previous studies have concentrated on the shallower flanks of the channel. The western flank has been subject to extensive biological investigation through the Internordic BIOFAR programme (Nørrevang et al. 1994; Fautin et al. 2005; Tyler et al. 2005) with particular attention being directed towards bank forming corals (Frederiksen et al. 1992; Jensen and Frederiksen 1992) and mass occurrences of large demosponges (Klitgaard 1995; Klitgaard et al. 1997). The biota of the West Shetland Shelf has been sampled using a trawl with a headline camera by Dyer et al. (1982).

In this study megafaunal species richness, standing stock, size and traces (*Lebensspuren*) along with the composition of the seabed will be assessed. The primary objectives are to classify the megabenthic assemblages of this area, and their traces, and relate these to environmental factors along the Faroe-Shetland Channel axis.

MATERIALS AND METHODS

Field sampling

Sampling was conducted as part of the UK Department of Trade and Industry (DTI) Strategic Environmental Assessment (SEA) process. The work was carried out from the Royal Research Ship *Charles Darwin* during cruises 119 (August 1999) and 123 (August 2000). Seabed sampling was carried out according to protocols developed in the AFEN region (Bett 2001). Ten photographic transects were undertaken, arranged along the length of the Faroe-Shetland Channel axis at depths of 1006-1660m (Table 3.1). Seabed survey photography was undertaken using the NOC WASP, wide-angle seabed photography, vehicle (Chapter 2). This vehicle was typically operated for one hour at the seabed, yielding some 250 still photographs (35mm Kodak Vision 250D colour negative) and continuous video footage (mini digital video cassette).

Table 3.1: Station data for WASP deployments in the Faroe-Shetland Channel axis. Seabed start and end position and depth are given together with the number and area of resultant photographs analysed.

Site	Station number	Date	Latitude	Longitude	Depth (m)	No. photos analysed	Seabed area analysed (m^2)
FSC1	55276	03/08/00 04/08/00	60°28.98´N 60°28.45´N	4°37.02´W 4°36.60´W	1017 1007	207	1042
FSC2	55310	10/08/00 10/08/00	60°40.15´N 60°40.34´N	4°23.88´W 4°24.06´W	1068 1069	172	1008
FSC3	55311	23/08/99 23/08/99	60°49.81´N 60°49.64´N	4°10.47´W 4°10.80´W	1085 1084	63	322
FSC4	55312	23/08/99 23/08/99	60°59.92´N 60°59.81´N	4°00.80´W 4°01.70´W	1119 1119	64	307
FSC5	55313	11/08/00 11/08/00	61°11.66´N 61°10.77´N	3°52.92´W 3°52.28´W	1090 1105	68	326
FSC6	55314	12/08/00 12/08/00	61°23.07´N 61°22.59´N	3°39.96´W 3°38.46´W	1154 1142	119	488
FSC7	55315	12/08/00 12/08/00	61°32.97´N 61°32.59´N	3°23.34´W 3°22.49´W	1384 1370	141	663
FSC8	55316	12/08/00 12/08/00	61°42.74´N 61°42.16´N	3°03.47´W 3°02.52´W	1487 1490	130	640
FSC9	55317	13/08/00 13/08/00	61°54.76´N 61°54.19´N	2°47.82´W 2°47.82´W	1602 1609	297	1129
FSC10	55392	26/08/00 26/08/00	62°04.91´N 62°04.99´N	2°36.18´W 2°34.86´W	1653 1660	224	885

Photo analysis

The megabenthic fauna in each photograph were recorded. Given the physical scale of the photographs we determined that only animals with a maximum dimension >5cm could be consistently identified. Altitude data (i.e. the height of the camera above the seabed) were printed directly onto each photograph allowing the scale of the image to be calculated. Megafaunal organisms were identified, counted and measured on each frame; their abundance converted to numbers per hectare and measured sizes converted to actual size using the altitude data. Recent *Lebensspuren* (i.e. life traces, tracks, burrows etc.) were classified, counted and their area measured. Seabed sediment type / grain size was assessed using the Wentworth index (Wentworth 1922) by examining 100 randomly chosen points overlaid onto selected photographs. A subsample of 30 photographs spaced approximately evenly along each transect were used to make the sediment assessment. Unsuitable photographs (high altitude or out of focus etc.) were discarded from all analyses.

Data analysis

Sediment

The finest sediment fraction distinguishable in photographs (sediment fraction <22mm) was divided further into smaller size classes, this was based on the proportion of sediments in each size class observed in DTI SEA sediment samples (Hughes et al. 2003). The combination of the photographic data with those from the analysis of physical samples allowed the full size range of sediment to be assessed for each site, from fine clays (2µm) to boulders (>256mm). Sediment parameters were calculated following the methods of Krumbein and Pettijohn (1938).

Diversity and composition

Species counts from individual photographs were pooled into ‘samples’ that covered $100m^2 \pm 1m^2$, although these ‘samples’ were essentially contiguous the course of the WASP vehicle was not pre-defined or constant. For these reasons each sample was considered a replicate. In some analyses we have treated these samples as replicates, in others we have used site totals.

Rarefaction (Hurlbert 1971) was used to compare species richness between sites along the Faroe-Shetland Channel. A range of other diversity indices (see e.g. Magurran 2003) were selected to cover patterns in both ‘rare’ and ‘common’ taxa: Berger-Parker Index, Simpsons λ' (Simpson 1949), Shannon Diversity Index, H' (Margalef 1968), Rarefaction, $ES_{(39)}$ (Hurlbert 1971) and S, the total species present. Univariate diversity indices were calculated using PRIMER (Clarke and Warwick 1994) and Biodiversity Pro (Version 2, Natural History Museum, London and Scottish Association for Marine Sciences, Oban). Species density (ES_{400m2}) was calculated from sample-based species accumulation curves using EstimateS software (Colwell 2005).

Initial multivariate analyses (hierarchical clustering and non-metric multidimensional scaling) were carried out using the PRIMER software package (Clarke and Warwick 1994). Following the general recommendations of Clarke and Warwick (1994) a fourth root transformation was applied to the faunal abundance data and the Bray-Curtis similarity measure employed. The BIO-ENV routine of PRIMER was used to assess potential environmental causes of the observed megafaunal distribution patterns (Clarke and Warwick 1994). A range of environmental variables (depth, sediment grain size, latitude, total organic carbon and total organic nitrogen), available from the DTI SEA survey (see Hughes et al. 2003) were examined in this way.

In addition canonical correspondence analysis (CCA) was undertaken using the PC-ORD programme (McCune and Mefford 1999) and was used to further assess the relationship between the environmental data and the structure of the megabenthic community. A Monte Carlo permutation test was undertaken to determine the significance of the relationship between the environmental variables and megabenthic community composition (Manly 1998). The ordinations presented here employed the linear combinations (LC) of variable scores as recommended by Palmer (1993).

Size and relative biomass

Relative biomass was estimated using approximate faunal bio-volume. Length to volume conversions were estimated based on the approximate shape of individual taxa and applied to body length measurements derived from the photographs.

RESULTS

Environment and physical setting

Photographic sediment analysis revealed the presence of high proportions of large size class sediments (i.e. boulders to gravel) at the southerly stations. At stations 1,3,4,5 and 6 a significant proportion of the seabed comprised coarse-grained sediments (>2mm); at stations 2 and 6-10, no coarse-grained sediments were recorded.

Sediment grain size data from core samples collected at the same study sites (see Hughes et al. 2003) show a highly significant negative correlation between mean grain size and latitude ($r' = -0.879$, $p < 0.001$). Very low sediment homogeneity was observed at all stations, with the large standard deviations indicating very poor sorting. There was a significant positive correlation between skewness and latitude ($r' = 0.636$, $p = 0.048$) indicating coarse skewed sediment sizes at the southerly stations.

A trend of reducing grain size with latitude was also observed ($r' = 0.915$, $p < 0.001$) when the size class data from photographic and conventional sediment analyses were combined to cover the entire spectrum of sediment size (table 3.2). Low sediment homogeneity was again apparent. A positive relationship with skewness ($r' = 0.855$, $p < 0.01$) and latitude was observed, again indicating coarser skewed sediments to the south.

Table 3.2: Summary of sediment particle size analysis from pooled DTI (see text) and photographically observed sediment size at each phototransect station in the Faroe-Shetland Channel axis.

Site Number	Median diameter (μm)	Median diameter (ø)	Mean diameter (μm)	Mean diameter (ø)	Standard deviation (ø)	Skewness (ø)
FSC1	36833	-5.20	5444	-2.61	3.90	0.76
FSC2	143	2.81	107	3.22	1.44	1.92
FSC3	235	2.09	903	0.08	4.40	-0.22
FSC4	2323	-4.54	2397	-1.31	4.63	0.41
FSC5	235	2.09	450	1.09	4.33	-0.41
FSC6	119	3.07	91	3.47	2.45	0.09
FSC7	38	4.70	35	4.85	1.91	0.06
FSC8	24	5.39	26	5.28	2.15	-0.46
FSC9	18	5.82	22	5.52	2.18	-0.64
FSC10	13	6.23	18	5.83	2.17	-0.76

Hard substrata available for megafaunal colonization (grain size > 64mm) was high in all southern stations (except station 2) reflecting the abundance of exposed ice-rafted drop stones. No hard substrata were observed from station 7 northwards.

Total Organic Carbon (TOC) was found to increase significantly northwards ($r' = 0.867$, $p < 0.001$; Figure 3.2) along the Faroe-Shetland Channel axis. This increase was concurrent with a significant northward increase ($r' = 0.846$, $p < 0.01$) in Total Organic Nitrogen (TON), with a notable large step increase in TON between stations 5 and 6 (Figure 3.2).

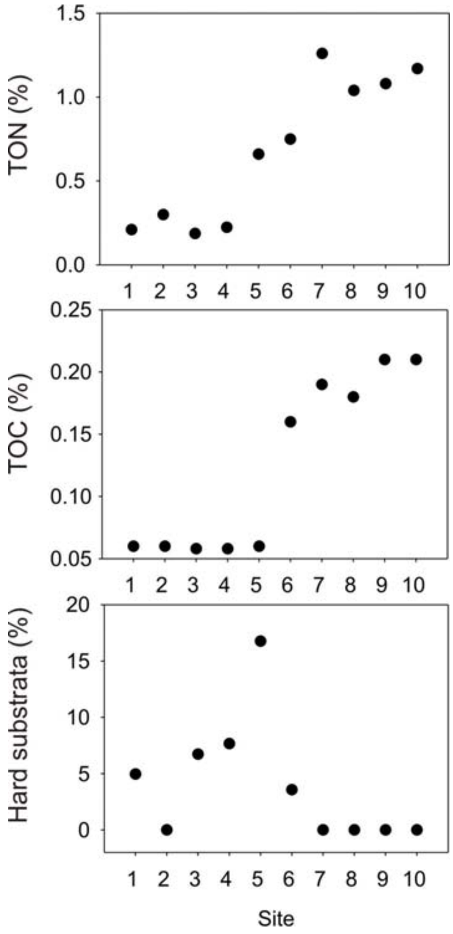


Figure 3.2: Total Organic Carbon (TOC), Total Organic Nitrogen (TON) and percentage area hard substrata (grain size > 64mm) at each study site on the Faroe-Shetland Channel axis.

Megafaunal density

Analysis of 1485 photographs revealed a total of 3826 megabenthic organisms from 57 nominal taxa in a total area of 6810 m^2. The density of megafauna ranges from 542 to 30,482 ha^{-1} with maximal densities towards the mid-section of the channel (Table 3.3). Tube dwelling polychaetes were very abundant, but, as it is not known if they were alive, megafaunal abundances are illustrated without them (Figure 3.3); the trend in abundance remains the same.

Size and biomass

Relative biomass (Figure 3.3) was found to be maximal in the mid channel stations with generally low relative biomass in the southern stations. At the northern stations biomass was consistently low. The observed megafauna of the Faroe-Shetland Channel were highly variable in size from the lower limit of consistent observation (5cm) to over 1 metre for the larger fish.

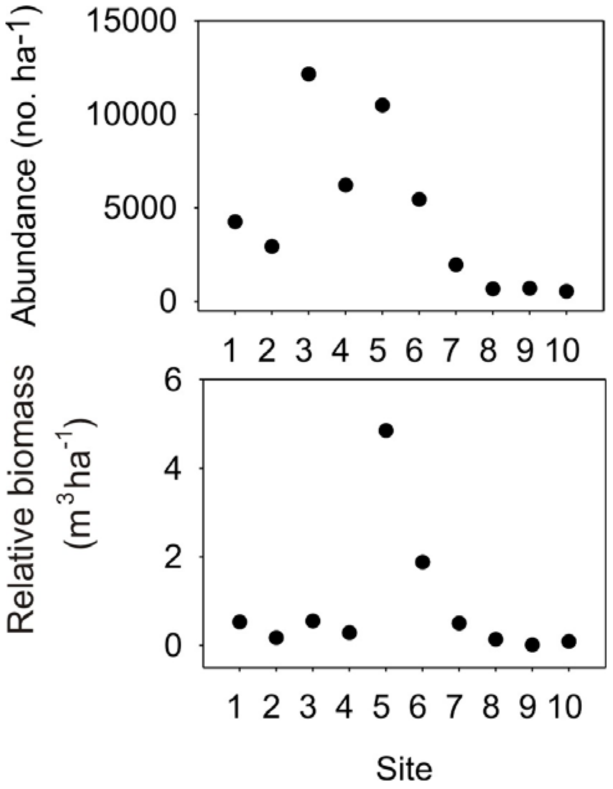


Figure 3.3: Abundance (numbers ha^{-1} excluding tube-dwelling polychaetes) and relative biomass (faunal volume m^3 ha^{-1}) of megafauna found at each phototransect site on the Faroe-Shetland Channel axis.

Table 3.3: Taxa found along Faroe-Shetland Channel Axis. Densities of each taxa recorded for each channel axis station (Numbers ha^{-1}).

	FSC1	FSC2	FSC3	FSC4	FSC5	FSC6	FSC7	FSC8	FSC9	FSC10
Chondrocladia gigantea	120	48	56	77	49	0	0	0	0	0
Indet. Sponge type 1	0	10	0	25	26	20	0	0	0	0
Indet. Sponge type 2	33	0	0	0	0	0	0	0	0	0
Indet. Sponge type 3	90	11	824	303	118	306	0	0	0	0
Indet. Sponge type 4	79	10	78	0	0	0	0	0	0	0
Indet. Sponge type 5	16	0	0	0	0	80	0	0	0	0
Stylocordyla borealis	15	958	0	0	0	0	45	0	0	0
Indet. Sponge type 6	12	0	0	0	0	0	0	0	0	0
Indet. Sponge type 7	0	22	0	0	0	0	0	0	0	0
Indet. Sponge type 8	0	0	140	91	263	0	0	0	0	0
Indet. Sponge type 9	0	0	0	0	0	24	0	0	0	0
Indet. Sea whip	0	0	0	0	0	16	18	0	9	0
Tubularia sp.	7	6	0	0	0	0	0	286	143	24
Cerianthus votgi?	0	123	2841	1951	2135	1662	0	0	0	0
Indet. Anemone type 2	119	37	157	42	0	0	0	0	0	0
Indet. Anemone type 3	0	0	0	23	0	0	22	0	0	0
Indet. Anemone type 4	1887	8	874	659	1696	249	0	0	0	0
Indet. Anemone type 5	20	0	0	0	0	0	0	0	0	0
Indet. Soft Coral type 1	1520	50	5624	220	4727	0	0	0	0	0
Indet. Soft Coral type 2	165	55	535	133	321	96	0	8	0	0
Indet. Soft Coral type 3	0	92	157	0	288	0	0	0	0	0
Indet. Soft Coral type 4	0	0	0	0	37	0	0	0	0	0
Umbellula encrinus	0	0	0	0	0	0	46	0	0	0
Indet. Sabellid	33	24	760	959	281	467	1003	325	450	448
Indet. Polynoid	0	0	0	0	0	16	10	0	41	17
Indet. Tube dwelling polychaete	0	0	25596	2696	4474	17524	0	0	0	0
Indet. Nemertine	9	195	0	0	0	23	12	0	0	0
Colus jeffreysianus	213	50	30	80	23	69	14	0	0	0
Indet. Gastropod	0	7	0	25	0	0	19	0	8	30
Indet. Octopus	32	0	0	0	0	0	0	0	0	0
Indet. Decapod	0	0	63	0	0	0	0	0	0	0
Colossendeis proboscidea	206	66	0	35	131	31	23	0	0	9
Indet. Pycnogonid type 1	246	552	1198	827	161	1161	15	0	0	0
Indet. Pycnogonid type 2	0	340	101	69	28	36	0	0	0	0
Indet. Pycnogonid type 3	0	105	0	0	0	0	0	0	0	0
Indet. Pycnogonid type 4	0	176	0	0	0	0	0	0	0	0
Indet. Pycnogonid type 5	0	8	0	129	50	16	0	0	0	0
Intet. Asteroid type 1	5	0	0	0	0	0	0	0	0	0
Intet. Asteroid type 2	4	0	0	31	0	0	0	0	0	0
Zoroaster fulgens	8	0	0	97	26	0	57	0	14	61
Stichastrella sp.	0	19	41	0	0	0	15	21	92	42
Poranid	0	14	0	0	0	0	0	0	0	0
Crossaster squamatus	30	0	240	43	292	36	0	0	0	0
Pteraster sp.	0	0	0	0	0	0	0	0	0	0
Hymenaster pellucidus	5	0	0	62	82	0	92	0	45	21
Plutonaster bifrons	0	0	0	0	0	27	13	33	0	0
Brisinga endecacnemos?	140	0	0	35	0	0	0	0	0	0
Indet. Brisingid	0	13	0	0	0	0	0	0	0	0
Ophiopleura borealis	0	0	0	217	156	795	34	13	0	0
aff. *Ophiophrixus spinosus*	0	0	0	21	0	137	0	0	0	0
Indet. Spatangoid	0	0	0	0	0	114	662	0	0	0
Indet. Comatulid Crinoid	60	0	0	0	0	18	0	0	0	0
Rhizocrinus lofotensis	0	0	0	0	0	17	11	0	0	0
Indet. Hemichordate	58	16	299	25	23	130	0	0	0	0
Gaidropsarus argentatus	105	47	0	42	59	178	14	0	19	0
Lycodes spp.	74	29	110	51	137	111	0	11	0	0
Raja hyperborea	13	11	0	0	0	0	23	22	5	0
Indet. Scorpionfish	8	13	0	31	0	0	0	0	0	0

Diversity

The number of ‘species’ present per site varied considerably from 33 (FSC1) to 8 (FSC 8 and 10) with a general decline with increasing latitude. The number of species found in an average m^2 had a range of 1.02 (FSC4) to 0.06 (FSC10) with maximal numbers found in the central channel sites.

Alpha diversity indices were compared (Figure 3.4) revealing a general decline in diversity from south to north. There are strong negative correlations between latitude and most diversity measures (S: $r' = -0.892$, $p < 0.001$; λ': $r' = 0.612$, $p = 0.06$; H': $r' = -0.697$, $p < 0.05$; ES(39): $r' = -0.720$, $p < 0.05$; Berger-Parker: $r' = 0.559$, $p = 0.093$). Highest species richness (Figure 3.4) was found at the shallower stations to the southwest of the channel, with a general trend of reducing richness to the northeast. Station 3 had a particularly low richness, as a result of the large numbers of tube dwelling polychaetes (i.e. high dominance) recorded at this site. Species density and H′ were generally high for the southern stations (1-6), reduced at station 7 and were very low for the northern stations (8-10). Species density and H′ followed the same pattern among stations as revealed by multivariate analysis (Figure 3.4; see further below).

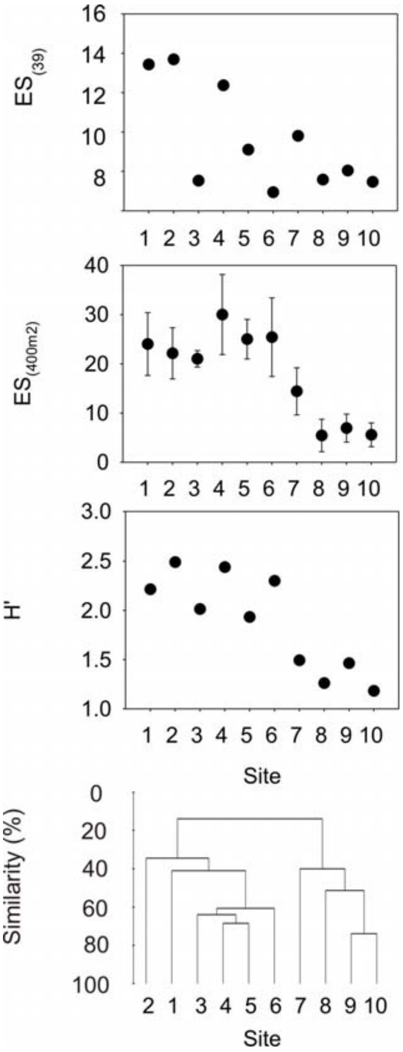


Figure 3.4: Megabenthos species diversity and composition along the Faroe-Shetland Channel axis: species richness (Rarefied $ES_{(n=39)}$), species density (Mao Tao S obs $_{(400m2)}$), Shannon-Wiener H´ (log e) and dendrogram (see text for details).

Community analysis

There was considerable variation in the dominant taxa at sites along the Faroe-Shetland Channel. The dominant megafaunal phylum at stations 3,4,6,7,8,9 and 10 was Annelida, (almost entirely tube dwelling forms). Maximal abundance reached 26,356 annelids ha^{-1} at station 3 where large dense patches of free-living tube dwelling forms were observed, these were also noted at stations 3 to 6. Sessile tube-dwelling sabellids were recorded at all stations reaching densities of 959 ha^{-1}.

Cnidaria, particularly anthozoans (actiniarians and cerianthids), made up a large proportion of the megafaunal community especially at the southern stations, being the dominant phylum at stations 1 and 5. Although their proportional dominance was highest at station 1 (69.6% megafauna), numerical abundance was highest at station 3 and station 5 (10,188 and 9,238 ha^{-1} respectively). Type 4 anemones were the most common in the southern stations being progressively replaced by cerianthids (type 1 aff. *Cerianthus votgi*). Very few anemones were recorded at station 7 and none at stations 8-10.

Arthropods, almost entirely represented by pycnogonids, were frequently encountered at southern stations, reaching densities of 1,362 ha^{-1} (station 3), but were absent or very rare at stations 7-10. The large, conspicuous *Colossendeis proboscidea* was present in low densities (up to 206 ha^{-1} but typically lower) at most stations. Smaller pycnogonids were more common at stations 2,3,4 and 6 with a maximal density of 1,299 ha^{-1} (station 3), they were rare at station 7 and not recorded at stations 8-10.

Echinoderms were present at all stations, becoming proportionally more abundant at the northern stations, representing 0.7-5.5% of the megafauna at stations 1-6 and 9.3-40.3% of the megafauna at stations 7-10. Numerical abundance of echinoderms broadly increased with latitude reaching a maximum of 1,144 ha^{-1} at station 6. Overall, asteroids made up the greatest proportion of the echinoderms (43.2%), ophiuroids were also important (34.6%) with echinoids (19.5%) and crinoids (2.7%) making up the remainder, no holothurians were observed. Asteroid numbers were low at stations 2,6 and 8 (46-63 ha^{-1}), intermediate at stations 1,7,9 and 10 (124-184 ha^{-1}) and high at stations 3-5 (237-400 ha^{-1}). Sunstars (*Crossaster squamatus*) were the numerically dominant asteroid. Almost equal total numbers of *Zoroaster fulgens*, *Stichastrella* sp., *Hymenaster pellucidus* and brisingids (aff. *Brisinga endecacnemos*) were observed. Ophiuroids (particularly aff. *Ophiopleura borealis*) were most common at stations in the mid section of the channel axis with densities of up to 933 ha^{-1}. Towards the south, megafaunal ophiuroid densities decreased, although large numbers (up to $54m^{-2}$) of smaller ophiuroids (*Ophiactis abyssicola*) were observed in some photographs. Ophiuroids were rare at stations 7 and 8 and absent at stations 9 and 10. Echinoids were only recorded at two stations, however they were common at station 7 (662 ha^{-1}) although lower numbers were observed at station 6 (114 ha^{-1}). Regular echinoids were not observed at any station and only shallow ploughing spatangoids (aff. *Spatangus raschi*) were observed from seabed photographs. Crinoids were the least abundant echinoderm class (2.7% echinoderms). Comatulid crinoids were only observed at station 1 (60 ha^{-1}). Small numbers of stalked crinoids (aff. *Rhizocrinus lofotensis*) were observed at stations 6 and 7 (up to 35 ha^{-1}).

Porifera (sponges) were present at stations 1-7 and represented a small proportion of the megafaunal communities at most of these sites. Their numbers were relatively high (reaching 1,097 ha^{-1}) although reduced northwards. Fish were present in low numbers (up to 288 ha^{-1}) at most sites although numbers were lower for stations 7-10. Mollusca were present in low numbers (up to 300 ha^{-1}) reducing towards the north. Other major taxa e.g. Hemichordata and Nemertea were recorded only rarely.

Multivariate community analysis including hierarchical clustering (Figure 3.4) and MDS analysis (Figure 3.5), revealed a clear grouping of stations into northern (stations 7-10) and southern (stations 1-6) areas. Within these two major groups there was further additional separation of station 2 from the other southern stations.

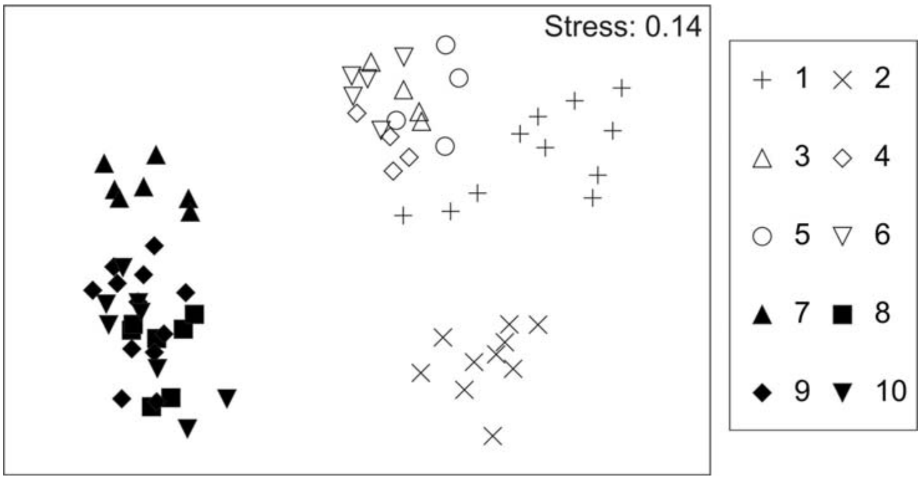


Figure 3.5: Multidimensional scaling ordination (see text for details) of megafauna composition along the Faroe-Shetland Channel axis (each point represents the data from a group of photographs covering $100m^2$ of seabed).

BIOENV analysis revealed that the single environmental variable which best groups the sites, in a manner consistent with the faunal patterns, was depth ($\rho w = 0.909$). The best 2-variable combinations are for depth and latitude ($\rho w = 0.849$) and for depth and total organic nitrogen ($\rho w = 0.829$). The x coordinates of the MDS plot were found to be highly correlated to depth ($r' = 0.879$, $p < 0.001$). This suggests that depth related factors are the most important physical drivers of the zonation of megafaunal communities in the Faroe-Shetland Channel.

Spearman rank correlations were preformed between all factors measured (Table 3.4). This highlights the correlations between many of the environmental factors (particularly depth, latitude, TOC, TON and grain size) and further reflects the difficulty in extracting the environmental causes for faunal variation.

Table 3.4: Spearman rank correlations between biological and environmental parameters for 10 Faroe-Shetland Channel axis study sites. Abundance (A; indiv. m^{-2}), relative biomass (B; m^{-3} ha^{-1}), number of species (S), Pielou evenness (J), Rarefied species richness (ES$_{39}$), Species density (ES$_{400m2}$), Shannon-Wiener Index (log e) (H′), Simpson's Index (λ′), Berger-Parker Index (B-P), x coordinates of MDS plot (xMDS), *Lebensspuren* density (Ln; traces m^{-2}), *Lebensspuren* area (La; trace area m^{-2}), depth (m), latitude (lat), width of the channel at 1000m depth (width), mean phi grain size (mp), standard deviation of phi grain size (std), skewness of phi grain size (skew), Total Organic Carbon (TOC) and Total Organic Nitrogen (TON). Values are r′ and its associated probability, * p<0.05, ** p<0.01, ns = not significant.

	Lat	A	B	S	J	ES$_{39}$	ES$_{400m2}$	H'	λ′	B-P	mdsx	Ln	La
Lat	__1.00**__	__-0.65*__	ns	__-0.89**__	ns	ns	__-0.79**__	__-0.70*__	ns	ns	__0.84**__	__0.70*__	__0.66*__
depth	__0.99**__	__-0.66*__	ns	__-0.87**__	ns	ns	__-0.92**__	__-0.69*__	ns	ns	__0.88**__	__0.66*__	__0.65*__
width	__0.96**__	ns	ns	__-0.87**__	ns	ns	__-0.72*__	__-0.65*__	ns	ns	__0.81**__	__0.69*__	__0.70*__
mp	__0.92**__	__-0.73*__	__-0.64*__	__-0.83**__	ns	ns	__-0.80**__	ns	ns	ns	__0.84**__	__0.70*__	__0.72*__
std	ns	__0.67*__	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
skew	__-0.86**__	ns	ns	__0.92**__	ns	__0.66*__	ns	__0.66*__	__-0.64*__	ns	ns	ns	ns
TOC	__0.87**__	__-0.71*__	ns	__-0.70*__	__-0.66*__	ns	__-0.79**__	ns	ns	ns	__0.82**__	__0.84**__	__0.82**__
TON	__0.87**__	__-0.75**__	ns	__-0.72*__	__-0.64*__	ns	__-0.82**__	ns	ns	ns	__0.80**__	__0.78**__	__0.78**__

On the CCA plot (Figure 3.6), axis 1 separates the northern from the southern group of stations, while axis 2 further separates stations based on habitat. Axis 1 on the canonical ordination plots was the most important (eigenvalue 0.61, species environment correlation 0.98) as eigenvalues > 0.5 are proposed by ter Braak (1986) to have a relatively good dispersal of species along the axes and account for a high percentage of variance in species composition. Axis 2 (eigenvalue 0.46, species environment correlation 0.97) separates the environmental variables based on sediment heterogeneity. The Monte Carlo analysis showed the CCA Eigenvalues to be extremely robust ($p < 0.01$ for all axes) as well as the species–environment correlations ($p < 0.01$ for all axes). This suggests that one of the environmental factors co-correlated with site (depth, latitude, TON and TOC) was most significant in defining the variability within the species data. Sediment parameters were also important particularly size range (sediment standard deviation), station 2, unusual for being shallow with fine sediment, was defined by sediment skewness.

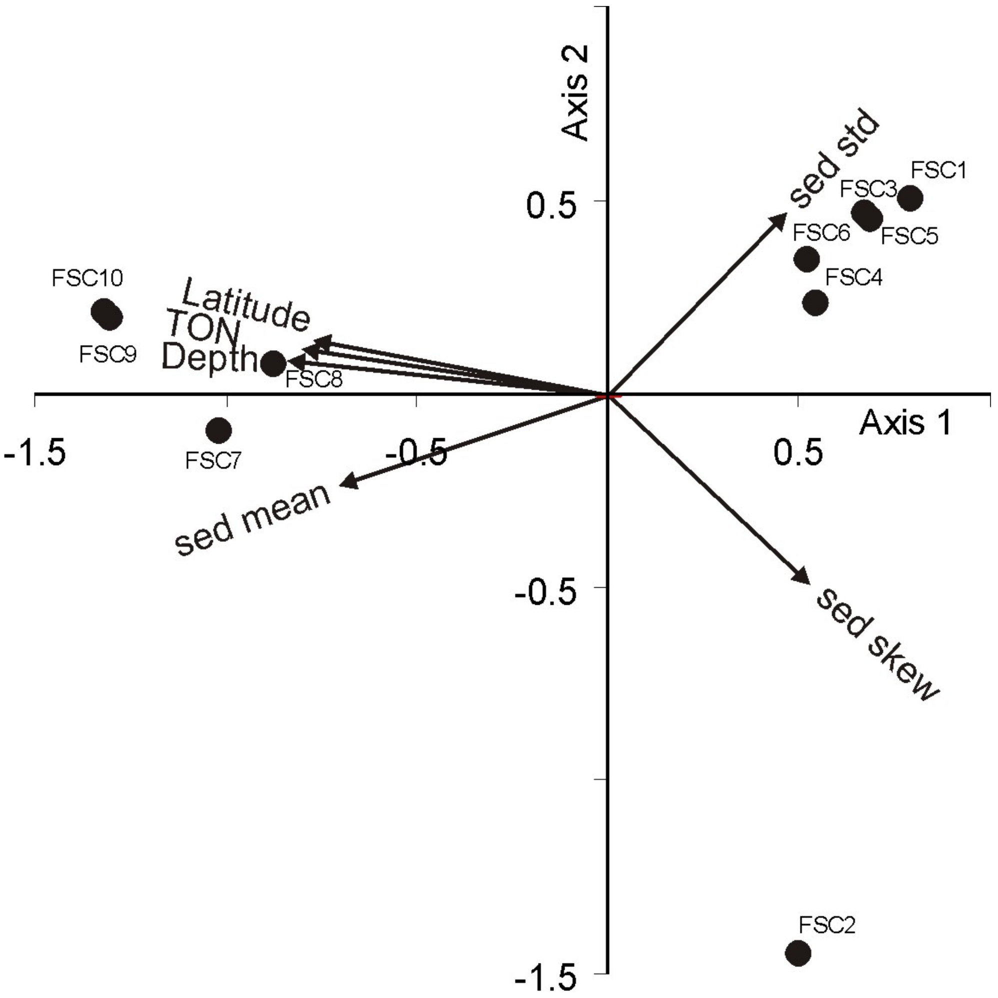


Figure 3.6: Canonical correspondence analysis of megabenthic species in the Faroe-Shetland Channel axis. Latitude (Latitude), Total Organic Nitrogen (TON), Site depth, m (Depth), mean phi sediment size (sed mean), sediment skewness (sed skew) and standard deviation of sediment size (sed std).

Lebensspuren

Lebensspuren were observed throughout the Faroe-Shetland Channel in all areas where the sediment was sufficiently soft to allow preservation of faunal traces. Twelve distinct *Lebensspuren* types were identified during the study (Figure 3.7). In some cases it was possible to identify the animal responsible for the trace (from trace form or by direct observation of trace formation). Unfortunately for many traces it was not possible to identify definitively the taxa responsible for their formation.

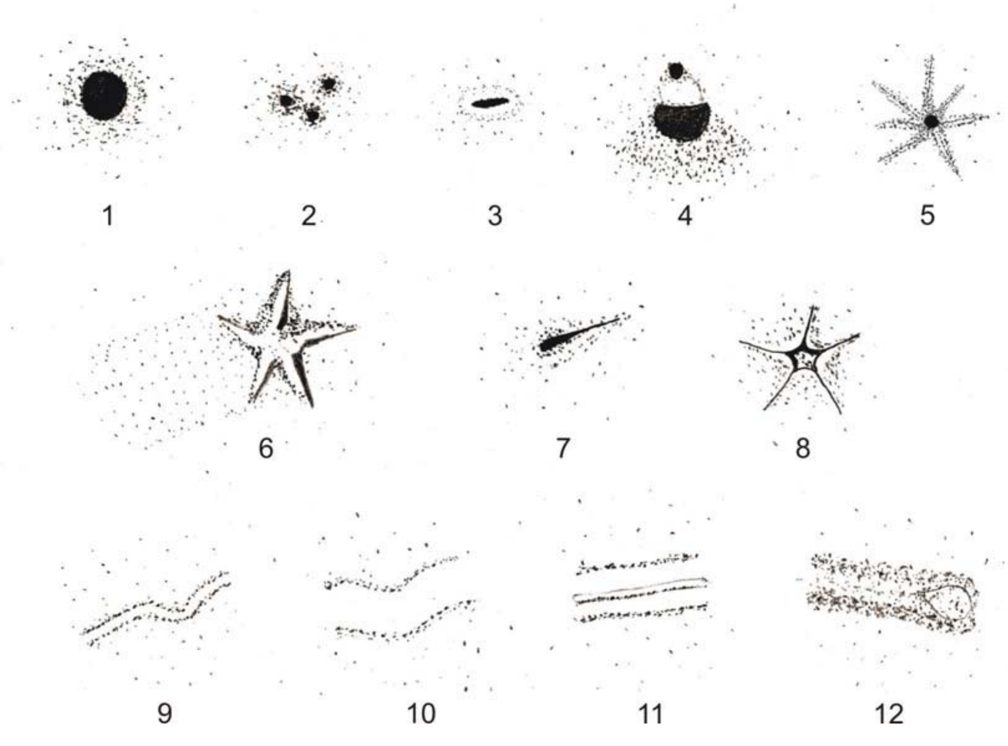


Figure 3.7: Faroe-Shetland Channel *Lebensspuren*. 1) Large circular holes, 2) small circular holes, 3) Slit shaped hole, 4) Ophiuroid inhabited burrow, 5) Spoke trace, 6) Asteroid trace, 7) Spike trace, 8) Ophiuroid trace, 9) Narrow plough, 10) Wide plough, 11) String plough, 12) Spatangoid trace. *Lebensspuren* 1-4 are caused by dwellings, 5 by feeding, 6-8 by resting and 9-12 by crawling. It is thought that trace 5 is produced by an Echiuran / sipunculid, 7 by a ray caudal fin and 9-11 by gastropods.

The occurrence of *Lebensspuren* (Figure 3.8) generally increased with latitude (r′ = 0.648, $p < 0.05$) although station 7 had a particularly high density of *Lebensspuren*. The area of seabed bioturbated by the presence of faunal traces (table 3.5) was not found to follow the same trend. Very little bioturbation was evident at stations 1 to 5 but at stations 6-10 there was a large step increase in bioturbation which remained high but decreased northwards.

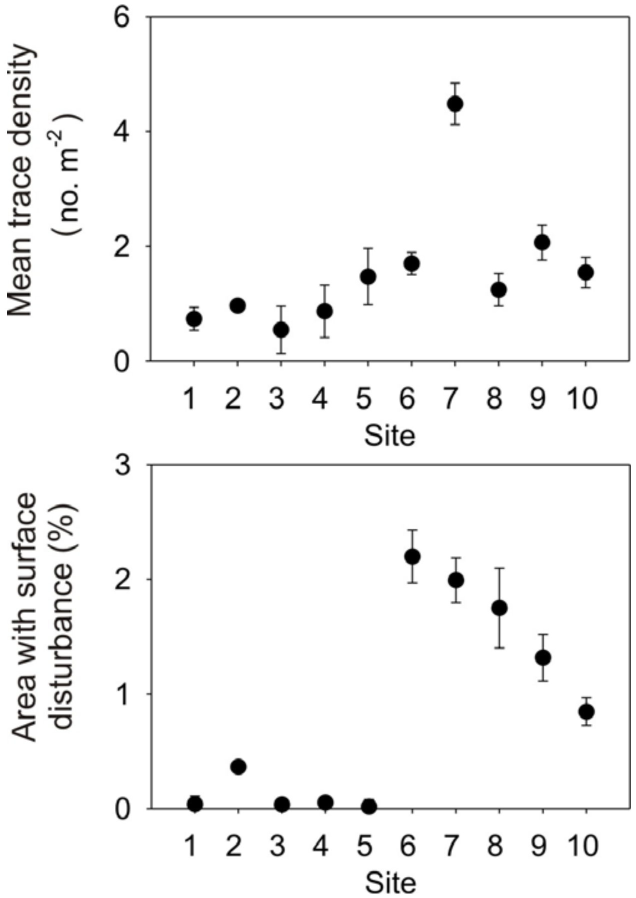


Figure 3.8: Mean number of *Lebensspuren* per photograph (number m^{-2}) and average percentage of seabed with surface disturbed by *Lebensspuren* per photograph at each site on the Faroe-Shetland Channel axis. Error bars represent 95% confidence intervals.

At the southern stations, *Lebensspuren* were dominated by crawling traces and although there was some evidence of burrowing in the finer sediments, there was no evidence of deposit feeders. At the northerly stations there appeared to be appreciable bioturbation by the action of deposit feeding echinoderms as well as crawling traces and burrows.

Small circular holes and narrow ploughs were the dominant trace forms throughout the Faroe-Shetland Channel particularly in terms of number (they both occupied only a small area). At the northerly stations asteroid traces became dominant in terms of number and particularly area. At stations 7 and 8 spatangoid ploughing traces were dominant in terms of area although there were high numbers of small circular holes at theses stations. Ophiuroid traces were also important at the latter stations.

Trace area and number were found to be significantly correlated with many physical parameters in the Faroe-Shetland Channel (Table 3.5). There was a particularly notable trends in bioturbation with Total Organic Nitrogen, with large step changes occurring in both these measures at station 6.

Table 3.5: The occurrence of *Lebensspuren* on the Faroe-Shetland Channel axis floor (see also Figure 3.6) No. represents number of *Lebensspuren* per hectare, area represents % seabed occupied by *Lebensspuren.*

	Trace	1	2	3	4	5	6	7	8	9	10	11	12	Total
FSC1	no.		5466							1599	79	211		7356
	area.		0.009							0.006	0.019	0.005		0.039
FSC2	no.		1300				86			8024				9410
	area.		0.011				0.005			0.348				0.364
FSC3	no.		2585							2879				5463
	area.		0.006							0.029				0.035
FSC4	no.		4371	2895					112	1308				8685
	area.		0.011	0.018					0.005	0.02				0.054
FSC5	no.		4160	10385						160				14705
	area.		0.009	0.003						0.003				0.015
FSC6	no.		1696				747		1300	13224	90			17057
	area.		0.029				0.609		0.819	0.691	0.049			2.197
FSC7	no.		38474			518	804	22	76	3187		23	1684	44787
	area.		0.161			0.022	0.313		0.002	0.336		0.01	1.145	1.989
FSC8	no.		1660			262	10031	130		278			73	12434
	area.		0.004			0.009	1.677	0.003		0.024			0.033	1.750
FSC9	no.	584	1000			190	18695	115		71				20655
	area.	0.007	0.002			0.003	1.3	0.002		0.003				1.317
FSC10	no.	3769	3769		39		7853							15429
	area.	0.103	0.017		0.008		0.717							0.845

DISCUSSION

Abundance and Biomass

Total megafaunal abundance was found to decrease with latitude, this appeared to be related to changes in seafloor habitat within the channel and was also found in macrofaunal studies in the same area (Bett 2001). Although changes in habitat have been shown to be important in determining deep-water abundances (Hecker 1994) it is difficult to separate the effects of this from other physical factors important in driving abundance patterns, particularly depth. This has been found throughout the Arctic (Piepenburg et al. 2001) and is thought to be related to reductions in organic matter supply to the benthos with depth (Gage and Tyler 1991). In studies of the macrofauna of the Faroe-Shetland Channel the opposite was observed in shallower water, with increasing abundance and biomass with depth to around 1000m (Bett 2001; Narayanaswamy et al. 2005). However at these depths large scale hydrographic patterns appear to play an important role. Hydrographic properties are relatively constant below this depth and in comparable depth waters abundance trends in macrofauna followed a very similar pattern to that found here (Bett 2001). Megafaunal abundance in the Faroe-Shetland Channel, although variable (1.02 - 0.06 individuals m^{-2}), is generally similar to other Arctic megafaunal studies (Figure 3.9). The peak in biomass in the central channel stations, observed from the relative biomass estimates, was similar to maximal faunal abundance and may have resulted from the occurrence of conditions suitable for both deposit and filter feeding megafauna. Similar patterns were observed in macrofaunal biomass in the Faroe-Shetland Channel (Bett 2001).

Diversity

A reduction in species richness, evenness and diversity was observed with depth in this study, this is contrary to the general pattern in the Atlantic (Rex et al. 1997) and Arctic (Piepenburg et al. 1997; Starmans and Gutt 2002), but this trend seems to be typical for the Faroe-Shetland Channel (Bett 2001; Axelsson 2003). The decrease in diversity in the Faroe-Shetland Channel megafauna with depth parallels a corresponding decline in macrobenthic diversity (Bett 2001; Narayanaswamy et al. 2005). It is likely that the faunal change observed in the deep Faroe-Shetland Channel axis is the result of a combination of change in a number of physical parameters. It would seem probable that a combination of principally depth and sediment type and heterogeneity was responsible for changes in the megafaunal communities investigated here.

Despite showing an opposite trend with depth, species richness in the Faroe-Shetland Channel stations appears consistent with other studies in Arctic areas. Starmans and Gutt (2002) found very similar numbers of taxa (mean 13.5) in stations off northeast Greenland at 180-375m depth. Piepenburg et al. (2001) found lower numbers of taxa in a wider area (10 in 2358 x 1m^2 photos) in northeast Greenland; however, at lower latitudes off east Greenland (75°N), 91 taxa were found in 297m^2 of seafloor at 190-2800m depth. Species diversity measures are given in several Arctic studies and are broadly comparable to those found in this study (Figure 3.9). The distinct reduction of taxa with site (i.e. latitude) observed in the Faroe-Shetland Channel is consistent with the reduction in species richness with latitude observed by Rex et al. (1993). However, the small change in latitude over stations in the present study suggest an alternative explanation. The changes in the fauna of the Faroe-Shetland Channel axis may have been driven by the influence of different biogeographic regions, e.g. the Atlantic Rockall Trough and the Norwegian Sea. From multidimensional community analysis, the megafauna of the northern group of stations was found to be distinctly different from that of the southern group. This may reflect patterns of colonization in the Faroe-Shetland Channel linked to invasion of the channel by deeper water species from the Norwegian Sea after isolation of deep-waters following the Quaternary glaciation (Dahl et al. 1976). Low diversities in the deep Faroe-Shetland Channel, as in the Norwegian Sea, reflect a young ecosystem (e.g. Paul and Menzies 1974). There are significant thermal and physical barriers between the deep Faroe-Shetland Channel and the Rockall Trough which prevented the invasion of many Atlantic deep-sea species that occurred in the northern Atlantic and the shallow waters of the Channel (Bett 2001; Narayanaswamy et al. 2005).

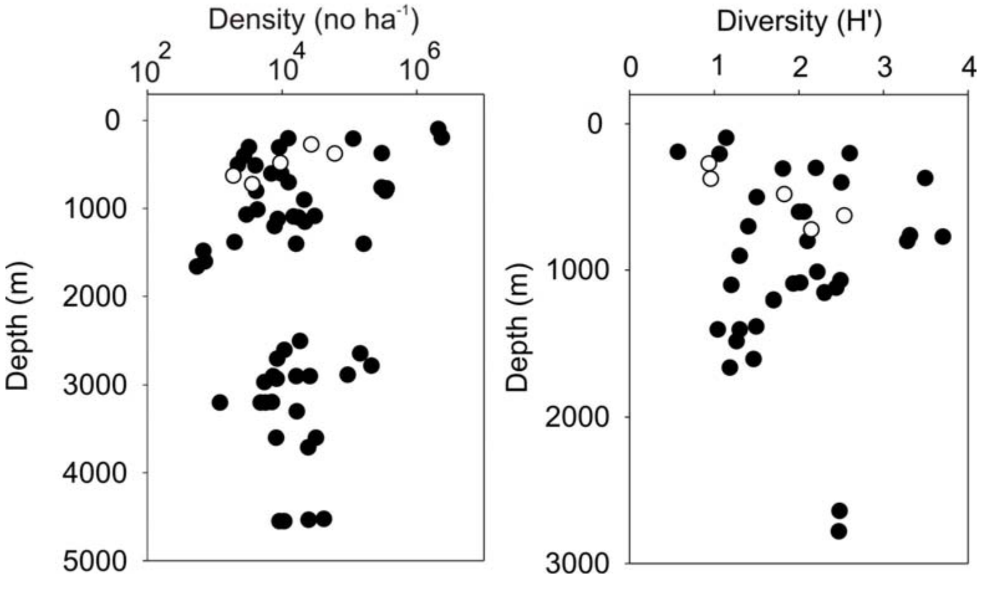


Figure 3.9: Variations in megafaunal abundance and Shannon-Wiener diversity in Arctic water studies (open circle: present study; solid circle: Dahl et al. 1976; Christiansen and Thiel 1992; Mayer and Piepenburg 1996; Starmans et al. 1999; Piepenburg et al. 2001; Axelsson 2003).

The faunal boundary observed at the Faroe-Shetland Channel is consistent with a global boundary believed to occur at around 1000-1400m depth (Day and Pearcy 1968; Rowe and Menzies 1969; Sanders and Hessler 1969; Dayton and Hessler 1972; Rex 1977; Hecker 1990). The depth at which faunal boundaries occur varies with the taxon studied and geographical location (Gage and Tyler 1991). In this study a faunal boundary for asteroids and ophiuroids was found to occur between 1100 and 1200m, this is similar to the faunal boundary for asteroids found by Howell et al. (2002) at 1100m in the Porcupine Seabight, northeast Atlantic and a faunal boundary for echinoderms found in the Rockall Trough (Gage 1986) at 800-1000m. This study revealed a major faunal boundary in the megafauna of the Faroe-Shetland Channel at around 1200m. Our results appear to correspond approximately with macrofauna in other north Atlantic studies, in the Hebridean Margin a highly depth-related differentiation in species composition was found (Gage et al. 1998; Bett 2001), with an overlying major environmental change occurring between 1,200 and 1,400 m.

The issue of how species diversity changes with depth is prevalent through the deep-sea literature (Sanders and Hessler 1969; Rex 1973; Poore and Wilson 1993; Smith et al. 1998). Most deep-sea species diversity literature focuses on macro- or meio-benthic fauna, reflecting the availability of gear for quantitative sampling of these fractions. Megabenthic organisms, those large enough to be identified in photographs (Grassle et al. 1975), are classically sampled using trawls that can only provide a semi-quantitative estimate of megabenthic diversity. Advances in deep-sea camera technology (Ewing et al. 1967) and in particular the use of towed camera platforms (Huggett 1987) has allowed large-scale quantitative assessment of megabenthic species diversity and standing stock, permitting comparison of deep-sea megabenthic diversity with that of other faunal groups.

Species distribution patterns

The dominant phyla found in this study are similar in proportion to those found in the Norwegian Sea, Hebridean Margin and the Rockall Trough (Dahl et al. 1976; Gage et al. 1985; Gage 1986; Christiansen and Thiel 1992; Gray 1994; Thurston et al. 1998). Compared to the Atlantic, however, there were notable differences, particularly in the absence of holothurians in the FSC, typically the dominant taxon in the bathyal Atlantic (Thurston et al. 1994) the apparent absence of reptant decapods and regular urchins from the deep FSC is also notable. Megafaunal comparisons between the FSC and the Barents Sea around Svalbard (Piepenburg et al. 1996) reveal a similar overall suite of taxa, however the faunal compositions of distinct communities identified by Piepenburg et al. did not correspond to faunal groups found in the FSC. The Norwegian Sea, in common with other basins populated comparatively recently (after the quaternary glaciation) has relatively few species compared with the much older fauna of the Atlantic basin (Dahl et al. 1976). Compared with the Faroe-Shetland Channel, the fauna of the deep Norwegian Sea has a number of clear differences, there are very low numbers of ophiuroids and high numbers of holothurians (particularly *Elpidia glacialis*) in the Norwegian Sea, although the numbers of actiniarians, gastropods, pycnogonids and sponges are broadly similar (Dahl et al. 1976). Many of the megabenthic species of the Faroe-Shetland Channel are very poorly known, with the pioneering works by Wyville Thomson (Thomson 1872a; Thomson 1872b; Thomson 1873) remaining some of the most informative studies on many of these organisms. As many of the physical parameters measured were inter-correlated it is difficult to assess causes for the observed faunal pattern. The apparent north-south zonation observed is likely the result of several direct and indirect processes operating on various spatial and temporal scales (Carney et al. 1983).

There are differences in sedimentary regime between the northern and the southern stations which appear to be an important factor governing faunal distribution in the FSC (Fautin et al. 2005; Tyler et al. 2005); this has often been cited elsewhere as the cause for faunal change, especially on the upper slope (Carey 1965; Haedrich et al. 1975; Starmans et al. 1999). The availability of hard substrata, such as ice-rafted stones and boulders, may also have restricted the distributions of sessile species such as sponges and soft corals (Gage and Tyler 1991). In this study a separation of the fauna in station 2 (with no hard substrata) in multivariate community analysis was likely driven by changes in habitat between this and neighbouring stations. Seabed properties have been shown to influence the abundance of Arctic megafauna (Mayer and Piepenburg 1996; Ambrose et al. 2001). The photographs of the seafloor offered little else in the way of explanation, e.g. no significant strong current indicators were observed. However, if the width of the Faroe-Shetland Channel is used as a proxy for the current regime, with constant volume flow and reduction in width of the channel (at 1000m depth) southwards (from 119km to 25km) this implies higher current speeds to the south. Current speed has been repeatedly shown to influence deep-sea faunal community composition with higher current speeds selecting filter feeding fauna and low speeds favouring deposit feeders (Christiansen and Thiel 1992; Rosenberg 1995; Starmans et al. 1999; Gage et al. 2000).

Lebensspuren

Lebensspuren were found to be common in the more northerly areas of the Faroe-Shetland Channel, this reflected the nature of the seabed, the fauna present and their feeding strategy. At the southern sites there was a predominance of hard substrata, and few megafaunal deposit feeders were observed, these deposit feeders are typically responsible for bulk of *Lebensspuren* production (Heezen and Hollister 1971). At the northern sites, with no hard substrata, megafaunal deposit feeders were more common; TOC and TON levels were also found to be higher in the sediments perhaps indicating that this lifestyle was more profitable. The concurrent large step increases in TON (which can indicate sediment nutritional quality) and area bioturbated would suggest a possible link between food quality and the abundance of megafaunal deposit feeders in the deep Faroe-Shetland Channel, as has been observed elsewhere (Billett et al. 2001; Ginger et al. 2001). Large megafaunal deposit feeders typically produce large *Lebensspuren* from their foraging and feeding activities, the most notable in the present case being asteroids (*Stichastrella* sp. and *Zoroaster fulgens*), these are important bioturbators (Heezen and Hollister 1971). In the FSC the ratio of megafaunal suspension to deposit feeders changed from higher abundance of suspension feeders at the southern sites to higher abundance of deposit feeders at the northern sites, this was also found on the Hebridean Margin (Gage et al. 1998). The abundance of several faunal groups in certain stations, particularly spatangoids that form large *Lebensspuren*, is also responsible for the variation in traces observed. It is not (always) possible to tell the age of *Lebensspuren*, although they are typically less than a few years old (Heezen and Hollister 1971); hence the rate of removal of *Lebensspuren* is very important in interpreting the abundance and area estimates of megafaunal bioturbation (Wheatcroft et al. 1989). When the traces found in the Faroe-Shetland Channel are compared to those found in the high Arctic by Kitchell et al. (1978) and Kitchell and Clark (1979) the highest affinities are found with their ‘Biofaces 2’ which were characteristic traces for the continental rise stations. They found low trace diversity, compared with that of the Faroe-Shetland Channel with two trace types dominating the entire Canadian Abyssal Plain (CAP). Trace coverage on the CAP was much higher than in the Faroe-Shetland Channel, with 49% of stations having 70-100% areal coverage of traces and a further 43% being characterized by 35-75% coverage. Many of the traces identified in the Faroe-Shetland Channel have been recorded by Ewing and Davis (1967) in their comprehensive analysis of megafaunal traces, these included the spike trace (their group IIIA9), the narrow plough (group IIIA13), the asteroid trace (group IIIB1), the ophiuroid trace (group IIIB2), the spoke trace (group IIIB3) and the wide plough (group VA1).

CHAPTER 4 – EFFECTS OF DISTURBANCE ON COLD-WATER FAROE-SHETLAND CHANNEL COMMUNITIES

INTRODUCTION

The link between diversity and ecosystem function in marine systems is complex and while specific relationships are difficult to define, it is generally agreed that there is a positive relationship between diversity and ecosystem function (Emmerson et al. 2001, Hughes & Petchey 2001, Loreau et al. 2002, Raffaelli et al. 2002, Covich et al. 2004). Ecosystem function has been measured as a considerable number of variables and investigated using a large array of experimental approaches (Covich et al. 2004). Direct experimentation, as used in terrestrial and shallow-water systems, is practically very difficult in the deep sea, but the nature of megafaunal communities allows remote quantification of community parameters such as diversity and abundance, with accuracy, over relatively wide areas, through the use of imaging technology e.g. Remotely Operated Vehicles (ROV) (Starmans & Gutt 2002). Community parameters, such as abundance and diversity, are frequently measured as indicators of ecosystem wellbeing (Magurran 2003) and can be used as a proxy for ecosystem function in studies of the effects of disturbance on biological systems. The rate of local extinction of species with disturbance may be greater in organisms of larger size (Solan et al. 2004) emphasising the importance of monitoring the diversity of megafauna.

Megafauna play an important role in benthic systems (Smith & Hamilton 1983), particularly in arctic waters (Piepenburg et al. 1996), contributing significantly to benthic biomass (Schwinghamer 1981, Sibuet & Lawrence 1981, Christiansen & Thiel 1992), organic matter recycling (Smith 1992, Smith et al. 1993) and total benthic energy turnover (Walker et al. 1987, Piepenburg et al. 1995). Megafauna have an important role in ecosystem function particularly in dispersing and redistributing organic matter as well as significant vertical and horizontal sediment redistribution (Smith 1985, Smith et al. 1993) important in the recovery of benthic systems from disturbance (Romero-Wetzel & Gerlach 1991). Quantitative understanding of megafaunal abundances and spatial pattern is important in assessing ecosystem effects and resilience to / recovery from physical anthropogenic disturbance, an impact that is becoming more widespread in the deep sea (Bluhm 2001). Seabed imaging highlights ecological pattern and structure in deep-water benthic systems, allowing a detailed assessment of the ecosystem that is not possible with traditional trawl or grab studies (Solan et al. 2002). Video allows focus on patterns within megafaunal species assemblages at scales relevant to community pattern and the areal extent of disturbance (Hewitt et al. 1998) without introducing additional disturbance through the act of physical sampling. The real time observation and manipulation capability of ROVs is important for detailed study and collection of voucher specimens permitting identification of species that may not be possible, and is often limiting, in other photographic studies (Thurston et al. 1994).

The benthic communities of the Faroe-Shetland Channel experience anthropogenic disturbance primarily from trawl fishing (Bullough et al. 1998) and increasingly from the activities of the oil and gas industry (Davies & Kingston 1992, Olsgard & Gray 1995). Disturbance is important in natural benthic communities as a source of temporal and spatial heterogeneity (Sousa 1984) that may act to maintain species diversity (Dayton & Hessler 1972). Diversity is maintained by preventing competitive exclusion by dominant species in an assemblage (Connell 1978) and, particularly in the deep-sea, by providing increased habitat diversity and niche availability (Gage 1996). As the magnitude of disturbance further increases, diversity may be reduced as physical stresses reach levels that exclude many species. Anthropogenic disturbance is often sufficient to cause some loss of diversity in marine systems, particularly in the deep sea (Bluhm et al. 1995, Borowski & Thiel 1998). As the oil industry expands to deeper waters in the Faroe-Shetland Channel, it is important to characterise and understand the natural communities and detect reliably the effects anthropogenic disturbance is having on community ecology (Underwood 1994). There is also a need for ecological research to become more concerned with problems of anthropogenic influence on natural systems at spatial and temporal scales of relevance to the organisms and habitats affected (e.g. Peters 1991).

The main objectives of this study are to determine: (1) the effects of physical anthropogenic disturbance on megafaunal ecosystem functioning in a deep-water area, and (2) aspects of the ecology of megafaunal communities in the cold waters of the Faroe-Shetland Channel that aid understanding of the effects of present and future disturbance.

MATERIALS AND METHODS

Study area

The West of Shetland hydrocarbon fields are located on the southern flank of the Faroe-Shetland channel (Figure 4.1). This area supports a high diversity of deep-water habitats and fauna which have been reviewed for the majority of the Faroe-Shetland

Channel in the U.K. Atlantic Margin Environmental Survey (Bett 2001). The Faroe-Shetland Channel harbours a wide variety of megafaunal species, but, despite the long duration of study in this area (Thomson 1873) there have been relatively few detailed studies on the megafauna. This is especially true for the megafaunal communities living in the cold, arctic water in the deeper areas (>600m) of the channel (Bett 2001). From what is known, the abundance of hard substratum (iceberg rafted drop stones) leads to a well developed encrusting epifauna with crustaceans and echinoderms being important faunal components on softer substrata (Bett 2001).

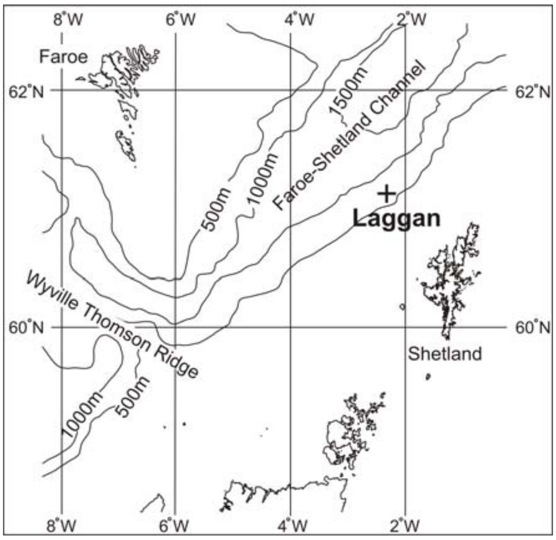


Figure 4.1: Chart showing the location of the Laggan study site in the Faroe-Shetland Channel.

The Faroe-Shetland Channel is an important area for exchange of water between the Arctic and Atlantic oceans with warm Atlantic water (>8°C) overlaying cold, subzero temperature, Norwegian Sea Deep Water (2 to -1°C) (Turrell et al. 1999). The boundary between the warm and cold waters is dynamic and may occur variously between 400 and 600m depth (Bett 2001). The benthic ecology of the Faroe-Shetland Channel is dominated by changes in hydrography as well as depth and sedimentary properties. Macrofaunal diversity is shown to be strongly linked with hydrography, with a diversity maximum at the boundary between warm and cold waters and declining diversity with greater depth (Bett 2001; Narayanaswamy et al. 2005).

At the Laggan study site (Figure 4.1), the benthic fauna experience low water temperatures (measured by ROV temperature probe as -1 to 2°C over the seven days prior to this study), moderate currents (circa 0.25m s^{-1}, estimated from ROV footage) predominantly to the north east and strong enough to form mobile bedforms (sand ripples, 150mm wavelength, indicating currents up to 0.6 m s^{-1}) in the newly deposited drill spoil (Stride 1982). ADCP current meter data (Figure 4.2) from a depth of 494m revealed a complex pattern. Tidal cycles (semi-diurnal and spring/neap) are evident as is the near-consistent flow to the northeast, this is likely to be Norwegian Sea Arctic Intermediate water, with temperatures of 2 - 0°C (Turrell et al. 1999). There is also a short period (centred 10/04/2004) of southwesterly flow which, with temperature observations of -1°C, indicate the presence of Faroe-Shetland Channel Bottom Water (Turrell et al. 1999). The residual current observed (38 day record) had a flow direction of 040° and an average speed of 0.16 cm s^{-1}.

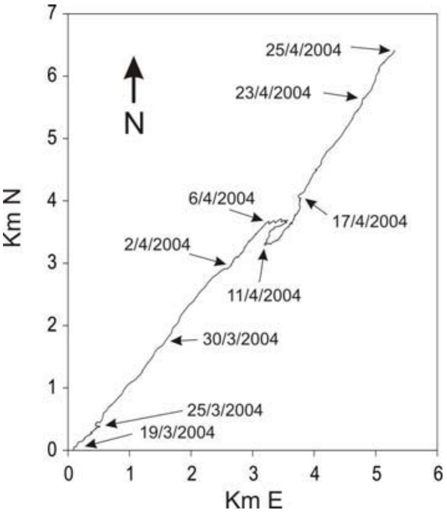


Figure 4.2: ADCP current meter progressive vector plot, 494m water depth at Laggan site. Data courtesy of Fugro.

The present investigations were carried out onboard the semi-submersible drilling platform “Jack Bates” (600m water depth, 60°56.72´N 02°53.48´W) between 14 and 23 April 2004 at the Laggan field. During drilling of the well investigated (drilling commenced 25 March 2004) 2700 tonnes of drill cuttings (1080m^3) and 3000 tonnes of water based mud (2528m^3) were discharged.

For the purposes of this study, the seabed around the source of disturbance was divided into 50m zones radiating from the blow out preventer (BOP), a structure on top of the well, put in place after the initial drilling disturbance was caused. The distance of the ROV from the BOP was measured using sonar fixes on a clear sonar target. The extent of drill cuttings was characterised as follows: ‘complete cuttings’ (>95% cuttings coverage), ‘visible cuttings’ (where patches of cuttings were visible on ROV video) and ‘no cuttings’ (where no cuttings could be seen on the ROV video). Graduated poles were placed on the seabed before drilling to assess spoil depth. The seabed drilling activity provided the indicator for physical disturbance examined in this study.

Data collection

Data were collected using an industry-operated work-class Clansman ROV equipped with a colour video camera (Remote Ocean Systems) and digital still camera (Kongsberg OE14-208), flash (Kongsberg OE11-242) and Sonar (Tritech). Cameras were mounted on a pan and tilt unit at the front of the ROV, which enabled oblique video to be taken. Before each transect the video was zoomed out to maximum extent and the camera was set to its most vertical angle (47° below the horizontal). Video transects were conducted radiating from the BOP, the ROV was run in a straight line on a set bearing at a constant speed ($0.3 \mathrm{ms}^{-1}$) and altitude (0.2m). Transects were typically 250m in length, the maximum extension of the ROV's tether. Transect width (0.91m) was calculated from the camera acceptance angles (θ = horizontal angle, ω = vertical angle), the angle of the camera from vertical (δ) and vehicle altitude (a):

$$width = 2.\sin(0.5\theta).\sqrt{(a.\sin(90-\delta-0.5\omega))^2}+a^2)$$

Transect width was also verified by passing over objects of known size on the seafloor. The optical resolution of the cameras permitted all organisms larger than 5 cm to be reliably identified. In addition to transects, ROV suction sampling, detailed inspection and still photography of selected individual organisms were used to aid species identification.

Pre-drilling qualitative video surveys of the immediate area around the drill site had previously been undertaken to ascertain the general nature of the seabed and megafaunal community prior to disturbance by drilling.

Data analysis

Video transects were replayed at half speed and all visible organisms were counted along the entire transect. Colonial organisms were counted as single individuals. Infaunal species, when seen, were counted if enough of their body was visible for identification. Only benthic fish were counted, i.e. those fish that dwell on and feed at the seabed. Abundances were then standardised to numbers per hectare.

Two separate classification schemes were adopted, distance from point source of disturbance and visible seabed disturbance. (1) Distance was used as a proxy for intensity of initial disturbance, which is assumed to occur approximately symmetrically around the source of disturbance. Initial disturbance is thought to result in very high sediment deposition rates and turbidity. (2) Visible seabed disturbance reflects the actual situation present at Laggan, it is different from the initial impact as a result of longer term redeposition of material in predominant currents; visible seabed disturbance represents the more sustained effects of disturbance through smothering. For analysis by distance from disturbance, each transect was partitioned into 50m lengths. For analysis by visible disturbance categories, each transect was partitioned into 3 visible disturbance categories (complete, visible and no cuttings), numbers were standardised to densities as partitions were not of equal length. For both analyses, within each partition, counts from three randomly chosen transects were pooled to form each sampling unit (resulting in 27 sampling units for distance and 18 for visible disturbance).

Megafauna were divided with respect to motility into mobile and sessile taxa. Fauna were also divided by predominant feeding mode into sestonivores (filter and suspension feeders), deposit feeders and predators/scavengers.

A range of univariate diversity indices were calculated to assess both the dominance and species richness aspects of diversity (Magurran 2003, Gotelli & Colwell 2001). These measures were principally calculated using PRIMER (see below), the Berger-Parker index calculated by spreadsheet, and sample based species density rarefaction implemented using “EstimateS” software (Colwell et al. 2004).

Community analysis is based on densities of all taxa, a square root transformation was applied to buffer the influence of domianant taxa (Field et al. 1982). Similarities were calculated using Bray-Curtis coefficients (Bray & Curtis 1957). The similarity values were subjected to both classification (hierarchical group-average clustering) and ordination (non-metric multi-dimensional scaling) using the software PRIMER (Clarke & Warwick 2001). Other PRIMER routines (e.g. ANOSIM and MVDISP) were also used to further examine the results of the community analyses (Clarke & Warwick 2001).

RESULTS

Analysis of ROV video footage revealed a total of 2135 megabenthic organisms from 27 nominal taxa (Table 4.1) in a total area surveyed of 3767m^2. Arthropods (39% megafauna, up to 4786 ha^{-1}) were predominantly *Pandalus borealis* although included hermit crabs, tube dwelling amphipods and *Colossendeis* sp. pycnogonids. Porifera (34% total megafauna, up to 3797 ha^{-1}) were grouped morphologically into taxa but could not be identified further. Echinoderms (23% total megafauna, up to 2418 ha^{-1}) were dominated by the urchin *Echinus elegans*, asteroids (*Ceramaster granularis granularis* and *Henricia pertusa*) although other asteroids, ophiuroids and comatulid crinoids were also present. The ophiuroid *Ophiactis abyssicola* was very common (~ 100 m^{-2}), as seen in high resolution still photographs and suction samples although it was too small to be identified from the transect survey video footage. The remainder of the megabenthos (4%) comprised of molluscs, cnidarians (actiniarians and alcyonarians) and benthic fish.

Table 4.1: Abundance and composition of megafaunal communities around the Laggan site, tabulated by distance from disturbance source, and by level of disturbance (full, total seabed smothering; partial, disturbance visible on seabed; none, no visible disturbance to seabed).

					Density (no. ha^{-1})				
	Functional group	0-50m	50-100m	100-150m	150-200m	200-250m	Full	Partial	none
Sponges									
Indet. encrusting sponge	Sestonivore	0	293	1600	1439	952	88	728	1526
Indet. Sponge	Sestonivore	0	183	1868	1622	842	135	896	1549
Indet. Sponge 2	Sestonivore	0	12	122	131	18	13	75	92
Indet. Sponge 3	Sestonivore	0	0	12	0	0	0	0	6
Indet. Sponge 4	Sestonivore	0	0	122	118	18	0	19	109
Indet. Sponge 5	Sestonivore	0	24	12	52	37	0	37	40
Indet. Hexactinellid	Sestonivore	0	24	73	131	0	0	112	69
Cnidaria									
Indet. Actinarian	Sestonivore	0	49	147	170	37	13	75	144
Indet. Alcyonacean	Sestonivore	0	0	37	52	18	0	0	46
Mollusca									
Colus icelandicus	Predator/scavenger	0	0	24	39	0	0	0	29
Sepiola atlantica	Predator	0	0	12	0	0	0	0	6
Arthropoda									
Pandalus borealis	Predator/scavenger	12	415	4664	3872	1538	249	2558	3600
Pagurus sp.	Predator/scavenger	0	24	122	131	110	7	131	115
Indet. Tube dwelling amphipods	Sestonivore	0	0	0	39	0	0	0	17
Colossendeis sp.	Predator	0	12	0	13	0	0	19	6
Echinodermata									
Henricia pertusa	Predator	12	110	635	484	275	34	411	513
Indet. Long armed Asteroid	Predator	0	0	24	0	0	0	0	12
Ceramaster granularis	Predator	61	171	598	432	476	40	429	564
Indet. White asteroid	Predator	0	0	0	0	18	0	0	6
Pteraster militaris	Predator	0	12	134	131	92	27	93	104
Echinus elegans	Deposit feeder	85	232	928	968	403	101	654	852
Heliometra glacialis	Sestonivore	37	24	98	92	55	13	112	98
Fish									
Indet. Juvenile fish	Predator	12	37	85	13	18	13	75	40
Lycodes esmarkii	Predator	24	12	171	39	0	7	112	81
Gaidropsarus argentatus	Predator	0	0	0	0	18	0	0	6
Raja hyperborea	Predator	0	0	0	13	0	0	0	6
Cottunculus microps	Predator	0	0	24	0	0	0	0	12
Additional species									
Epimeria loricata	(Amphipod)								
Pardalisca abyssi	(Amphipod)								
Atylus smitti	(Amphipod)								
Nymphon sp.	(Pycnogonid)								
Ophiactis abyssicola	(Ophiuroid)								
Myxine glutinosa	(Hagfish)								
Sebastes sp.	(Redfish)								
Brosme brosme	(Tuskfish)								

Pre-disturbance and beyond the disturbed area there was a highly heterogeneous distribution of benthic megafauna. The distribution of megafauna in these ‘natural’ seabed areas was primarily driven by substratum type and the availability of suitable microhabitats. The stochastic arrangement of ice rafted cobbles and boulders is important in determining the small-scale distribution of the megabenthos. Most sessile filter feeders were attached to hard substrata; many of the echinoderms preferred softer sediments, being more common in gravel and sand areas.

Physical disturbance from drilling resulted in local scale (<100m) smothering of the benthos, particularly in the direction of the residual current (Figure 4.3). The disturbed area, with complete smothering (~ 28400m^2) was larger than typical as a result of repeat drilling. The seabed was smothered to a maximum depth of 1m, although typically a lesser thickness. Disturbance was visible over a wider area (>66800m^2) where disturbed sediment had collected in depressions and in the lee of ice-rafted boulders. Outside this area the seabed appeared to be unaltered when compared to pre-disturbance ROV footage from the study site; it consisted of a heterogeneous mix of sand, gravel and occasionally cobbles and boulders.

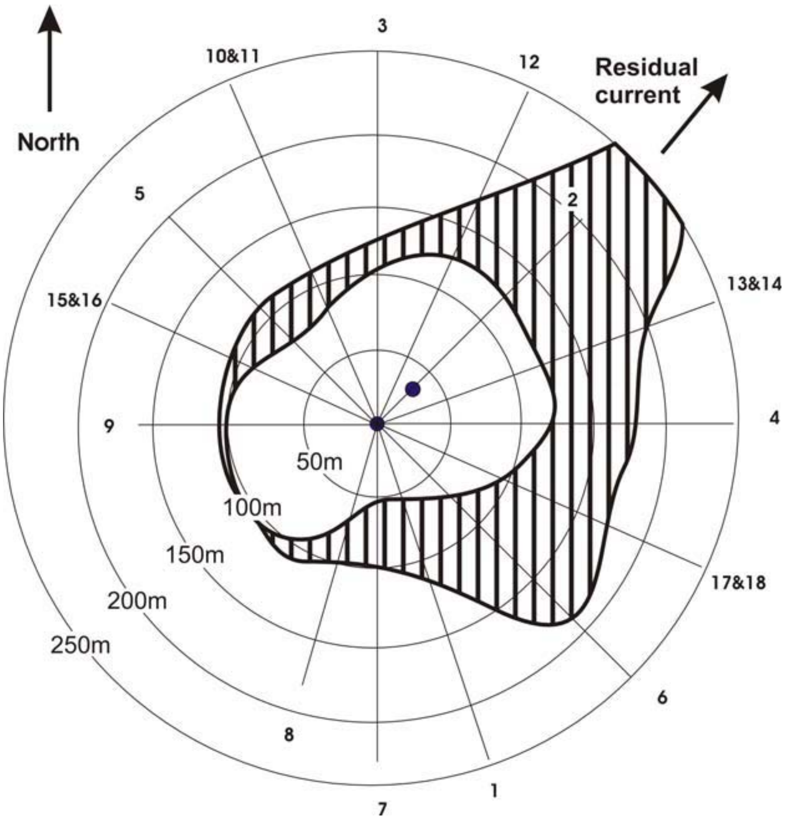


Figure 4.3: ROV transects (1-18) conducted around the Laggan site, showing the extent of complete (central white area) and partial (hatched area) physical disturbance of the seabed, and 50m zones radiating from the disturbance source. The filled circles represent drilling locations.

Complete seabed disturbance resulted in low total megafaunal abundance with typically only small numbers of errant benthic megafauna. Larger boulders occasionally protruded above the level of smothering, acting as islands of megafaunal abundance; these boulders account for almost all observed benthic megafauna in the complete spoil areas. The seabed drilling structure did not appear to attract large numbers of fish as seen in other West of Shetland locations (authors' personal observations), although eelpouts (*Lycodes esmarkii*) were observed sheltering beneath it. Total megafauna abundance was significantly different between disturbance regimes (Kruskal Wallis, H = 25.31, df = 3, 17 p < 0.001), being higher in partially disturbed areas than those with full disturbance (Moods median test Chi-Sq = 5.33, $p < 0.05$) although there were no significant differences in abundance between partially disturbed areas and those with no disturbance (Moods median Chi-Sq = 1.33, $p = 0.25$). Total abundance was very low near the source of disturbance (0-50m zone; Table 4.2), it was highest at intermediate distances from the source of disturbance (11,514 individuals ha^{-1} at 100-150m) and reduced somewhat with further increasing distance (Figure 4.4).

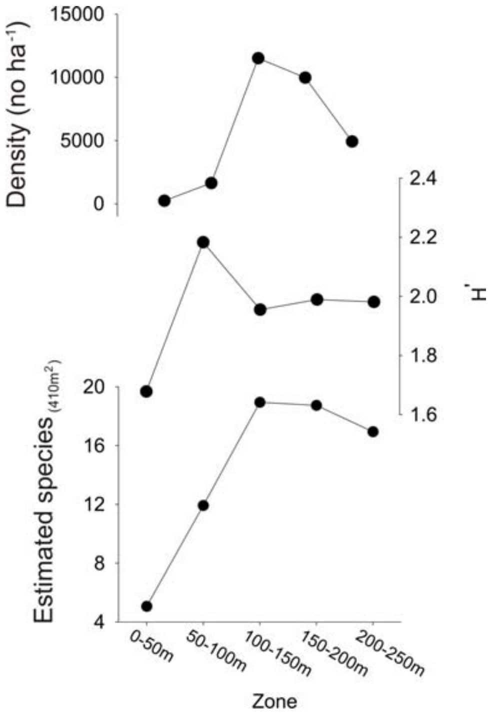


Figure 4.4: Variations in faunal density and diversity (H´, Shannon-Wiener Index; ES$_{(area)}$, Mao Tao estimate of species density) around the Laggan site with distance from source of disturbance.

Univariate diversity indices (Table 4.2) indicated depressed megafaunal diversity in both the 50m zone and the complete disturbance zone (Figure 4.3), with further reaching effects noted for rarer species (type I indices). Shannon-Wiener diversity was elevated in the 50-100m zone (Table 4.2; Figure 4.4), dropping slightly beyond 100m. Estimated species density (Figure 4.4) increased from very low values near the source of disturbance to maximal levels at intermediate distances, slightly declining with increased distance. The fauna in both the completely disturbed and 0-50m zone formed a distinct grouping on the Multi-Dimensional Scaling (MDS) ordination, with low similarities with the less disturbed areas (26.0% for 0-50m; 48.6% for complete disturbance; Figure 4.5 A). Analysis of similarities (ANOSIM) indicated statistically significant ($p < 0.05$) differences between the 0-50m zone, the completely disturbed area and all other zones (Table 4.3).

Table 4.2: Variations in megafaunal species diversity measures around the Laggan site, tabulated by (A) distance from disturbance source, and (B) level of disturbance (mean density (no. ha^{-1}); B-P, Berger-Parker index; SI, Simpson's index [1-λ′]; H′, Shannon-Wiener index [$\log_e$]; ES(n), rarefied species richness; ES(area), Mau Tao estimate of species density).

A

Zone	Density (no. ha^{-1})	B-P	SI	H'	ES(240)	S	ES(410m^2)
0- 50m	244	0.35	0.78	1.68	7.00	7	5.06
50-100m	1636	0.25	0.85	2.18	15.32	16	11.92
100-150m	11514	0.41	0.78	1.95	16.54	22	18.94
150-200m	9982	0.39	0.79	1.99	16.77	21	18.73
200-250m	4927	0.31	0.82	1.98	14.15	17	16.94

B

Level of disturbance	Density (no. ha^{-1})	B-P	SI	H'	ES(500)	S	ES(545m^2)
Complete disturbance	740	0.34	0.78	1.85	12.91	13	21.73
Partial disturbance	6536	0.39	0.82	2.12	16.75	17	17.13
No disturbance	9647	0.37	0.81	2.06	20.61	27	5.83

Table 4.3: Tabulation of PRIMER ANOSIM R-statistics from tests of variation in megafaunal community composition around the Laggan site, by (A) distance from disturbance source, and (B) level of disturbance (ns, p > 0.05.*, p < 0.05; **, p < 0.001).

A

	50-100m	100-150m	150-200m	200-250m
0-50m	0.342 *	0.987 **	0.985 **	0.932 *
50-100m	-	0.544 **	0.483 **	ns
100-150m	-	-	ns	ns
150-200m	-	-	-	ns

B

	Partial disturbance	No disturbance
Complete disturbance	0.328 *	0.391 *
Partial disturbance	-	ns

The megafaunal communities in partially disturbed areas were not distinct from those with no disturbance (Table 4.3). The benthic community in the area with no visible disturbance was quite homogeneous in composition, i.e. the undisturbed sample units formed a very tight group in the MDS plot (Figure 4.5A: MVDISP = 0.41), whereas more scatter is evident in those from disturbed areas (Fig. 5 A; MVDISP: partial disturbance = 0.99, full disturbance = 1.59). Megafaunal community composition becomes more consistent with distance from the disturbance source (Figure 4.5 B). ANOSIM reveals a distinct fauna in the areas >100m away from the disturbance source with significant differences from closer, more disturbed areas (Table 4.3). This trend is clear from the MDS plot (Figure 4.5 B) with a distinct grouping of comparatively “undisturbed” sites (65.0% similarity; mean MVDISP = 0.66), as distinct from the diffuse spread of the “disturbed” sites (mean MVDISP = 1.45).

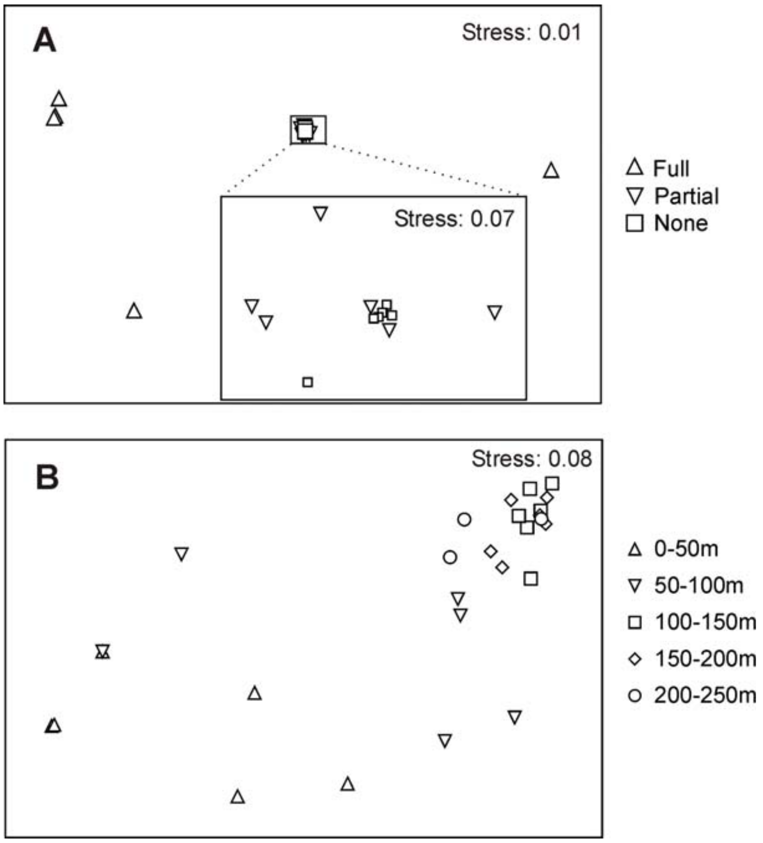


Figure 4.5: Non-metric multi-dimensional scaling ordination of the megafaunal communities around the Laggan site. (A) Assessed by level of disturbance, and (B) by distance from disturbance source.

Mobile megafaunal density was higher than sessile in all disturbance regimes. The total abundance of sessile fauna increased with reduced disturbance, motile fauna had highest abundance at intermediate disturbance. The proportion of motile to sessile forms is broadly similar except in the partial disturbance zone where there is a higher proportion of mobile fauna (Figure 4.6 A). The total abundance of sessile and motile forms increased with distance from the source of disturbance, peaking at intermediate values, but the proportional abundance remained broadly similar except close to the source of disturbance where motile fauna were proportionally much more abundant than sessile (Figure 4.6 B).

Predator / scavengers were consistently the most abundant feeding group and deposit feeders the least abundant group in all disturbance regimes. The abundance of all feeding groups increased with reduced disturbance (Figure 4.6 C) and are all highest in the 100-150m zone (Figure 4.6 D). The proportional abundance of each group did not change significantly with distance from disturbance except close to the source of disturbance where there was a reduced proportional abundance of sestonivores and increased proportional abundance of deposit feeders.

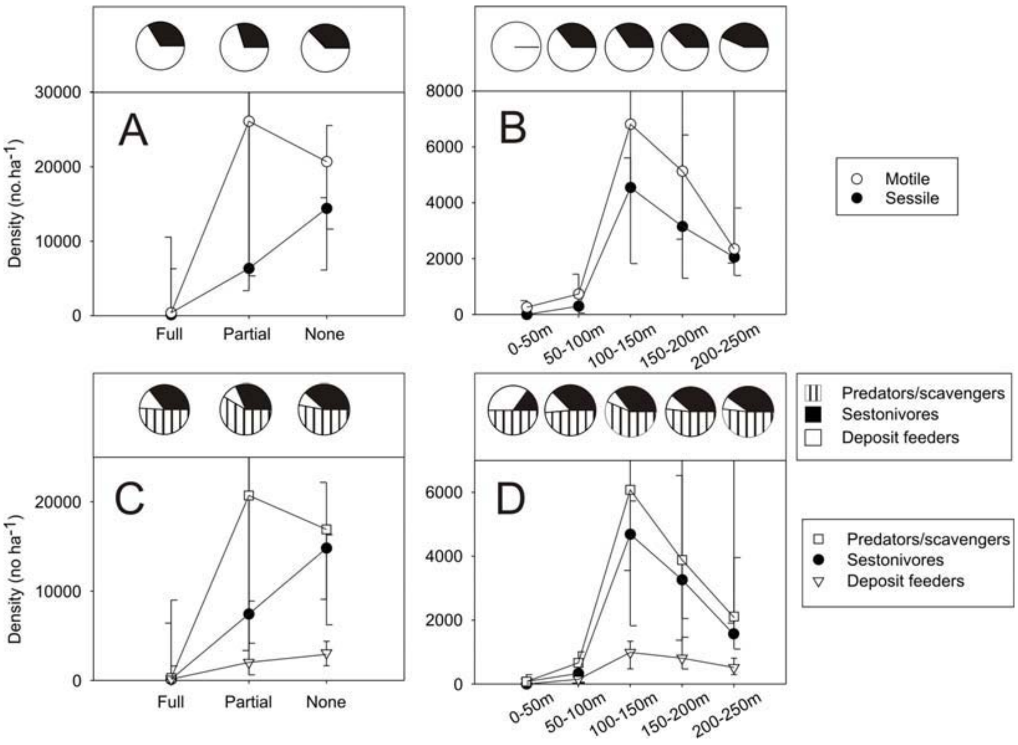


Figure 4.6: Variations in the median abundance and composition of megafaunal functional groups around the Laggan site. Illustrating faunal motility (A and B) and feeding mode (C and D) in relation to disturbance level (A and C) and distance from disturbance source (B and D). Error bars represent 95% confidence intervals calculated using a 1-sample sign test; pie charts show corresponding proportional abundance of functional groups.

In the above, we have analysed disturbance in terms of both observed seabed disturbance and distance from disturbance source. The asymmetric distribution of drill cuttings (see Figure 4.3) results in an ‘imperfect’ match between distance and apparent disturbance. We have therefore also examined community parameters for trends with disturbance within distance zones (Figure 4.7). Total megafaunal abundance (Figure 4.7A) in disturbed areas increased with distance from disturbance source; in the less disturbed areas, total abundance peaked at intermediate distances. The proportional abundance of motile fauna (Figure 4.7B) was generally higher than sessile in disturbed areas, with highest proportional abundance of motile fauna at intermediate distances from disturbance. In undisturbed areas motile to sessile faunal proportional abundances reduced with distance from disturbance, to approximately equal abundances at 150-200m from disturbance. Species richness (Figure 4.7C) was consistently high in less disturbed areas; in more disturbed areas richness increased with distance. Species diversity measures have revealed significantly reduced diversity with proximity to disturbance source but, in the intermediate zones depicted (Figure 4.7D) there is no significant change in H′ with distance within the disturbed ($H = 5.46$, $p = 0.07$) or less disturbed areas ($H = 6.98$, $p = 0.07$).

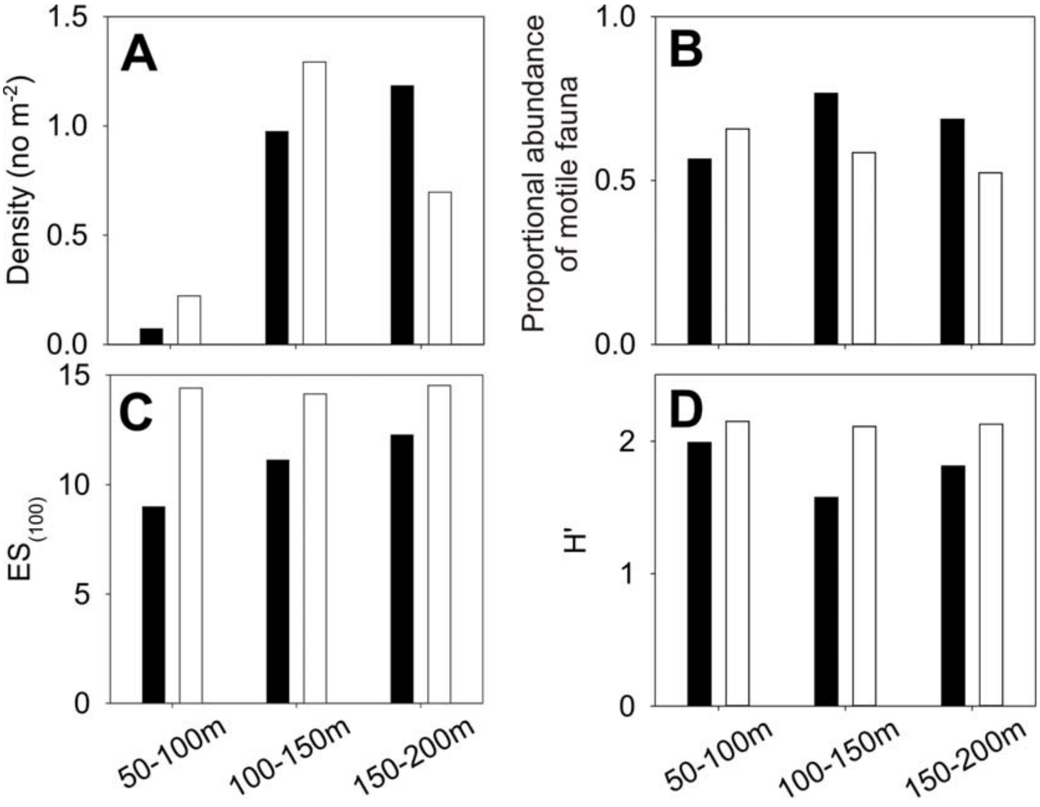


Figure 4.7: Comparisons of megafaunal abundance and diversity in more (black bars) and less disturbed (white bars) areas within three distance zones around the Laggan site (H´, Shannon-Wiener index; ES$_{(n)}$, rarefied species richness).

DISCUSSION

Megafaunal abundance at Laggan was significantly reduced by disturbance. Megafaunal numbers were very low in disturbed areas and close to the disturbance source. As this study was completed within a month of the initial disturbance, this reflected the initial disturbance of the communities by physical smothering and burial of organisms also observed in other studies (Stronkhorst et al. 2003). Highly motile organisms responded by moving away from the disturbance, as has been noted in many previous studies (e.g. Bluhm 2001), but for less motile taxa, motility was inversely proportional with mortality. Outside the area of complete disturbance megafaunal taxa responded differently to disturbance, likely a result of a complex interaction of factors including feeding mode, motility, particle removal rate and rate of sedimentation.

Predator / scavenger abundances increased dramatically in the disturbed zones at Laggan as a result of increased mortality of other taxa and potentially increased available food (i.e. carrion) as observed in shallow-water studies (Ramsay et al. 1998; Dolmer et al. 2001). There may have also been some enrichment effects, with recently exposed sub-surface sediments providing a food source for meio- and macro-faunal prey species.

The sestonivores increased in abundance with reduction in disturbance at Laggan. Although such taxa may experience enrichment effects these would likely be outside the zone of this study (i.e. >250m) and over periods of longer duration than the present study. Survival of sestonivores at Laggan was shown to be directly related to motility. The impact of disturbance on sessile forms would be related directly to levels of suspended solids and to their ability to clear particles from their feeding and respiratory surfaces, as observed in many shallow-water sessile organisms (Rogers 1990). Disturbance may also have sub-lethal effects on megabenthic organisms, particularly sessile forms, that are not addressed in this study.

Deposit feeder abundance was not significantly different between partial and undisturbed areas at Laggan, these taxa are typically adapted to handling large amounts of particulate material and so may not be as susceptible to increased sedimentation. Deposit feeders, such as epibenthic echinoids and holothurians, are likely to be amongst the first recolonisers of the disturbed area. The increased availability of fine particles may reduce the need to sort through larger mixed size sediment complexes (Hudson et al. 2004) potentially allowing greater turnover and increased reprocessing of organic material within disturbed areas. In undisturbed areas, deposit feeder abundance may be limited by high abundances of suspension feeders (Gray 1974). The reduction in suspension feeders resulting from disturbance, along with the changes to the substratum observed at Laggan, may have promoted the preferential recolonisation of impacted areas by epibenthic deposit feeders, thereby changing overall species composition and allowing deposit feeders to dominate the disturbance/recolonisation community.

At Laggan faunal abundances increased with reductions in disturbance. In this study it is not known if abundances are at or near ‘normal’ levels, an indication of this can be gained from comparison with other, undisturbed ecosystems in similar physical environments (Figure 4.8). The megafaunal communities of the Laggan area, although not arctic by location, essentially inhabit arctic waters from the Norwegian Sea, alternating between Norwegian Sea Arctic Intermediate Water and Faroe-Shetland

Channel Bottom Water (Turrell et al. 1999). It is therefore most relevant to compare the Laggan communities with those of the Norwegian Sea and the Arctic rather than the geographically closer Rockall Trough. Abundances were compared with respect to depth as it has been shown to have important controls on faunal abundances (Piepenburg et al. 2001). While megafaunal abundance at Laggan was variable in areas of no or limited disturbance (244 to 11,514 individuals ha^{-1}), it is towards the low end of values found in other undisturbed arctic megafaunal studies. Faunal abundances typically increase until a point is reached where all available resources are utilised and inter- and intra-specific density-dependant processes limit abundances of each species (Begon et al. 1990). In disturbed areas, faunal abundance was clearly reduced in comparison to other studies. Faunal abundance provides an indication of ecosystem production, and the low abundances of this study may reflect a reduction in ecosystem production as a result of disturbance. These comparisons must be tentative as a result of physical differences between sites or methodological variation, particularly the inclusion of smaller faunal size classes in other studies. Nevertheless, the observed reductions in abundance with disturbance at Laggan suggest significant changes in ecosystem function.

Diversity increased with distance from the source of disturbance at Laggan. Some diversity indices showed a small decrease in diversity at maximal distance and minimal disturbance. Diversity was depressed by high disturbance but intermediate levels have been found to increase diversity levels in certain environments (e.g. Connell 1978). The trend observed at Laggan was very slight and may be attributed to reduced sampling effort at minimal disturbance sites. The whole community multivariate measures reflected a clear trend of increased similarity of megabenthic communities with decreased disturbance. This trend is commonly observed in community measures in many marine disturbance settings (Clarke and Warwick 2001).

The megafaunal diversity of Laggan, as with abundance, was variable with extent and degree of disturbance. The Shannon-Wiener diversity at Laggan was broadly similar to comparable studies of megafaunal diversity in undisturbed arctic areas (Figure 4.8), although this should interpreted cautiously given the differences in sampling methodology between studies. Shannon-Wiener diversity in disturbed areas at Laggan was low, but within the values recorded at undisturbed sites elsewhere; this may result from the typically high dominance levels observed in many undisturbed arctic megafaunal studies (Piepenburg et al. 2001; Starmans and Gutt 2002). At Laggan, H′ is driven by low richness and high evenness; unfortunately richness cannot readily be compared between studies (Gray 2000). The similarity of diversity at Laggan and in other arctic megafaunal communities suggests that the less disturbed ecosystems at Laggan have similar ‘function’ to those in comparable, undisturbed areas. Diversity is best used as a measure for ecosystem health in conjunction with information on the functioning of specific ecological aspects of the community (Raffaelli et al. 2002). Changes in diversity with initial disturbance may not adversely affect ecosystem functioning, in many cases a high diversity can act to buffer the effects of first disturbance. However, as species are displaced by disturbance it becomes increasingly likely that species dominating the functionality of an ecosystem will disappear (Hughes and Petchey 2001). Suites of species responsible for specific functions may get smaller thus increasing the susceptibility of the ecosystem to further disturbance (De Ruiter et al. 2002). In the deep-water ecosystem at Laggan there appear to be only a few megafaunal species that are responsible for some major ecosystem functions, particularly those associated with processing of soft sediments. Disturbance may have impacted the ability of the Laggan ecosystem to utilise available resources as a result of differences in species resource use and the effects of interactions among species (Hughes and Petchey 2001).

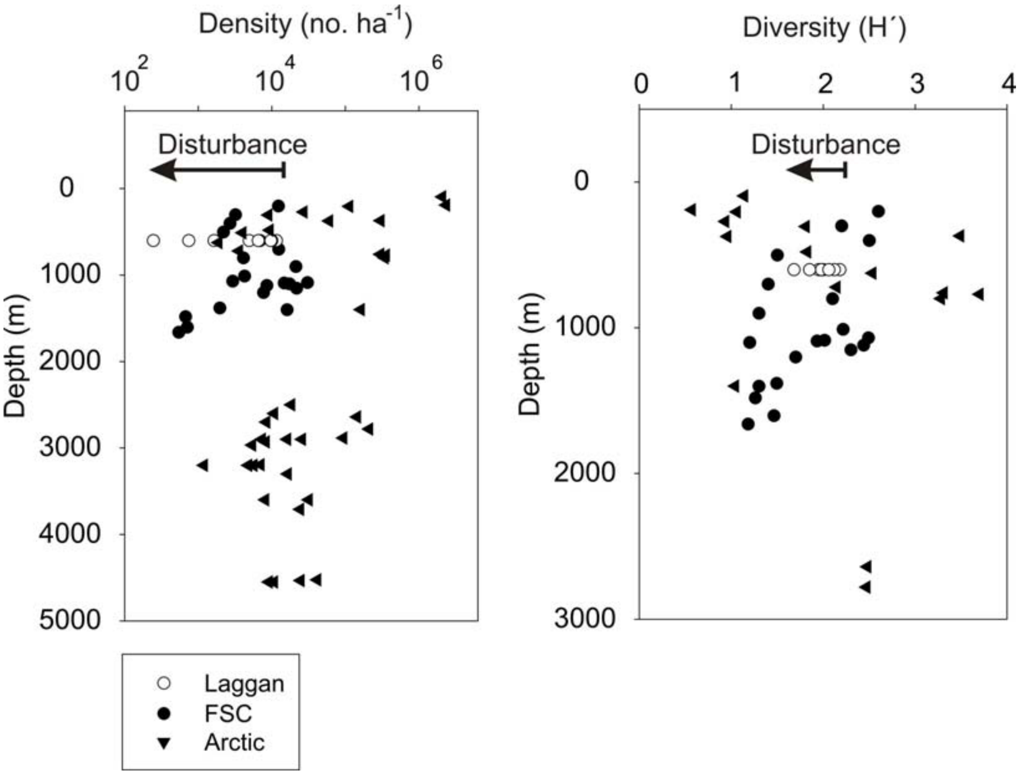


Figure 4.8: Comparisons of megafaunal abundance and Shannon-Wiener diversity (H´) with depth for this study (Laggan site: open circles; increased disturbance is indicated with an arrow), studies in the Faroe-Shetland Channel (solid circles: FSC values from Chapter 3 and (Axelsson 2003)) and other arctic studies (solid triangles: Dahl et al. 1976, Christiansen & Thiel 1992, Mayer & Piepenburg 1996, Starmans et al. 1999, Piepenburg et al. 2001).

The relative changes in megafaunal diversity and abundance with physical anthropogenic disturbance recorded at Laggan are common to other areas despite differences in the community composition. As an example, megafaunal communities at

Laggan are significantly different from those at shallower depths in the Faroe-Shetland Channel (authors' personal observations) with virtually no megafaunal species common between Laggan (600m) and shallower study sites (508m) as a result of the large changes in water mass properties (particularly temperature) that occur between these depths in the Faroe-Shetland Channel. While diversity and abundance were higher in these shallower communities, both of these measures decreased in a similar way with disturbance.

The extent of visible seabed disturbance at Laggan is relatively small in comparison with other studies of well sites (Davies et al. 1981; Olsgard and Gray 1995) but larger than found at previous well locations in this area (Block 206/1, TOTAL 2004). The widespread effects on the fauna from drilling activity on the Norwegian continental shelf (Olsgard and Gray 1995) did not appear to have occurred around Laggan. Many of these effects were attributed to the discharge of cuttings contaminated with oil-based drilling mud, in Laggan only water-based muds were discharged to the seabed (TOTAL 2004). Note , however, that comparisons with studies on macrofauna (e.g. Olsgard and Gray 1995) should be treated with caution as only megafauna were analysed in the present study.

The effects of physical disturbance at Laggan were manifested as the partial or complete defaunation of disturbed patches through physical smothering and (presumed) direct mortality. Numerous additional effects of disturbance on sediment properties were observed which may impact subsequent community recovery. Changes to sediment topography were noted as a result of disturbance, such changes can alter near bed hydrodynamics (Thrush et al. 1992) and may therefore affect the deposition of particles, such as organic matter and benthic invertebrate larvae (Dernie et al. 2003), this may be particularly important in the high current regimes to the West of Shetland. Reduced sediment heterogeneity was apparent in the disturbed areas at Laggan; this has been shown to lead to reduced diversity in the deep sea (Levin et al. 2001). The blanketing of the seabed with sediment of a different composition, such as occurred at Laggan, has been shown elsewhere to result in conditions unfavourable to the typical resident communities, reducing immigration of mobile fauna and limiting larval settlement (Snelgrove et al. 1999), and increasing recovery time. The increase in suspended particulate loading as a result of disturbance at Laggan may have lead to clogging of filter feeding apparatus of some organisms (Sharma et al. 2001).

At Laggan the most obvious environmental change with disturbance was a change from coarse to fine sediment, in studies of disturbance by trawling in shallow water, recovery was quickest in areas of coarse sediment (Thrush et al. 1995) but more stable, muddy areas recovered slowly (Tuck et al. 1998). Measured rates of recovery for mobile species from fishing disturbance were largely as a result of immigration, since what is known of life histories of benthic species (Brey 1999) suggested that population regeneration would not occur on these time scale.

Although megafauna are not typically assessed to provide indication of impact, this study along with others (Bluhm 2001; Rodrigues et al. 2001; Sharma et al. 2001) shows the utility of megabenthic assessment. The use of photography in megabenthic assessment has advantages over more commonly used trawl sampling techniques (Thurston et al. 1998). Photography allows quantitative data to be obtained on the abundance of megafauna, unlike trawls which at best provide semi-quantitative estimates of abundance (Grassle et al. 1975). Trawling is difficult in the West of Shetland area with a high risk of gear loss as a result of the large boulders present (e.g. Bett et al. 1997). Photography preserves ecological information that is lost with trawling, particularly the relationship between fauna and local habitat as well as the small-scale distribution of megabenthic organisms (Parry et al. 2002; Teixido et al. 2002). Use of ROVs allows quantitative assessment of megabenthos at a very high resolution over a wide area and unlike other photographic assessments (e.g. Hersey 1967) allowed concurrent detailed observation and sampling of the fauna, permitting positive identification of species. ROV sampling allows fragile species to be seen *in situ* then collected with minimal damage. The real-time nature of sampling also allowed the quality of the video footage to be continually assessed and transects repeated if necessary.

Summarising, this study indicates that physical disturbance in deep-water areas can have significant impacts on megafaunal communities, reducing the abundance and diversity of fauna and modifying community composition. In the case of the present study of drilling impact, the areal extent of the main effects appears to be relatively small. This work suggests the utility of ROV systems for the high resolution investigation of deep-water impacts on megafaunal communities.

CHAPTER 5: ECOLOGY OF BENTHIC MEGAFAUNAL COMMUNITIES AT KANGERDLUGSSUAQ FJORD MOUTH, EAST GREENLAND

INTRODUCTION

Changes in physical factors have long been shown to be integral in controlling ecosystem structure (e.g. Connell 1972) and this has been shown repeatedly in Arctic waters (Curtis 1975; Piepenburg and Schmid 1996a; Piepenburg et al. 1997; Piepenburg and Schmid 1997). Of these, depth is often seen as one of the greatest, and its effects have been shown to be very important in structuring marine ecosystems (Gage and Tyler 1991) as well as controlling diversity (Rex et al. 1997; Holte et al. 2004) and density (Filatova 1982). Habitat has also been found to be very important in governing the distribution of deep-sea fauna (e.g. Barthel and Tendal 1993), with reductions in habitat heterogeneity leading to reduced diversity (Levin et al. 2001). Physical disturbance is a key factor in controlling spatial and temporal variations in the composition of benthic communities (Probert 1984; Sousa 1984; Hall et al. 1994) particularly in polar areas (Conlan et al. 1998; Gutt and Piepenburg 2003). The effects of disturbance on community patterns can occur on very short to evolutionary time-scales and depend on the effects to specific species activity, life history and recruitment (Sousa 1980; Clarke 1983; Connell and Keough 1985; Gutt 2001; Conlan and Kvitek 2005; Thatje et al. 2005) as well as interspecific interactions (Gutt and Starmans 2001; Barnes and Kuklinski 2003). The presence of ice is very important in the biology of the Arctic regions causing wide scale disturbance of the seabed (Gutt et al. 1996; Conlan et al. 1998) as well as reducing potential surface production (Andersen 1989; Gutt 2001) and as a means of transporting sediment to marine environments (Syvitski et al. 2001).

The megafauna are an important constituent of many deep-sea benthic communities particularly in Arctic waters (Piepenburg et al. 1996). Motile species of epibenthic megafauna contribute significantly to the dispersal of large food falls and vertical and horizontal sediment mixing through bioturbation and bioirrigation activity (Smith 1985; Romero-Wetzel and Gerlach 1991; Smith et al. 1993). Megafaunal species may be important components in the overall energy budget of the deep sea (Lauerman et al. 1996), a quantitative understanding of their densities and spatial patterns is necessary in order to assess their contribution to energy flow through these systems (Smith 1992; Lauerman et al. 1996).

In this study, the effects of physical factors, particularly depth and sediment type, on megabenthic density, diversity and distribution is assessed through quantitative data derived from seafloor images obtained from both a towed camera platform and some of the first Autonomous Underwater Vehicle (AUV) photographs obtained of the seabed (Jones et al. 2005). This study will expand existing faunal studies of the East Greenland slope to include the megafauna, and provide an insight into the ecology of Arctic slope epibenthic megafaunal communities and how they are influenced by their physical environment, particularly depth, disturbance, habitat type and hydrography.

MATERIAL AND METHODS

Study area

East Greenland is largely influenced by Arctic waters, its shelf being dominated by the cold southward-flowing East Greenland Current as far south as Kangerdlugssuaq (Figure 5.1). There is continual ice presence in the fjords and over the shelf and slope areas, ranging from continuous sea ice in the winter to low ice cover in summer (Toudal 1999). Between Kangerdlugssuaq and Angmagssalik, Bertlesen (1937) found strongly contrasting faunas suggesting that a major biogeographic boundary occurs (Madsen 1936), separating more typical boreal marine fauna from true arctic forms. This is concurrent with an abrupt change in the mean sea temperatures between these areas (Stein 2000). The seabed in this area is composed primarily of heterogeneous glacimarine sediments both from melt water runoff and ice-rafting (Syvitski et al. 1996; Dowdeswell et al. 1998; Smith and Andrews 2000). It is also heavily impacted by ice, particularly the scouring of the seabed by larger icebergs to depths of 550m (Dowdeswell et al. 1993).

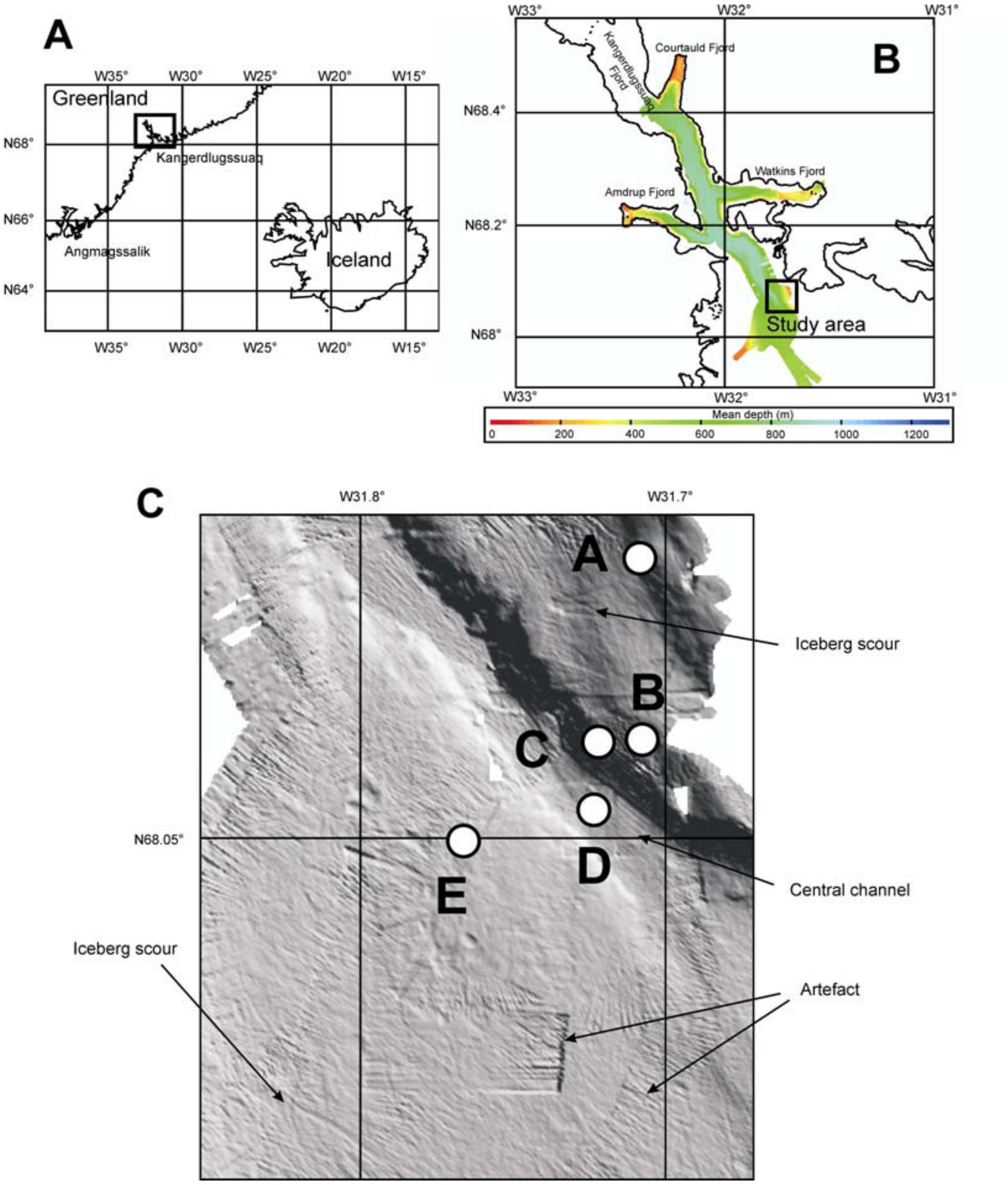


Figure 5.1: (A) Location of study area, (B) swath bathymetry of Kangerdlugssuaq Fjord and C) bathymetry of sampling sites (sun position north-east, showing the position of the sampling sites as well as iceberg ploughmarks on the seabed). Swath data collected and processed by J. Evans et al. (Dowdeswell 2004).

The benthic communities of east Greenland have had a long history of study (Curtis 1975) dating from the publication of *Fauna Groenlandica* (Fabricius 1780). Results of early expeditions to the area, particularly the *Ingolf* expedition (1895 and 1896) in the south of Greenland and the *Denmark* expedition (1906-1908) to the east, were compiled as the *Conspectus Faunae Groenlandicae*, published in the journal *Meddelelser om Grønland* between 1898 and 1917. The *Godthaab* expedition of 1928, whilst taking extensive collections of benthic fauna, did not venture to east Greenland (Kramp 1963). The first quantitative benthic investigations of north eastern Greenland fjords, Franz Joseph Fjord (73°N) and Scoresby Sund (70°N), were undertaken by Spärck (1933) and Thorson (1934). The benthic biology of the eastern fjords, Kangerdlugssuaq (68°N) and Angmagssalik (65°N), were investigated by Bertelsen (1937) as part of the 7th *Thule* expedition. A brief mention of the megafauna within the Kangerdlugssuaq fjord system has been made as part of more general sedimentological investigations (Syvitski et al. (1996). Studies to date have generally been carried out in shallow water, typically to a maximum depth of 200m. Modern studies in the area have concentrated on deeper water faunas particularly off north eastern Greenland (Dahl et al. 1976; Piepenburg and Schmid 1996b; Starmans et al. 1999; Piepenburg et al. 2001) although Piepenburg et al. (2001) sampled macrofauna from 390-1570m in the Denmark Strait just south of Scoresby Sund. There have been no bathyal megafaunal investigations in East Greenland south of 75°N.

Field sampling

Sampling was conducted as part of the UK National Environment Research Council (NERC) Autosub Under Ice (AUI) thematic programme on board the Royal Research Ship *James Clark Ross* (cruise JR106; see Dowdeswell 2004).

Sampling was carried out along a bathymetric gradient at the mouth of the Kangerdlugssuaq Fjord, east Greenland (Figure 5.1). Stratified random sampling was carried out along the depth gradient. One photographic transect was carried out within each of 5 approximately equally spaced depth bands (Table 5.1). Seabed survey photography was undertaken using the National Oceanography Centre (NOC) Wide Angle Seabed Photography (WASP) vehicle and the NOC Autosub Autonomous Underwater Vehicle (AUV) (Babb 1993; Jones et al. 2005).

Table 5.1: Study site data: Site identifier (A-E), station number (unique identifier of camera deployment), date of observations, central position of observations, average water depth (m), total area analysed (m^2), total seafloor area (%) with hard substrata (>64mm sediment size) and number of $100m^2$ samples used in analysis.

Site	Station	Date	Lat (°N)	Long (°W)	Depth (m)	Area photographed (m^2)	Hard substrata (%)	Number of 'samples'
A	56508#1	08 Sep 2004	68.0842	31.7060	270	335	1.7	4
B	56509#1	08 Sep 2004	68.0677	31.7043	374	476	1.1	5
C	56512#1	09 Sep 2004	68.0665	31.7205	481	243	3.6	3
D	56503#1	03 Sep 2004	68.0513	31.7723	625	1084	0.9	11
E	56513#1	09 Sep 2004	68.0557	31.7290	722	430	4.0	5

The WASP vehicle (Huggett 1987) is an off-bottom (2-4 m) towed camera platform, operated using an acoustic telemetry system, carrying a vertically-mounted still camera, and a vertically-mounted video camera. This vehicle was typically operated for one hour at the seabed, yielding some 250 still photographs (35mm Kodak Vision 250D colour negative) and continuous video footage (mini digital video cassette). The course of the WASP vehicle was not pre-defined or on a constant heading.

Autosub is a long range, deep diving, AUV. It carries a wide variety of physical, biological and chemical sensors including a vertically-mounted digital still camera (Jones et al. 2005), swath bathymetry system, Seatex MRU 6 attitude sensor (for magnetic heading, pitch and roll), Digiquartz 430 kT 700 bar pressure sensor (for depth data) and Simrad Mesotech 808 echo sounder (for altitude information). The vehicle was programmed to operate at 10m above the seabed for part of a longer mission in the fjord mouth. Agassiz trawl and rock dredge samples were obtained to aid in the identification of the fauna observed in photographs.

Photo analysis

The megabenthic fauna in each photograph were recorded. Given the physical scale of the photographs it was determined that only animals with a maximum dimension >5cm could be consistently identified. Altitude data (i.e. the height of the camera above the seabed) were printed directly onto each photograph allowing the scale of the image to be calculated using the following equation, where a = camera altitude, θ = horizontal camera acceptance angle, ω = vertical camera acceptance angle:

$$\text{Area of photograph} = 4a^2 \tan\left(\frac{\theta}{2}\right)\tan\left(\frac{\omega}{2}\right)$$

Megafaunal organisms were identified, counted and measured on each frame and their numbers converted to numbers per hectare. Sabellid tubes were counted, but as it was not possible to ascertain whether they were alive, they were omitted from the calculation of diversity indices and density values. Sponge colonies were counted as individuals when no visible separation between colonies was observed. Only benthic fish were counted i.e. those fish that dwell on and feed on the seabed. Recent *Lebensspuren* were classified, counted and their area measured.

Seabed type/grain size was assessed using Wentworth sediment size classes (Wentworth 1922) under 100 randomly chosen points overlaid on the photograph. A subsample of 30 photographs spaced evenly along the transect was used for each site. Hard substrata were taken as sediments classified as cobble or larger (>64mm maximum dimension). Unsuitable photographs (high altitude or out of focus) were discounted from all analyses.

Data analysis

Species counts of individual photographs (from the whole series of photographs at each site) were pooled at random, without replacement, into 'samples' that covered $100m^2$ ± $1m^2$. In the last 'sample' per station, if there were insufficient samples to cover $100m^2$, random photographs from throughout the sampling site were pooled until $100m^2$ was reached. Although the original photographs were contiguous, the transects were conducted in random locations (within depth stratifications) and the course of the WASP vehicle was not pre-defined or constant. For these reasons each sample was considered a replicate. In analyses 'samples' have been treated as replicates for all further analysis except for the investigation of spatial pattern where non-randomised individual photograph counts were used.

Taxon accumulation curves (Colwell et al. 2004) were used to compare species richness between sites at Kangerdlugssuaq. Dominance was assessed using the Berger-Parker index (Berger and Parker 1970). A selection of diversity indices (see e.g. Magurran 2003) were used to cover patterns in both ‘rare’ and ‘common’ taxa: Simpson’s λ' (Simpson 1949), Shannon Diversity Index, H' (Margalef 1968), Rarefaction, $ES_{(n)}$ (Hurlbert 1971) and S, the total species present. Univariate diversity indices were calculated using PRIMER (Clarke and Warwick 2001) and Biodiversity Pro (Version 2, Natural History Museum, London and Scottish Association for Marine Sciences, Oban). Species richness estimates were calculated from sample-based species accumulation curves using EstimateS software (Colwell 2005).

The within-transect spatial distribution of the fauna was analysed using a standardised Morisita's index of dispersion (Krebs 1998). The level of iceberg disturbance at each site was assessed qualitatively by reference to seabed ploughmark features observed in the WASP video footage, such as elevated ridges of sediment, displaced sediment, or scour related sediment lineation.

Multivariate analyses (hierarchical clustering and non-metric multidimensional scaling) were carried out using the PRIMER software package (Clarke and Warwick 2001). Following the general recommendations of Clarke and Warwick (2001) a square root transformation was applied to the faunal density data and the Bray-Curtis similarity measure employed (Bray and Curtis 1957).

RESULTS

Environment and physical setting

Seabed sediments ranged from mud to boulders characteristic of ice-rafting. All sites were characterised by a predominance of fine muddy sediment although the amount of hard substrata present was variable (Table 5.1). A significant difference in mean sediment size was observed between sites (Kruskal-Wallis $H = 73.52$ $df = 4$, $p<0.001$), although non-parametric post-hoc comparisons after Miller (1981) revealed that the sediments at sites A, B and D were not significantly different from each other consisting predominantly of fine material with very little available hard surface. Sediments at sites C and E were not significantly different from each other but had significantly more coarse-grained material than A, B and D, and therefore more hard surface available.

Swath bathymetry and backscatter data collected during the cruise (Dowdeswell 2004) from the fjord mouth area (Figure 5.1) indicates that iceberg ploughmarks are numerous (>5 km^{-2}) down to 300m, infrequent (1-5 km^{-2}) between 300m and 500m and virtually absent deeper than 500m; note that it was only possible to enumerate large ploughmarks (>20m minimum dimension) from these swath data. From the WASP photographs and video it appears that the density of iceberg ploughmarks is higher at the shallow sites (A & B) than the swath bathymetry suggests, whilst at intermediate (C) and deep sites (D & E) no evidence of iceberg disturbance was observed using visual imaging techniques.

Bottom water temperatures determined from CTD casts (Dowdeswell 2004) were similar at all sites (Figure 5.2) slightly decreasing with water depth from around 1 to 1.5°C at shallow sites to around 0.5 to 1°C at the deep sites.

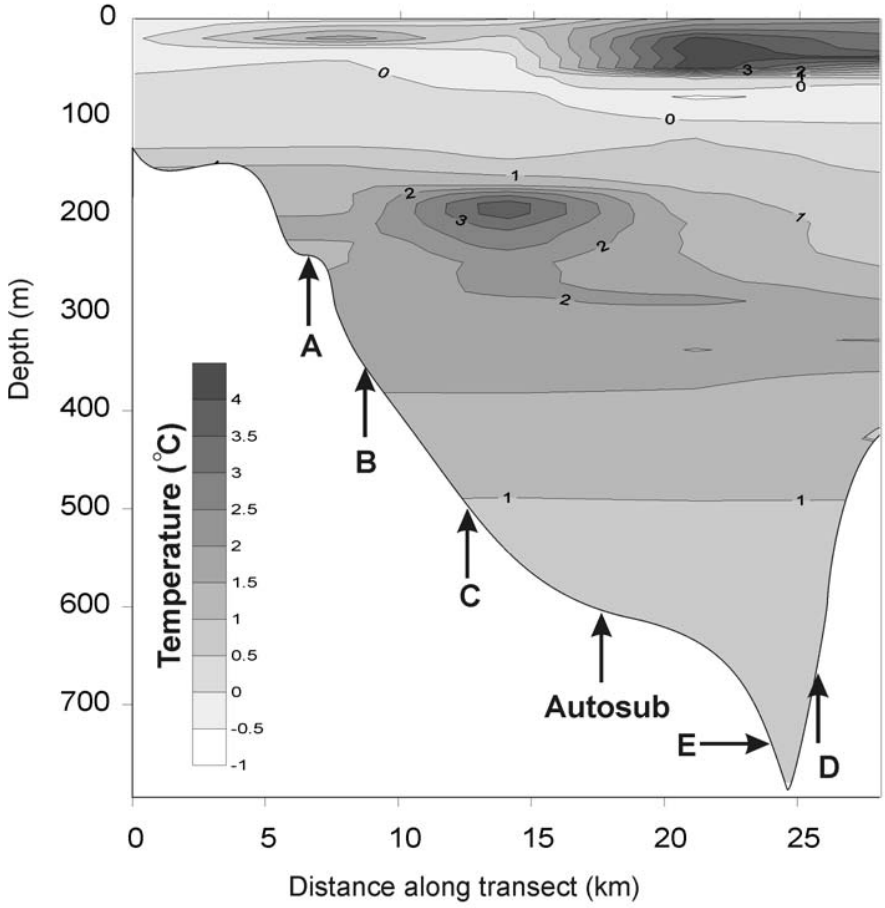


Figure 5.2: Temperature section through the mouth of Kangerdlugssuaq fjord showing positions of study sites. Data collected by K. Heywood et al. (Dowdeswell 2004).

Density

A total of 4351 megabenthic organisms were observed from 45 nominal taxa in an area of 2568 m^2 (Table 5.2). There is a significant difference in the density of total megafauna between sites (Kruskal-Wallis H = 19.67, df = 4, p<0.001; Figure 5.3), and a significant negative correlation between density and depth (r′ = -0.70, p<0.001). Densities are highest at stations A and B, notable for the presence of high numbers of the comatulid crinoid *Poliometra prolixa*.

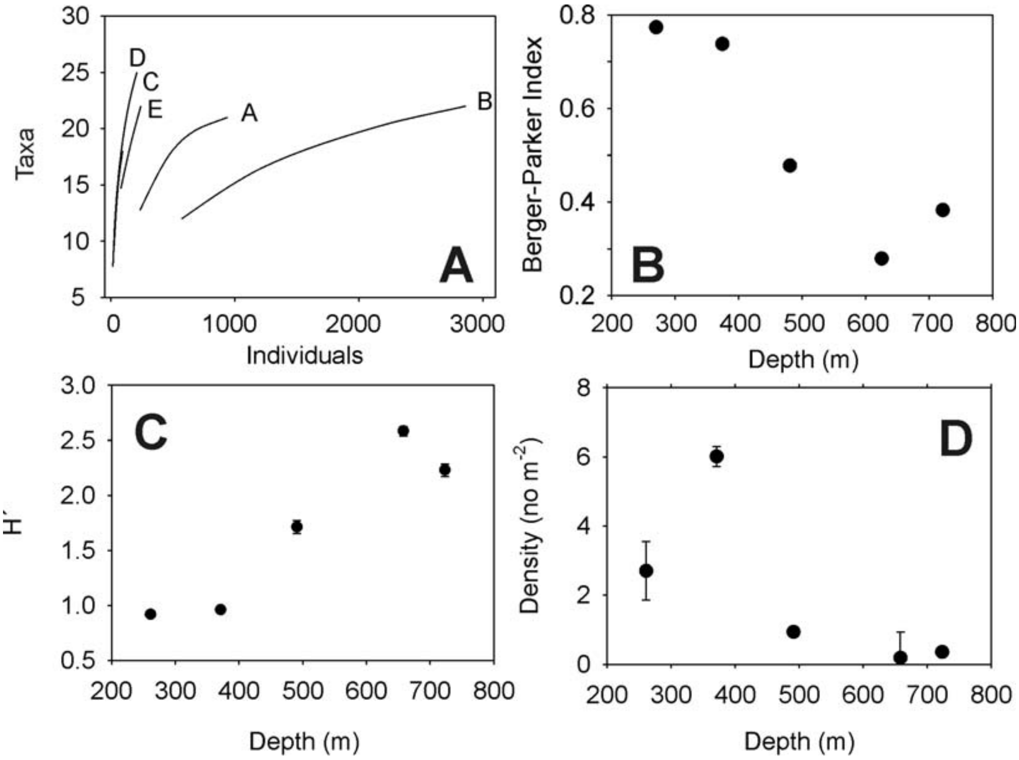


Figure 5.3: Megafaunal diversity and density for Kangerdlugssuaq study sites. (A) Taxon accumulation curves (showing species richness), (B) variations in dominance (Berger-Parker index), (C) Shannon-Wiener Diversity (H′ log e) and (D) faunal density (no m^{-2}). Error (H′ and density shown with 95% confidence intervals).

Table 5.2: Composition and density of epibenthic megafauna at Kangerdlugssuaq, Greenland investigated by means of seafloor photography.

			Numbers (ha^{-1})				
Phylum	Class	Species	A	B	C	D	E
Cnidaria	Actiniaria	Indet. anemone 1	27	15	28	26	44
		Indet. anemone 2	0	0	223	58	53
		Indet. anemone 3	87	0	0	24	0
		Indet. anemone 4	298	1,374	521	14	30
		Indet. anemone 5	61	0	395	0	0
		Indet. anemone 6	0	0	168	0	0
	Ceriantharia	*Cerianthus* sp.	0	20	0	410	129
	Alcyonaria	Indet. Alcyonarian	14	94	0	0	0
		Alcyonium sp.	0	0	97	0	0
	Pennatulida	Indet. pennatulid	0	0	0	25	0
	Scleractinia	*Stylaster* sp.	2,350	8,106	5,384	1,488	580
Porifera	Demospongia	*Stylocordyla borealis*	172	109	311	181	567
		Chondrocladia gigantea	0	20	0	68	0
		Indet. spikey sponge	0	0	42	104	126
		Indet. tube sponge	0	0	0	197	0
		Indet. ear shaped sponge	0	63	20	14	74
		Indet. encrusting sponge	98	669	65	0	0
		Indet. perforated sponge	0	17	76	0	193
		Indet. bottle shaped sponge	0	0	34	0	486
		Indet. ball shaped sponge	0	0	0	0	1,653
Echinodermata	Crinoidea	*Poliometra prolixa*	26,539	50,603	532	0	21
	Ophiuroidea	*Ophiura sarsi*	0	0	0	142	0
		Ophiacantha bidentata	50	1,303	229	148	0
		Ophioscolex glacialis	72	214	0	319	0
		Aff. *Ophiactis abyssicola*	3,543	8,111	2,996	0	183
		Gorgonocephalus sp.	0	0	76	0	0
	Asteroidea	Indet. star 1	0	15	68	66	154
		Indet. star 2	0	0	0	26	0
		Aff. *Pteraster* sp.	0	0	0	5	0
		Hymenaster pellucidus	430	213	0	106	0
		Luidia sp.	107	164	67	0	27
		Aff. *Porania* sp.	0	46	0	0	0
Mollusca	Cephalopoda	*Sepia* sp.	19	0	0	0	0
	Gastropoda	Indet. whelk	106	249	204	27	64
Arthropoda	Pycnogonida	*Colossendeis* sp.	120	0	31	0	25
	Decapoda	*Pandalus borealis*	0	19	0	0	0
Annelida		Indet. terebellid	0	0	0	134	0
		Indet. purple proboscis	0	0	0	31	0
		Indet. errant polychaete	42	0	0	24	17
		Indet. sabellid	5,305	10,238	29,513	46,543	46,717
Hemichordata		Indet. ascidian	117	34	0	0	0
Chordata		*Lycodes* sp.	95	0	0	106	87
		Amblyraja sp.	0	0	0	9	0
		Aff. *Eumicrotremus spinosus*	0	29	37	0	0

Diversity

Species richness increased with depth (Figure 5.3) with a clear division between low richness at sites at A and B and higher richness in the deeper stations (C-E). Evenness was low (high dominance) at the shallow sites as a result of the high relative abundances of the crinoid *Poliometra prolixa*. At the deep sites, communities had more even distribution of individuals among taxa (Figure 5.3; Table 5.3). The combined result of low richness and low evenness at the shallow sites resulted in low diversity across all univariate indices (Figure 5.3; Table 5.3). Heterogeneity diversity (as measured by H´) was significantly different between sites (Kruskal-Wallis H = 23.35, df = 4, $p<0.001$) with a significant positive correlation between heterogeneity diversity and depth (r´ = 0.395, $p<0.05$). The shallower stations tended to have high densities but low species richness, whereas the deeper stations show significantly lower densities but elevated species richness. The combined effects of high species dominance (low evenness) at the shallow stations and the increasing patterns of species richness resulted in an increasing diversity with depth. The increase of diversity (in all indices) with depth reflects increased diversity in the entire megafaunal community from rare to common taxa.

Community composition

Overall the observed megafauna were dominated by echinoderms (77.7%), although cnidarians (16.8%) and sponges (4.2%) were also important. Echinoderms are clearly dominant at sites A (89.3%) and B (85.7%), with cnidarians dominant at C (59.2%) and D (51.5%) and sponges dominant at site E (75.32%).

Classification and ordination of stations, based on root-transformed taxon density and Bray-Curtis similarities, revealed a distinct depth zonation in the distribution of megabenthic assemblages. ANOSIM revealed significant differences between stations ($R=0.816$, $p<0.001$). Three faunistic zones were discernable in the cluster diagram and MDS plot (Figure 5.4):

Shallow. Clearly dominant at the shallow stations was the crinoid *Poliometra prolixa* (40,253 ha^{-1}, 63.6%), sabellids while important (12.3%) were not as abundant as in other zones. Ophiuroids were seen frequently at this zone (9.7%) as was the “deep-water” coral *Stylaster* (8.9%).

Intermediate. A single station (C) represents an intermediate situation between the shallow and deep faunas, it is more closely allied to the shallow stations (mean Bray-Curtis similarities: 43% similarity to shallow, 25% similarity to deep) than the deep but does possess faunal elements of each. Densities of *Poliometra* were significantly reduced (1.3%) with only occasional specimens observed, sabellids were dominant (71.8%), coral (13.1%) and ophiuroids (7.3%) were abundant, actiniarians were also relatively abundant (3.2%).

Deep. This group encompassed those stations in water depths of 625 to 725m. Sabellids were highly abundant, dominating faunal numbers (92.2%), *Stylaster* was also important (2.5%) as were demosponges (1.8%) and cerianthids (0.7%).

Variations in the availability of hard substrata did not appear to influence community parameters at the between-site scale.

Table 5.3: Characteristics of sites and epibenthic faunistic zones distinguished in the Kangerdlugssuaq area. For each zone, stations included, water depth (m), number of species found, dominant species, evenness (Pielou's J´), Mean density of total epifauna ± 95% confidence interval, Rarefied estimated number of species (ES_{220}), Shannon-Wiener diversity index, H´ (base log e), Simpson's Index (1-λ´) and Berger-Parker Index (B-P).

Cluster	stations	Depth (m)	species number	Dominant species	Evenness (J')	Density No. m^{-2} ± C. I.	$ES_{(220)}$	H'	1- Lambda'	B-P
	A	270.2	20	coral, *Poliometra*, brittle 4	0.312	3.435 ± 0.748	9.641	0.934	0.387	0.774
	B	374.4	22	sabellid, coral, *Poliometra*, brittle 4	0.309	7.149 ± 0.844	7.639	0.956	0.432	0.738
	C	480.8	22	sabellid, coral, brittle 4, anemone 4	0.590	1.16 ± 0.291	21.720	1.825	0.713	0.478
	D	625.3	25	sabellid, coral, cerianthid, brittle 3	0.788	0.3752 ± 0.1312	22.898	2.535	0.877	0.279
	E	721.6	19	sabellid, sponge, coral	0.728	0.4513 ± 0.1242	18.843	2.145	0.812	0.383
Shallow	A, B	261-375	28	coral, *Poliometra*, brittle 4	0.289	5.551 ± 0.633	9.774	0.962	0.4221	0.749
Intermediate	C	480-501	22	sabellid, coral, brittle 4, anemone 4	0.590	1.160 ± 0.291	21.72	1.825	0.7132	0.478
Deep	D, E	625-725	32	sabellid, coral, sponge, cerianthid	0.797	0.395 ± 0.102	28.7	2.761	0.9065	0.147

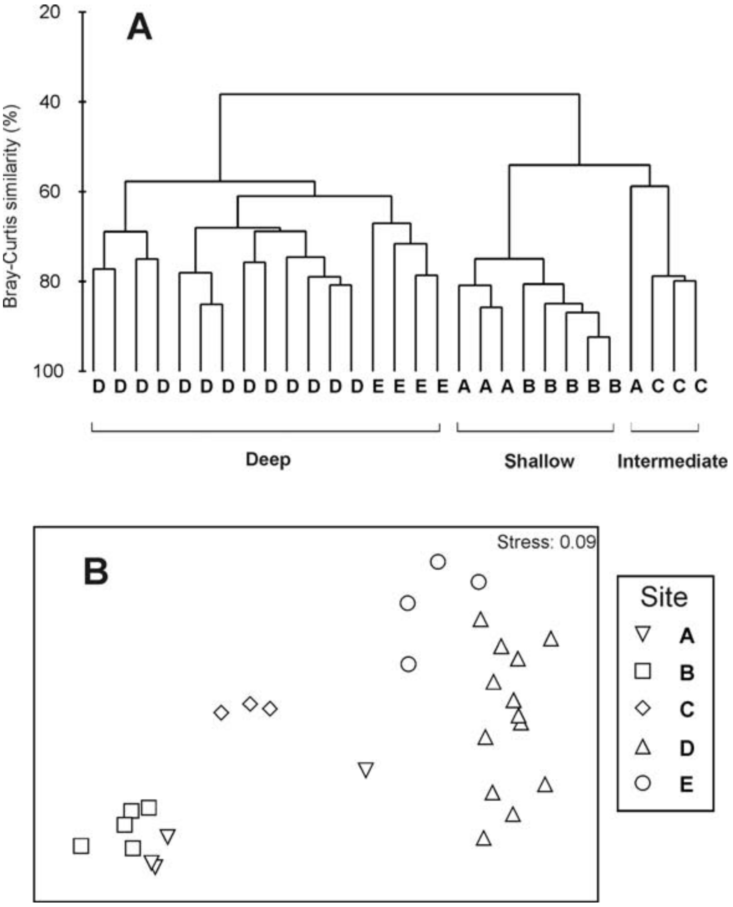


Figure 5.4: Multivariate analysis of Kangerdlugssuaq megabenthos. (A) Dendrogram and (B) multidimensional scaling ordination (see text for details of analysis).

Small-scale patchiness

While inter-station analyses of the faunal data revealed zonation in the distribution of epibenthic assemblages, within-station evaluation of the transects (Figure 5.5) provided small scale distributional information for the most abundant epibenthic species, the crinoid *Poliometra* (sites A and B), stylasterine corals (sites C and D) and sponges (site E).

Poliometra was highly abundant at the shallower sites (A and B). Crinoid densities were very high, reaching a mean value of 50,603 ha^{-1}, although their distribution along transects was patchy (Figure 5.5) with counts ranging from 0 to 53 individuals in a single photographic frame (0 to 17.71 m^{-2}). Dispersion of *Poliometra* was found to be significantly clumped at both sites (Standardised Morisita Index I_p=0.505 $p<0.05$ for site A; I_p=0.501, $p<0.05$ for site B). *Poliometra* was observed to occur in preference on topographical elevations such as sediment ridges and boulders.

Stylasterine coral was highly abundant in all stations, but only dominant in stations C and D. Their densities reached a mean of 8106 ha^{-1} but in some cases the distribution was patchy (Figure 5.5) with counts ranging from 0 to 25 colonies per frame (0 to 8.5 m^{-2}). Dispersion of stylasterines was found to be significantly clumped at site D (also in B although it was not dominant) and random at site C (Standardised Morisita Index I_p=0.501, $p<0.05$ for site B; I_p=-0.396, ns for site C and I_p=0.532 $p<0.05$ for site D). Stylasterine colonies had no obvious affinities with particular seabed characteristics.

Sponges were important at all sites, but were only dominant at site E. Their densities reached a mean of 2532 ha^{-1}, with counts ranging from 0 to 4 colonies per frame (0 to 1.77 m^{-2}). Dispersion of sponges was found to be random (Standardised Morisita Index I_p= -0.11, ns). Sponge colonies were observed to occur predominantly associated with hard substrata, particularly with larger sized cobbles and boulders.

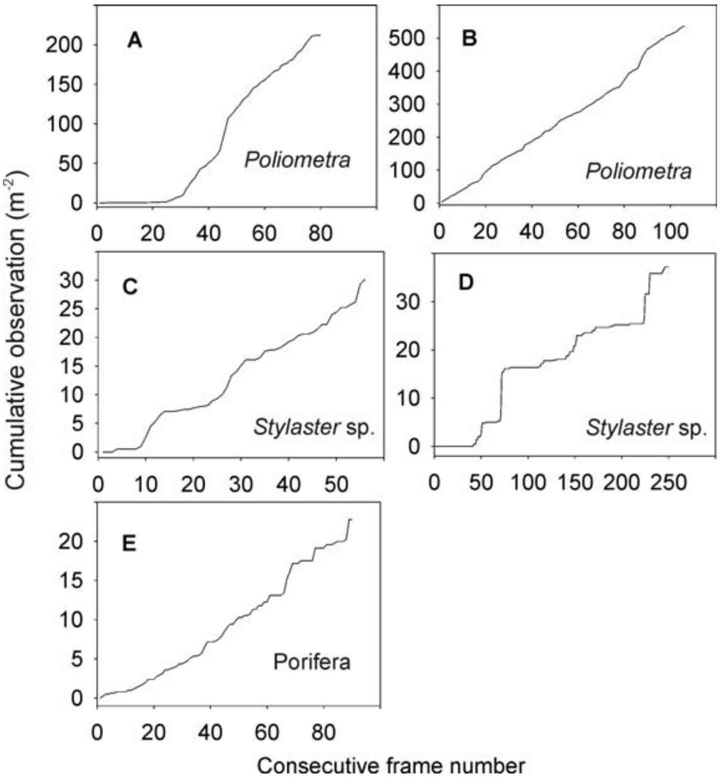


Figure 5.5: Spatial variation in the distribution of selected (dominant) taxa along phototransects.

Traces

Faunal traces of varying nature were observed in the soft sediments at all sites. Nine distinct trace types were observed (Figure 5.6). For some trace types it was possible to identify causative organisms (or group of organisms) from trace form or direct observation of trace formation. While only a small percentage of the total seabed area was disturbed by faunal traces, considerable numbers of traces were observed (Table 5.4).

Trace density (Kruskal-Wallis H = 13.95, df = 4, $p<0.05$) and area (Kruskal-Wallis H = 9.95, df = 4, $p<0.05$) were significantly different between sites. There was a significant positive correlation between trace number and depth ($r' = 0.76$, $p<0.001$), primarily driven by particularly high trace density at one of the deeper sites (site D). Many trace forms had higher numbers and areal coverage in the deeper sites (Table 5.4).

Multivariate comparisons, based on root-transformed data and Bray-Curtis similarities of trace assemblages, revealed significant differences between sites in both trace number (ANOSIM R=0.561, $p<0.001$) and trace area (ANOSIM R=0.390, $p<0.001$). Trace number and area followed the same trend, being low in the shallow sites (A, B and C) and generally high in the deep sites (D and E). This trend was the opposite of that found for faunal density; faunal density was highest in the shallow sites but very low in the deep sites. The proportion of infaunal to epifaunal traces was found to change across the bathymetric gradient. Traces produced by infaunal organisms represent 49% of total trace numbers at site A, at the other sites there was 83-89% of infaunal traces.

Table 5.4: *Lebensspuren* observed in photographs of the bathyal Kangerdlugssuaq area, Greenland. No. represents number of *Lebensspuren* per hectare, area represents proportion (0-1) of total area sampled occupied by *Lebensspuren* (x10^5 to show small values).

Trace name	Origin	Trace type	A		B		C		D		E	
			No.	Area	No.	Area	No.	Area	No.	Area	No.	Area
Large circular hole	unknown	Dwelling	383	0.19	478	1.60	131	0.83	8888	11.09	5382	11.54
Small circular hole	unknown	Dwelling	995	0.57	1791	0.63	4857	0.29	57223	1.04	8416	1.16
Molpadid mound	Holothurian	Dwelling	77	0.59	0	0	0	0	116	1.52	0	0
Asteroid trace	Asteroid	Resting trace	153	1.89	0	0	0	0	871	4.77	734	109.00
Ophiuroid trace	Ophiuroid	Resting trace	0	0	0	0	0	0	2440	27.17	0	0
Narrow plough	Gastropod	Crawling trace	1148	31.95	299	8.61	919	11.76	1336	13.54	734	15.58
Wide plough	Gastropod?	Crawling trace	0	0	119	16.65	0	0	3950	402.42	98	30.11
Faecal plough	Holothurian	Crawling trace	230	2.41	60	0.78	131	1.60	116	0.30	49	10.56
Crenulated plough	Fish?	Crawling trace	0	0	0	0	0	0	2498	563.63	0	0
		Total	2986	37.42	2747	26.67	6039	13.65	77440	1014.38	15412	166.41

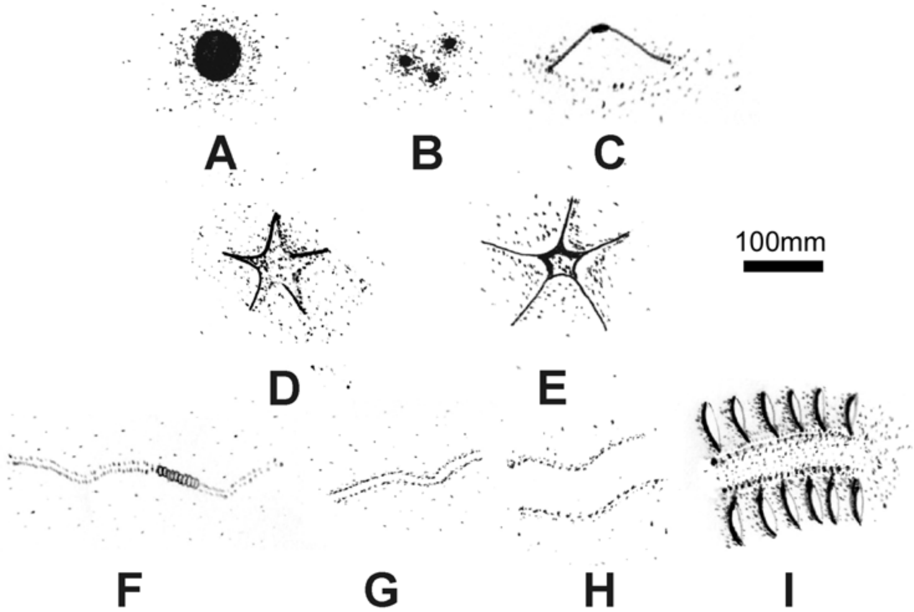


Figure 5.6: Megafaunal traces recorded in seabed photographs of the bathyal Kangerdlugssuaq area, Greenland. (A) large circular hole, (B) small circular hole, (C) molpadid mound, (D) asteroid trace, (E) ophiuroid trace, (F) holothurian faecal plough, (G) narrow plough, (H) wide plough, (I) crenulated plough.

DISCUSSION

Density

The density of megafauna was observed to decrease by over an order of magnitude with increasing depth at Kangerdlugssuaq. This could not be explained with changes in hydrography, which was relatively constant between sites, or seafloor habitat, which also showed no distinct trends with depth. Variability in the supply of food is a major controlling factor of benthic faunal density. Benthic communities depend on the downward flux of organic matter for food. In open ocean environments, this decreases with depth (Lampitt et al. 2001) and is manifested in reductions in benthic community density with depth throughout the oceans (Gage and Tyler 1991). The situation at Kangerdlugssuaq is much more complex, with very high input of glacially derived sediment (from 0.6 - 2.4 cm a^{-1}) and meltwater flux (around 4 km^3 a^{-1}), both with potentially elevated nutrient levels (Syvitski et al. 1996; Smith and Andrews 2000). This is combined with very high ice cover, both from sea ice and the high volume of iceberg influx (15 km^3 a^{-1}), which will severely limit surface primary production for at least 8 months of the year where the fjord is entirely ice covered (Syvitski et al. 1996). The result of these factors is likely high phytoplankton production for <4 ice-free months, possibly around 5.3 mmol C m^{-1} d^{-1} as measured in a similar fjord in NE Greenland (Rysgaard et al. 1996), although potentially as high as 95 mmol C m^{-1} d^{-1} as measured off the coast of NE Greenland (Smith et al. 1995). High flux of organic matter to the seafloor has been found during these blooms, with as much as 50-80% of phytoplankton stock sinking to the bottom (Wassmann 1991). Water currents predominantly flow out of the fjord (Syvitski et al. 1996; Dowdeswell 2004) so it is unlikely that high quality organic matter will be advected from surface primary production in less ice-impacted waters outside the fjord. The combination of these factors suggest that there is not much variation in surface organic matter supply between study sites, especially given their spatial proximity. Density variations are still likely related to reductions in available food with depth. There are tidally-reversing currents and horizontal mixing occurring around the study area (Dowdeswell 2004) that will pass much of the sinking organic matter over the dense beds of suspension feeders (particularly crinoids) in shallow water. Beds of suspension feeders have been shown to reduce available food supplies significantly (Fabricius and Dommisse 2000; Tweddle et al. 2005). This will likely reduce the available food supply to the deeper stations and hence reduce faunal densities.

Megafaunal density in this study was highly variable (1881 to 60,132 individuals ha^{-1}). Such densities and the major reductions in density with depth are consistent with other Arctic megafaunal studies (Figure 5.7). Absolute densities and bathymetric pattern in the density of Arctic fauna is likely governed by a complex of interdependent factors (primary production, flux rates, ice cover and seafloor properties) which vary at each location investigated (Ambrose and Renauld 1995; Brandt 1995). For example, in an area of high primary production, the Northeast Water Polynya, Piepenburg et al. (2001) found higher megafaunal densities than in this study. Analysis of all published megafaunal density values for the Greenland Sea, Norwegian Sea and Denmark Strait reveal a significant negative correlation between total density and depth ($r' = -0.355$, $p<0.05$).

Diversity

Analysis of the benthic species distribution revealed a conspicuous depth zonation at Kangerdlugssuaq, in which the benthic assemblage of the shallow stations could be clearly distinguished from that of the deeper parts of the fjord mouth. Similar bathymetric zonation patterns in Greenland have been reported for the megafauna, epifauna and selected species (Piepenburg and Schmid 1996b; Piepenburg et al. 1997; Starmans et al. 1999; Starmans and Gutt 2002). Diversity is frequently found to increase to intermediate depths in open ocean environments (Rex et al. 1997); possibly being driven by: increased large-scale environmental stability (Sanders 1968), patchiness of food resources, and localized autochthonous disturbances (Grassle 1991). The situation at Kangerdlugssuaq is considerably more complex with additional controls on diversity from the disturbance effects of grounding ice and the related effects of high sedimentation (Wlodarska-Kowalczuk et al. 2005). In the shallower waters of Kangerdlugssuaq, seabed disturbance by icebergs plays an important role in regulating local benthic diversity, as seen at local scales in the Arctic (Conlan et al. 1998) and Antarctic (Gutt and Piepenburg 2003; Teixido et al. 2004). In shallow waters it appears that the high levels of disturbance from iceberg activity is acting to reduce local diversity. There is a movement of around 1200 icebergs per year out of the fjord, past the study sites, and with an average keel depth of 250m (Syvitski et al. 1996) suggesting that the shallow study sites are disturbed regularly. In deeper waters there is a lower frequency of disturbance which will allow communities to build up their species complement, through succession, acting to increase diversity (Connell 1978). Small-scale, low intensity disturbance in the deeper waters will occur from the periodic deposition of iceberg drop stones, increasing diversity by providing new habitat for colonisation and potentially allowing several successional stages to be assessed within individual photographs. The reductions in diversity with local disturbance found here have been shown on a regional scale to increase diversity, where, within a heterogeneous mosaic landscape, co-existence of different successional stages would act to prevent a steady-state climax community at the large scale (Gutt and Piepenburg 2003).

Megafaunal diversity in this study showed a similar increase with depth to others in the literature but is difficult to compare directly as a result of the numerous diversity indices and sampling methods in use (Magurran 2003). The diversity recorded in this study is comparable with similar photographic studies of Arctic megafauna to the east of Greenland (Figure 5.7). When all available diversity measurements are compared with depth an overall positive correlation is evident ($r' = 0.526$, $p<0.05$) for H' (the most widely quoted index). However there is a unimodal peak in diversity at around 600-800m, with reducing diversity at both shallower and deeper depths. This peak in diversity occurs at about the average limit of iceberg disturbance over the last 10,000 years (Dowdeswell et al. 1993). It may be that ice-related disturbance reduces shallow water diversity throughout the Greenland Sea and Denmark Strait area.

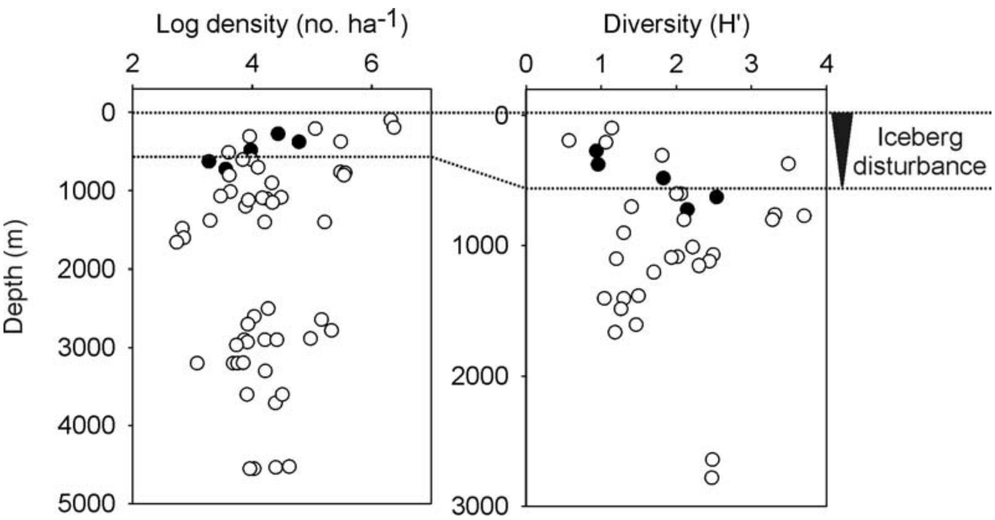


Figure 5.7: Comparisons of megafaunal density (log numbers ha^{-1}) and Shannon-Wiener diversity (H′) with depth for this study (solid circles), and other arctic water studies (open circles) after (Dahl et al. 1976; Christiansen and Thiel 1992; Mayer and Piepenburg 1996; Starmans et al. 1999; Piepenburg et al. 2001; Axelsson 2003; data in this thesis).

Species richness is difficult to compare between studies as a result of differences in sample size or sampling method (Gray 2000). The present study recorded a comparable taxon richness to other Arctic photographic studies. However, it is apparent from the taxon accumulation curves that there may be many more species present, supported by widespread trawl sampling on the Northeast Greenland Shelf where Piepenburg and Schmidt (1996b) found over 200 megabenthic species.

Community patterns

Organisms are broadly constrained by depth as a result of their physiological tolerance to pressure. While this sets lethal limits, the bathymetric zone in which species are abundant is narrowed by other local factors (Rowe 1983; Billett 1991; Howell et al. 2002). While changes in hydrographic regime have been shown to be important in the zonation of benthic fauna (Gage et al. 1995; Callaway et al. 2002), in this case, with negligible differences in hydrographic properties between stations, it is unlikely that this is an important structuring force driving community patterns. However, many environmental parameters are correlated with water depth. One of the major ecosystem-structuring forces on the Greenland continental shelf is disturbance from icebergs (Gutt et al. 1996). Grounding ice modifies seabed topography, reworks the sediment, and ploughs and crushes the seabed biota (Conlan et al. 1998). Scouring by icebergs has been shown to be a significant process in water depths < 550 m (Dowdeswell et al. 1993). Iceberg scouring intensity varies inversely with water depth. The most intense scouring occurs at depths of < 300-400 m (Dowdeswell et al. 1993). Gutt et al. (1996) show that the seafloor in open-ocean Arctic Greenland was disturbed by icebergs statistically once every 53 years. At Kangerdlugssuaq, it would seem that the frequency of disturbance is much higher than this (Syvitski et al. 1996). *In situ* photographs and videos taken here and elsewhere have demonstrated that iceberg grounding in polar regions locally causes considerable damage to benthic communities (Gutt et al. 1996; Gutt and Starmans 2001; Gutt and Piepenburg 2003; Teixido et al. 2004). Scavenger abundances have been found to increase as a result of ice disturbance related mortality and damage (Conlan et al. 1998). At Kangerdlugssuaq very low densities of scavenging fauna were observed, these often highly mobile fauna may only present at high densities in very recently disturbed areas and move around following disturbance events. All motile species can move into disturbed areas quickly. This is apparent at the shallow stations at Kangerdlugssuaq where, in clearly disturbed areas, there are very high densities of mobile organisms compared to sessile species, particularly evident in

Poliometra prolixa although also in the ophiuroids (e.g. *Ophiacantha bidentata* and *Ophiactis abyssicola*) and asteroids (e.g. *Hymenaster pellucidus*). In less disturbed patches, the ratio is more equal. Sessile organisms are eradicated by initial disturbance and subsequently pioneer species begin to grow in high densities on the impacted substratum, being replaced by a succession of species, going through a number of stages of recolonisation before recovery (Teixido et al. 2004), there is insufficient evidence in this study or other literature on Arctic interspecific interactions, growth or reproductive rates to evaluate the successional hierarchy of fauna in this area. In the shallow sites it appears that areas are frequently disturbed and remain in a state of incomplete recovery as found in other polar areas (Gutt et al. 1996). Disturbance also has implications beyond direct impacts to fauna, the action of ice ploughing changes the seafloor topography. Suspension feeding fauna, such as crinoids have been found here to aggregate on topographic highs where flow rates are increased (Muschenheim 1987; Wildish and Kristmanson 1997), this was predicted, but found to occur in the shallow Canadian Arctic (Conlan et al. 1998). In the deeper sites, where iceberg disturbance is less frequent or ancient, the high rates of sediment deposition at Kangerdlugssuaq will have covered all visible evidence of disturbance, essentially homogenising the environment, as well as providing habitat for infaunal organisms, such as molpadid holothurians. Stochastic deposition of ice-rafted drop stones continually creates habitat for many taxa. In some cases, post depositional processes, such as iceberg ploughing, can produce patches of larger sized sediments. The distribution of hard substrata explains variations in the distribution of stylasterine corals, many sponges and other attached taxa.

Traces

Trace numbers increased, despite decreases in total faunal density, at greater depths. This may reflect a number of changes, including the dominant feeding mode: deposit feeding increased at greater depths increasing trace formation; this is coupled with a reduction in physical or biological factors that remove traces. Changes in feeding pattern with depth have been found in many assemblages (Carey 1972; Gage and Tyler 1991; Flach et al. 1998) and reflect a move towards deposit feeding with depth, with deposit feeding more likely to produce traces. Traces found at Kangerdlugssuaq suggest a much higher infaunal density or activity in the deep areas (>500m).

Trace numbers and area may have been reduced in the shallow sites as a result of physical or biological forces acting to remove them. However these effects will be relatively small over the time-scale for typical trace duration, likely to be less than a year with measured sedimentation rates (Hollister et al. 1975; Syvitski et al. 1996). Although disturbance rates are higher, and there is some evidence that sedimentation may be elevated slightly in shallower sites closer to the glacier fronts (Syvitski et al. 1996), trace densities are likely to be more reflective of the communities present than the forces removing them.

There is a considerably higher proportion of epifaunal organisms at the shallowest site when compared with the other infaunal-dominated sites. In some situations infaunal organisms have been found to be more susceptible to disturbance (Jennings et al. 2001), hence less abundant in the shallow sites. Epifauna, particularly mobile forms, can respond quickly to disturbance events, they have been shown to recolonise disturbed areas within hours (Ramsay et al. 1998). Disturbed areas at Kangerdlugssuaq have large sediment sizes and topographic highs favourable to suspension feeding epibenthos, these conditions may further reduce infaunal organism density through reductions in food and larval supply.

CHAPTER 6: ECOLOGY OF BENTHIC MEGAFAUNAL COMMUNITIES IN THE FIMBUL ICE SHELF REGION, WEDDELL SEA, ANTARCTICA

INTRODUCTION

Considerable research has been carried out on Antarctic benthic communities during the last decades, mainly related to aspects of systematics, zoogeography, reproduction and foraging biology (Dayton 1990; Arntz et al. 1994; Gutt 2000). Studies on patterns and processes are important in understanding development, structure and function of Antarctic benthic communities (Hedgpeth 1971; Dell 1972; White 1984; Arntz et al. 1994; Clarke 1996; Teixido et al. 2002). Knowledge of the density, spatial distribution and diversity of species within a community is fundamental to understanding ecosystems (Sousa 1980; Paine and Levin 1981; Connell et al. 1997; Newell et al. 1998).

The influence of ice is a characteristic feature of Antarctic communities, impacting benthic communities through both direct processes such as ice scouring (Barnes 1999; Teixido et al. 2004) and indirect processes including changes to surface water productivity caused by the presence of seasonal sea ice (Andersen 1989; Gutt 2001). Disturbance from icebergs is among the most significant disturbances that any large ecosystem on earth experiences (Gutt and Starmans 2001). Natural disturbance is widely recognised as an important determinant of the occurrence and density of species (Dayton 1971; Pickett and White 1985; Huston 1994; Paine et al. 1998; Sousa 2001). Disturbance effects on communities depend on the individual life histories of the species present, and the dispersal and recruitment patterns of their offspring (Grassle and Grassle 1974; Sousa 1980; Connell and Keough 1985; Giangrande et al. 1994).

Environmental gradients are important in determining the distribution of benthic fauna and the structure of seabed communities (Garrabou et al. 2002). In the Antarctic, as elsewhere, depth is one of the most important marine environmental gradients (Dayton 1990; Arnaud and Hain 1992; Starmans et al. 1999). Community changes with depth concern not only the composition, but also the organization of the communities. Community parameters such as diversity, species richness and standing stock have been shown to be affected by depth (Rex et al. 1997; Gutt and Starmans 1998; Gutt et al. 1999; Gage et al. 2000).

Photography and image analysis are increasingly used to investigate the fauna of deep-sea environments (Smith et al. 1993; Priede and Merrett 1998; Lampitt et al. 2001; Solan et al. 2002). In the high Antarctic, despite the vast areas, only a few studies have investigated the megafauna quantitatively (e.g. Piepenburg et al. 1997; Gutt and Starmans 1998; Starmans et al. 1999; e.g. Barry et al. 2003). The bulk of work on Antarctic benthos has been carried out using trawling (e.g. Arnaud et al. 1998), which is at best semi-quantitative (Thurston et al. 1994). Towed camera platforms allow the megabenthos of large areas of seabed to be studied quantitatively without disturbing the environment under study. Photographs can provide an undisturbed view of the benthos over a wide area allowing the elucidation of large-scale faunal spatial patterns (Solan et al. 2002) revealing any heterogeneity in the distribution of assemblages that is lost with trawling (Clarke and Johnston 2003). Along with the geology of an area (Masson

2001), megafaunal species richness and standing stock are commonly assessed from photographs (Fell 1967; Bohnsack 1979; Gutt and Starmans 1998; Gutt et al. 1999).

This study aims to investigate the community structure, diversity and density of deep-water benthic megafauna in an area impacted by both seasonal and permanent ice. I aim to characterise patterns in benthic community structure in relation to major physical factors, particularly depth, habitat type and disturbance from icebergs. While communities have been separated in distinct areas in the Antarctic (Gutt and Starmans 1998), this work focuses on the effects of physical factors on the benthic fauna in a single area.

METHODS

Study area

The Fimbul Ice Shelf is the largest ice shelf in the north eastern Weddell Sea (Swithinbank 1957; Lunde 1961; Nost 2004). Jutulstraumen, the largest outlet glacier in the central Dronning Maud Land, feeds the central part of the Fimbul Ice Shelf. The eastern and north eastern Weddell Sea region has a very narrow continental shelf, with ice shelves occasionally overhanging the continental slope. The unique position of these ice shelves relative to the deep ocean makes them important areas for study and with a potentially unique fauna. Much of the Antarctic continental shelf is unusually deep as a result of scouring from ice shelves and depression by the enormous mass of continental ice (Clarke 1996). Continental shelves globally are typically 100-200m deep and 75km wide; those around Antarctica average over 450m deep and 125km wide. The southern Weddell Sea in particular has a very wide continental shelf predominantly covered with ice shelves (Clarke and Johnston 2003). The megafauna of the Weddell Sea is reasonably well studied, with publications on benthic megafaunal communities (Voss 1988; Galéron et al. 1992; Gutt and Starmans 1998), specific megafauna (Gutt 1991; Gutt et al. 1991; Barthel and Gutt 1992; Gutt and Koltun 1995; Gutt and Ekau 1996; Piepenburg et al. 1997; Tendal and Barthel 1997; Gutt 2002), and the effects of environmental factors on the megafauna (Gutt et al. 1996; Gutt 2000; Gutt 2001; Gutt and Starmans 2001; Gutt and Piepenburg 2003; Gutt and Starmans 2003; Teixido et al. 2004). Most Antarctic benthic work has been carried out on the continental shelves, with the slope and the deep sea far less well known. Recent work on deep water Antarctic benthos is addressing this shortfall (Clarke 2003; Brandt et al. 2004).

The surface waters of the north eastern Weddell Sea are heavily impacted by seasonal sea ice cover (Figure 6.1). The Fimbul ice sheet is around 200-300m thick at the ice edge (Nost 2004) in the area of study with a draft of 150-250m. The seabed of the narrow continental shelf slopes from around 500m to the east to around 200m at the west of the study site (Figure 6.2).

The distance from the edge of the ice-shelf was within 10km for all stations. The effects of km scale differences in distance were not considered in this study because of the general patterns of circulation around the study sites. There is a predominant south easterly flow of bottom currents at Fimbul (Nichols et al. in prep) which will result in a reduced significance of the distance from the ice shelf on the benthic communities, at least in terms of food supply.

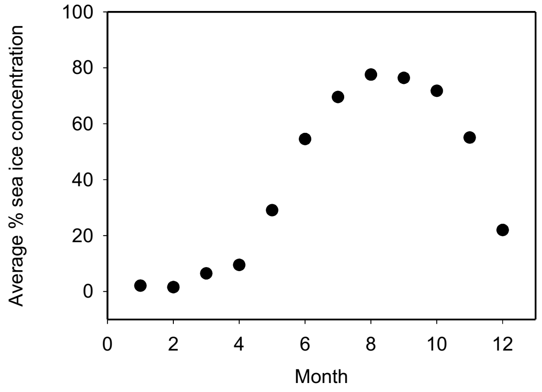


Figure 6.1: Average percentage concentration of sea ice in a 10 degree longitude section (0-10°W) of the southern ocean from 50°S to the ice shelf edge. Data averaged from NOAA/NMC/CAC Antarctic Monthly sea ice extent from 1973-1990. Data courtesy of National Snow and Ice Data Center, University of Colorado, USA.

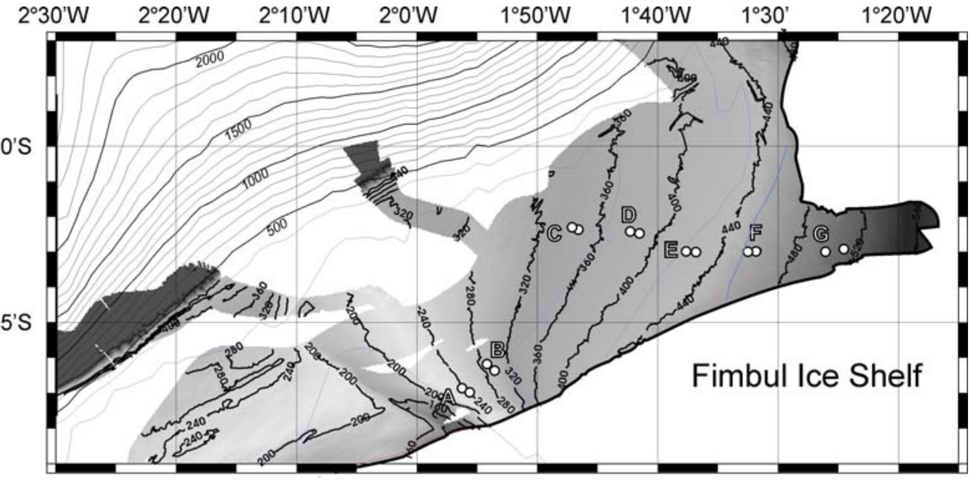


Figure 6.2: Processed EM120 Swath bathymetry of the study site on the edge of the Fimbul ice sheet, showing positions of WASP stations. Thick black line indicates edge of ice shelf.

Field sampling

Sampling was conducted as part of the UK National Environment Research Council (NERC) Autosub Under Ice (AUI) thematic programme on board the Royal Research Ship *James Clark Ross* cruise JR97. Sampling was carried out along a bathymetric gradient at the edge of the Fimbul ice sheet, in the north eastern Weddell Sea, Antarctica (Figure 6.2). Stratified random sampling was carried out along the depth gradient. One photographic transect was carried out within each of 7 approximately equally spaced depth bands (Table 6.1). Seabed survey photography was undertaken using the National Oceanography Centre (NOC) Wide Angle Seabed Photography (WASP) vehicle. The WASP vehicle (Huggett 1987) is an off-bottom (2-4 m) towed camera platform, operated using an acoustic telemetry system, carrying a vertically mounted still camera, and a vertically mounted video camera. This vehicle was typically operated for one hour at the seabed, yielding some 250 still photographs (35mm Kodak Vision 250D colour negative) and continuous video footage (mini digital video cassette).

Swath bathymetry was carried out using a hull mounted Kongsberg-Simrad EM120 multibeam swath bathymetry system. High resolution measurements were obtained over the WASP survey areas by low ship speed (10 km hr-1), low beam angle (30° beam angle) and high ping rate (0.5 Hz). See Nicholls (2005) for more details.

Rock dredge samples were obtained to aid in the identification of the fauna seen in the photographs. Rock dredges were hauled over the ground for 30 minutes at 0.7 knots.

The dredge had an opening 1m wide and 0.5m high, it had 10mm mesh net inside a chain mesh net.

Table 6.1: Station list. For each site: site name, unique cruise identifier, date of sampling, water depth (m), position in decimal degrees Latitude (°S) and Longitude (°W), total area photographed and analysed (m^2) and number of sampling units.

Site	station	date	depth (m)	start time	lat start (°S)	long start (°W)	end time	lat end (°S)	long end (°W)	Area analysed (m^2)	Number of 'samples'
A	56607#1	21/02/2005	245	22:44:39	70.1144	1.9377	23:16:00	70.1164	1.9268	498	5
B	56608#1	21/02/2005	300	23:55:27	70.1029	1.9033	00:30:00	70.1061	1.8927	423	5
C	56603#1	21/02/2005	340	09:34:00	70.0383	1.7853	10:05:30	70.0394	1.7765	423	5
D	56606#1	21/02/2005	388	20:44:57	70.0403	1.7048	21:19:30	70.0414	1.6921	351	4
E	56604#1	21/02/2005	425	11:58:22	70.0498	1.6275	12:34:00	70.0502	1.6134	489	5
F	56605#2	21/02/2005	465	18:50:51	70.0499	1.5418	19:22:00	70.0498	1.5305	420	5
G	56601#1	13/02/2005	510	20:26:36	70.0499	1.4341	21:30:00	70.0488	1.4090	947	10

Photo analysis

Megabenthic fauna in each photograph were recorded. Given the physical scale of the photographs I determined that only animals with a maximum dimension >5cm could be repeatedly identified. Altitude data (i.e. the height of the camera above the seabed) were printed directly onto each photograph allowing the scale of the image to be calculated using the following equation, where a = camera altitude, θ = horizontal camera acceptance angle, ω = vertical camera acceptance angle:

$$\text{Area of photograph} = 4a^2 \tan\left(\frac{\theta}{2}\right)\tan\left(\frac{\omega}{2}\right)$$

Megafaunal organisms were identified, counted and measured on each frame, and their abundance converted to densities (numbers per hectare). Sabellid tubes were counted, but as it was not possible to ascertain whether they were alive density values were treated with caution. Sponge colonies were counted as individuals when no visible divide between colonies was observed. Only benthic fish were counted i.e. those fish that dwell on and feed on the seabed. Unsuitable photographs (high altitude or out of focus) were discounted from all analysis, around 30% of photographs were discarded for each station.

Classification of disturbance

To investigate present community structure related to iceberg disturbance it is necessary to describe plough marks in terms of their extent and approximate age. This is very difficult to achieve in practice. An integrated approach was used here to classify disturbance in as much detail as possible by remote methods. Disturbance was investigated at three scales using different methods: swath bathymetry was used to identify iceberg plough features at a large scale (20-1000m), continuous video used to identify the broad patterns of visible effects of iceberg ploughing, such as patterns in sediment distribution and clear topographic differences from mechanical disturbance at plough edges (scale 5-20m) and still photography to identify biological patterns associated with iceberg ploughing (scale 0.05-5m).

Swath bathymetry, video and photographic observations revealed clear patterns in sedimentation related to disturbance, this was particularly clear in the deep sites (Figure 6.3). The seabed sediments were classified into three groups: coarse, intermediate and fine (Figure 6.3C, D and E respectively). Coarse sediment was defined as having <20% sediment smaller than pebbles (<4mm) and including >25% cobbles or larger (>64mm); fine sediment had >80% of sediment smaller than cobbles (<64mm) with no boulders (>256mm) visible; intermediate included the sediments in between. Operationally these sediment classifications were clearly distinct in photographs.

Data analysis

Species counts of individual photographs (from the whole series of photographs at each site) were pooled at random, without replacement, into 'samples' that covered $100m^2 \pm 1m^2$. In the last 'sample' per station, if there were insufficient samples to cover $100m^2$, random photographs from throughout the sampling site were pooled until $100m^2$ was reached. Although the original photographs were contiguous, the transects were conducted in random locations (within depth stratifications) and the course of the WASP vehicle was not pre-defined or constant. For these reasons each sample was considered a replicate. In analyses 'samples' have been treated as replicates, except for analysis of sediment groups. In analysis of sediment groups, the whole series of photographs for each site were divided into 3 groups based on sediment composition of the whole photograph (coarse, intermediate and fine) and faunal totals for each group used (standardised to numbers per ha).

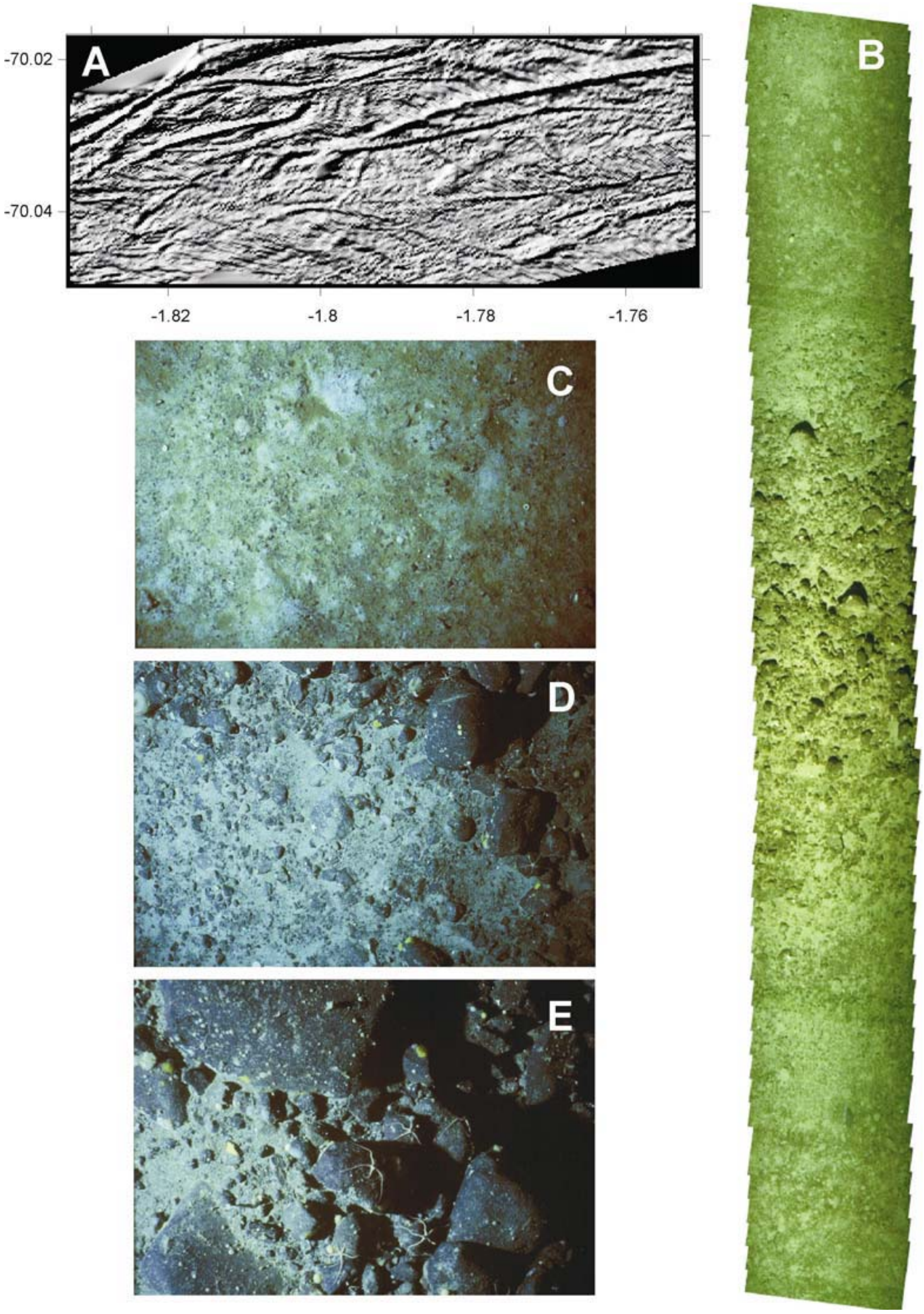


Figure 6.3: Seabed disturbance from iceberg ploughing. Swath bathymetry (site C) showing clear iceberg plough marks, latitude and longitude indicated (**A**); mosaic of seabed video (site G) covering approx. 30x3m of seafloor showing clear edge of ploughmark characterised by coarse sediment (**B**); seafloor photographs covering approx. 3x2m, examples of fine (**C**), intermediate (**D**) and coarse (**E**) sediment classifications (sites F, G, G respectively).

Taxon accumulation curves (Colwell et al. 2004) were used to compare species richness between sites at Fimbul. Dominance was assessed using the Berger-Parker index (Berger and Parker 1970). A selection of diversity indices (see e.g. Magurran 2003) were used to cover patterns in both ‘rare’ and ‘common’ taxa: Simpson’s λ' (Simpson 1949), Shannon Diversity Index, H' (Margalef 1968), Rarefaction, $ES_{(n)}$ (Hurlbert 1971) and S, the total species present. Univariate diversity indices were calculated using PRIMER (Clarke and Warwick 2001) and Biodiversity Pro (Version 2, Natural History Museum, London and Scottish Association for Marine Sciences, Oban). Species richness estimates were calculated from sample-based species accumulation curves using EstimateS software (Colwell 2005).

Multivariate analyses (hierarchical clustering and non-metric multidimensional scaling) were carried out using the PRIMER software package (Clarke and Warwick 2001). A square root transformation was applied to the faunal density data and the Bray-Curtis similarity measure employed (Bray and Curtis 1957; Clarke and Warwick 2001).

RESULTS

The seabed environment

The seabed was characterised by a heterogeneous mix of sediment type and size with clear evidence of iceberg ploughing. Swath bathymetry (Nicholls 2005) revealed a complex pattern of plough marks (e.g. Figure 6.3A) in the sediment at all sites (Lien et al. 1989), particularly in shallow waters where over 10 distinct ploughs (>20m minimum dimension) were observed per km^2. Video and photographs revealed changes in seabed composition between areas of coarse and fine sediment. The coarse sediment is elevated and forms long mounds. These features are related to ice ploughing, with the coarse material pushed up and out of the icebergs path. The fine material would appear to settle in the trench left behind after the iceberg has moved on. The intermediate sediments represent the transition phase found at the edge of the extent of disturbance. There is also evidence of deposition of coarse sediments from ice rafting (Lien et al. 1989), although this forms small patches of material distinct from the iceberg plough features.

Faunal density

Total faunal density was significantly negatively correlated with depth ($r' = -0.701$ $p<0.001$). This trend is apparent even with sabellids removed from analysis. As well as the overall trends, there is a significant difference in both sessile (Kruskal-Wallis $H = 24.35$, $df = 6$, $p<0.001$) and motile faunal density between sites (Figure 6.4; Kruskal-Wallis $H = 26.81$, $df = 6$, $p<0.001$). Sabellids increased the densities of sessile fauna at the shallow sites; even with their removal from analysis densities of sessile fauna still varied between sites (Kruskal-Wallis $H = 21.67$, $df = 6$, $p<0.001$). Both sessile ($r' = -0.54$, $p<0.001$) and motile faunal densities ($r' = -0.588$, $p<0.001$) were negatively correlated with depth. The ratio of sessile to motile taxa (not including sabellids) was significantly different between sites (Kruskal-Wallis $H = 27.86$, $df = 6$, $p<0.001$) and generally there was an increasing relative density of motile forms with depth, except at station G where relative densities of sessile forms were as high as at station A.

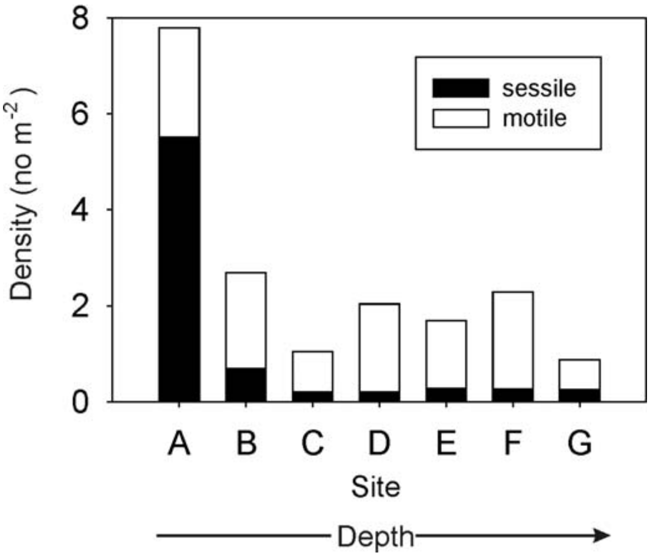


Figure 6.4: Total density of motile and sessile megafauna at each study site on the edge of the Fimbul ice sheet, Antarctica. Study sites can be seen in Figure 6.2.

Total density of fauna of all sites was significantly different depending on the sediment type (Figure 6.5; Kruskal-Wallis $H = 10.02$, $df = 2$, $p > 0.01$), total megafaunal density was highest in areas of coarse sediment. The underlying causes of this trend are habitat preferences of individual faunal groups (Figure 6.6). The majority of fauna observed have highest densities on coarse substrata with the notable exception of sabellids and holothurians. The highly dominant small ophiuroids elevated motile fauna densities in coarse sediment. With ophiuroids excluded there were approximately equal motile faunal densities in each sediment type. Most taxa had a notable preference for one sediment type.

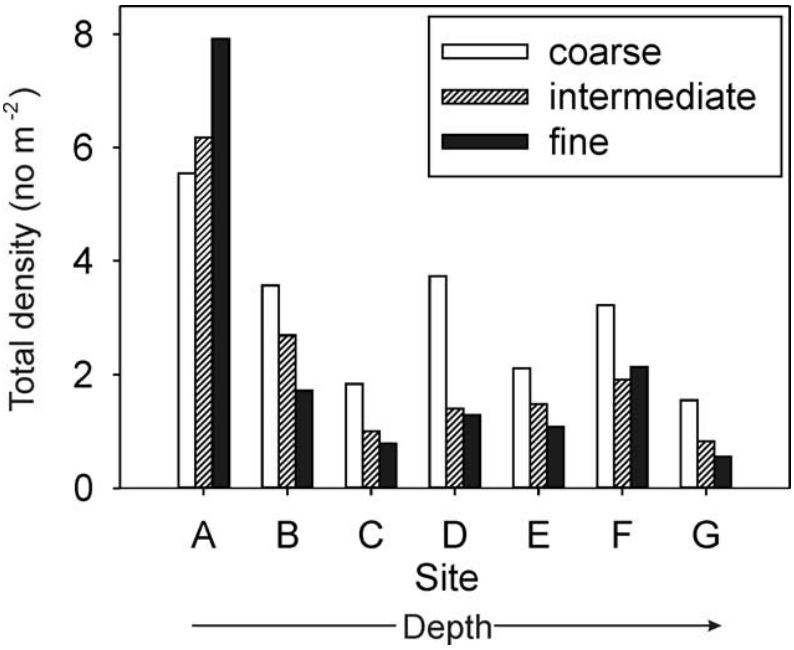


Figure 6.5: Total density of megafauna in different sediment types at each study site on the edge of the Fimbul ice sheet, Antarctica.

Table 6.2: Megafaunal taxa observed in Fimbul Ice Shelf region, NE Weddell Sea Antarctica. Densities quoted as number per hectare to reflect low densities of some taxa.

Phylum	Class	Taxa	Station total densities (no ha^{-1})						
			A	B	C	D	E	F	G
cnidarians	hydroida	Giant hydroid	0	0	24	0	20	48	0
		Indet. Hydroid	0	0	0	0	246	0	11
	actiniaria	Indet. Actinarian 1	40	95	71	57	0	0	32
		Indet. Actinarian 2	40	95	0	142	0	0	0
		Indet. Actinarian 3	0	0	0	0	41	0	21
		Indet. Actinarian 4	100	0	47	57	0	0	0
		Indet. Actinarian 5	100	473	118	199	164	119	42
		Indet. Actinarian 6	161	142	71	256	102	167	32
		Indet. Actinarian 7	20	24	0	0	20	0	11
		Indet. Actinarian 8	40	0	0	0	20	24	0
		Indet. Actinarian 9	0	378	142	0	0	0	11
		Indet. Actinarian 10	0	95	0	0	0	24	0
		Isotealia antarctica	40	260	0	114	102	95	0
	ceriantharia	Indet. Cerianthid	0	47	189	256	61	24	11
	gorgonacea	Indet. Gorgonian	0	0	0	0	0	24	0
	pennatulacea	Indet. Pennatulid	0	0	0	0	0	95	84
		Umbellula sp.	20	71	0	28	82	48	0
	scleractinia	Indet. Scleractinian	4,918	473	71	171	20	24	0
ctenophora	platyctenida	*Lyrocteis flavopallidus*	40	24	0	0	0	0	0
sponges	demospongia	*Chondrocladia* sp. ?	40	0	0	0	0	0	0
		Indet. Demosponge 1	1,706	567	213	171	61	95	32
		Indet. Demosponge 2	100	118	95	0	102	0	11
		Indet. Demosponge 3	201	24	0	57	0	0	0
		Indet. Demosponge 4	161	284	47	28	82	119	253
		Indet. Demosponge 5	482	47	71	0	41	71	0
		Indet. Demosponge 6	281	402	71	0	20	0	42
		Indet. Demosponge 7	0	47	0	28	0	0	0
		Indet. Demosponge 8	0	47	0	0	0	0	0
		Indet. Demosponge 9	0	47	0	0	0	0	0
		Indet. Demosponge 10	0	24	71	199	205	24	74
		Indet. Demosponge 11	0	0	24	0	20	71	21
		Indet. Encrusting Demosponge 1	221	307	24	0	82	214	918
		Indet. Encrusting Demosponge 2	0	0	0	0	82	262	602
		Kirkpatrickia variolosa	20	24	0	0	0	0	0
		Stylocordyla borealis	0	213	24	28	82	24	11
	hexactinellida	Indet. Hexactinellid 1	60	24	71	28	20	24	32
		Indet. Hexactinellid 2	20	0	0	0	0	0	11
		Rossella fibulata	0	24	118	0	0	0	0
		Rossella nuda	60	71	71	28	0	0	32
molluscs	gastropoda	*Amauropsis rossiana ??*	40	0	0	0	0	24	11
		Indet. Gastropod	0	47	0	28	0	0	0
		Indet. Nudibranch	0	0	24	0	0	0	0
	polyplacophora	Indet. Chiton	0	24	0	0	0	0	0
	bivalvia	Indet. Pectennid	0	24	24	0	0	0	11
	cephalopoda	Indet. Octopus	0	47	0	0	0	0	0
arthropods	chelicerata	Aff. *Dodecolopoda mawsoni*	120	95	0	0	0	24	0
polychaetes		Indet. Sabellid	46,167	2,506	284	114	512	0	84

		Indet. Polychaete	40	24	0	0	0	0	0
echinoderms	ophiuroids	Indet. Ophiuroid 1	13,890	5,864	5,465	12,393	8,901	17,037	4,360
		Indet. Ophiuroid 2	6,443	11,089	118	2,536	82	0	11
		Indet. Ophiuroid 3	562	260	0	0	0	0	11
		Indet. Ophiuroid 4	0	71	71	199	102	0	11
		Astrotoma agassizii	0	24	0	0	348	0	0
		Ophionotus victoriae	0	0	0	0	0	0	42
	crinoids	Indet. Comatulid crinoid	542	166	520	171	1,371	143	95
		Indet. Comatulid crinoid 2	20	24	24	57	102	0	11
		Pomachocrinus kerguelensis	40	0	24	28	41	48	0
	asteroids	Indet. Asteroid 1	141	284	237	199	143	95	53
		Indet. Asteroid 2	20	71	71	28	0	0	0
		Indet. Asteroid 3	20	47	0	0	0	0	0
		Indet. Asteroid 4	0	24	24	85	164	71	21
		Indet. Asteroid 5	20	47	0	28	20	71	0
		Hymenaster sp.	0	0	71	256	225	834	95
		Indet. Asteroid 6	0	0	0	0	0	0	11
		Indet. Asteroid 7	0	0	0	0	0	0	11
		Indet. Asteroid 8	40	71	615	456	164	167	11
		Odontaster validus	100	284	47	57	82	95	106
		Indet. Asteroid 9	0	24	24	85	41	167	63
		Indet. Asteroid 10	0	0	24	57	41	0	0
		Labidiaster annulatus	0	47	24	28	0	0	0
		Indet. Asteroid 11	0	0	0	0	20	0	0
	holothurians	Indet. Synallactid Holothurian	141	260	308	256	143	48	11
		Bathyplotes bongraini	60	213	142	57	389	71	42
		Pseudostichopus mollis	40	142	166	85	818	524	348
		Peniagone vignioni	100	0	213	798	593	453	222
		Staurocucumis turqueti ?	60	24	0	0	0	0	21
		Trachythyone parva ?	0	0	47	0	552	1,001	127
	echinoids	*Sterechinus antarcticus*	0	0	0	0	0	0	528
		Indet. Echinoid	0	0	0	0	0	0	84
fish		*Champsocephalus gunnari*	462	520	308	570	409	477	116

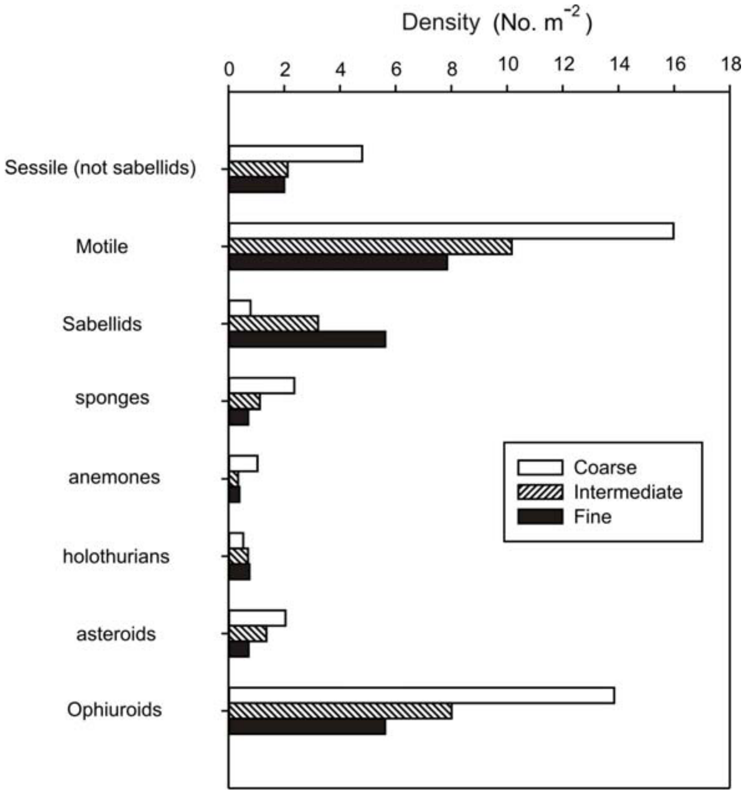


Figure 6.6: Density of selected megafaunal groups totalled across all sites for different sediment types on the edge of the Fimbul ice sheet, Antarctica.

Diversity

A total of 80 megabenthic taxa were distinguished from photographs (Table 6.2) with total numbers of taxa per site ranging from 38 (site F) to 56 (site B). Species accumulation curves (although not approaching asymptotic values) reveal changes in species richness between sites but no clear patterns with depth (Figure 6.8). The accumulation curve for site A is clearly different, driven by the dominance of sabellids at this site. The gradients of the species accumulation curves were very similar between sites. Rarefied estimates of species richness showed similar patterns to the species accumulation curves with low richness at site A and similar, higher richness for the other, deeper sites. Species density has been found to decline with depth (Figure 6.7).

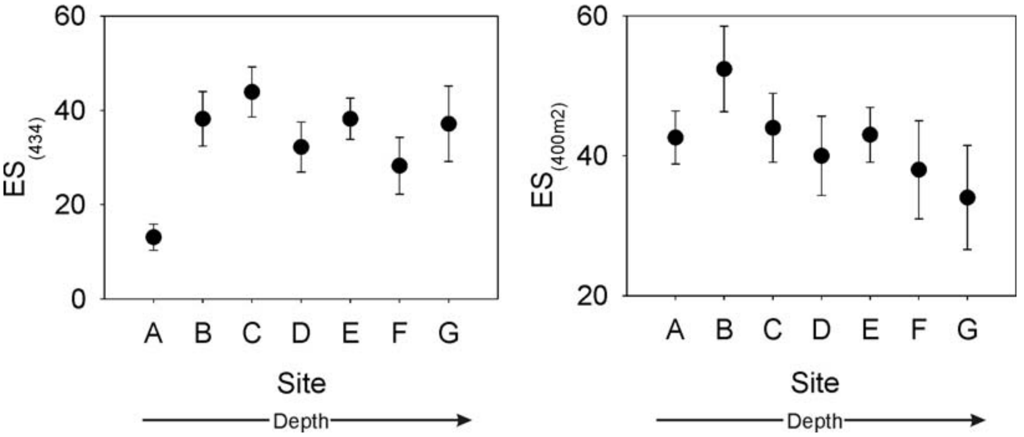


Figure 6.7: Megabenthos species diversity at each study site on the edge of the Fimbul ice sheet, Antarctica: species richness (Rarefied $ES_{(n=434)}$), species density (Mao Tao S obs $_{(400m2)}$).

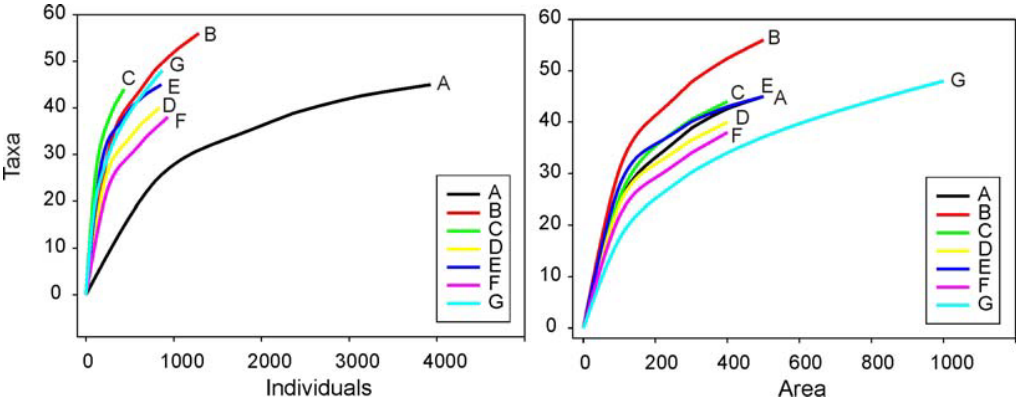


Figure 6.8: Taxon accumulation curves for study site on the edge of the Fimbul ice sheet, Antarctica: taxon accumulation per individual and taxon accumulation per unit area (m^2).

Heterogeneity diversity indices reveal significant changes in diversity between sites (H´ Kruskal-Wallis H = 24.80, df= 6 p<0.001). Indices show depressed diversity and evenness at sites A, D and F but there are no clear depth related patterns.

Heterogeneity diversity indices vary significantly with substratum (eg H´ Kruskal-Wallis H = 7.72, df = 2, p < 0.05). Within each site diversity changes with substratum, although there are no clear overall trends in diversity with substratum that are applicable to all sites (Figure 6.9). Depth and specific community composition control the changes in diversity that occur with changes in substratum. There were significant differences in Shannon Diversity between sediment groups (Kruskal-Wallis H = 7.72, df = 2, p<0.05). Diversity was highest in intermediate sediment areas and lowest in fine sediments.

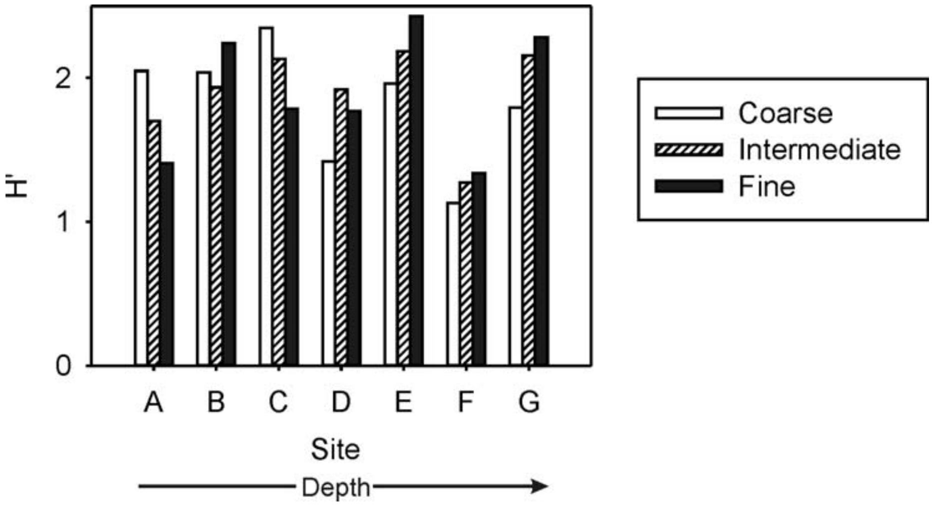


Figure 6.9: Species diversity (Shannon-Wiener, H´) of megafauna in different sediment types at each study site on the edge of the Fimbul ice sheet, Antarctica.

Community patterns

Analysis of photographs revealed a total of 8801 megabenthic organisms in an area of $3550m^2$ (Table 6.3). Overall echinoderms were the most abundant megafauna (57% megafauna; up to $2.2m^{-2}$), these were predominately ophiuroids (48.8%), although holothurians (3.6%), asteroids (3.4%), crinoids (1.8%) and echinoids (0.3%) were also represented. Sabellid polychaetes were important constituents of the total megafauna (27%) particularly as a result of large numbers at site A ($4.6m^{-2}$), their density reduced significantly with depth ($r' = -0.857$ $p<0.05$). Cnidarians were important (7.4%), these were predominantly actinarians (3.4%) and anthozoans (3.1%) but also included cerianthids, pennatulids and gorgonians. Sponges (5.7%) and fish (1.6%) were also important with the remainder of the megabenthos comprising of molluscs, arthropods and ctenophores.

Table 6.3: Characteristics of sites at the edge of the Fimbul ice sheet, Antarctica. For each station: water depth (m), density of total epifauna, dominant species, total number of species found, Rarefied estimated number of species, Shannon-Wiener diversity index, H′ (base log e), Simpson's Index (1- Lambda′), evenness (Pielou's J′) and dominance (Berger-Parker index, B-P).

Site	Depth (m)	Total density (No ha^{-1})	Dominant species	Species number	$ES_{(444)}$	H'	1-Lambda'	J'	B-P
A	245	77942	Sabellids, ophiuroid 1, Scleractinians	45	20.8	1.45	0.61	0.38	0.59
B	300	26765	Ophiuroid 1, sabellids, demosponges	56	41.3	2.23	0.77	0.55	0.41
C	340	10504	Ophiuroid 1, commatulids, ice fish	44	44.0	2.28	0.72	0.60	0.52
D	388	20427	Ophiuroid 1, *Peniagone*, ice fish	40	34.6	1.77	0.61	0.48	0.61
E	425	16942	Ophiuroids 1, commatulids, *Pseudostichopus*	45	39.1	2.19	0.71	0.57	0.53
F	465	22947	Ophiuroid 1, *Trachythyone*, *Hymenaster*	38	30.1	1.34	0.44	0.37	0.74
G	510	8804	Ophiuroid 1, encrusting sponge, *Sterechinus*	48	38.4	2.17	0.73	0.56	0.50

Multivariate analyses of whole community abundances reveal significant differences between stations (ANOSIM R=0.839, $p<0.001$). Both hierarchical clustering and Multi-Dimensional Scaling ordination reveal distinct between-site separation of communities (Figure 6.10). The pattern of multivariate similarity strongly suggests a gradient of species between sites (and depths) with a strong faunal discontinuity separating site A and B from the deeper sites. The pattern of points within each site is relatively diffuse indicating high within site heterogeneity.

Multivariate analyses of variance reveal significant differences in communities between different sediment types (ANOSIM R = 0.064, $p < 0.05$).

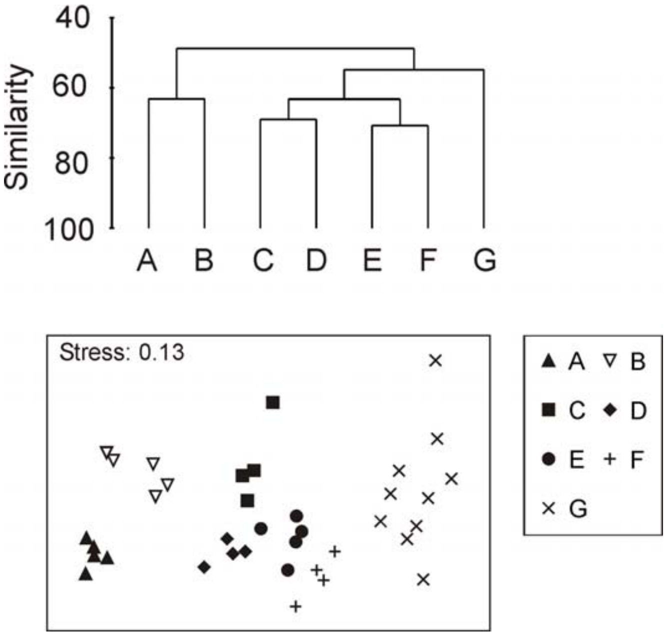


Figure 6.10: Megabenthos composition at the edge of the Fimbul ice sheet, Antarctica. Hierarchical clustering and multidimensional scaling ordination (see text for details) of megafauna composition (each point represents the data from a group of photographs covering 100m^2 of seabed).

DISCUSSION

Characterisation of the seabed environment

Physical disturbance from icebergs is widely regarded as one of the most important structuring forces for polar shelf communities (Gutt et al. 1996; Gutt and Piepenburg 2003; Thatje et al. 2005), while its effects are clear (Gutt et al. 1996) it is very difficult to measure the extent and impacts of disturbance (Thatje et al. 2005). The integrated approach used in this study facilitated investigation of extent of the plough disturbance, although there are several limitations in this method. While it is clear that the coarse material is produced at the edges of ploughmarks it is not always apparent if the fine sediment is inside or outside of the ploughmark, clearly a very important factor in establishing community patterns in relation to disturbance. The disturbance status of fine sediments is particularly a problem in deep water where visible disturbance inside the ploughmark is less obvious as a result of post-disturbance erosional processes. The presence of large hexactinellids, for example *Rossella* spp. (>400mm diameter in some cases), found throughout fine sediment areas indicate that these ploughs are likely to be very old (>500 years from Dayton 1979). An additional limitation of this classification scheme is that in shallow water, although generally applicable, the divisions are not as clear as in deep waters most likely owing to regular disturbance.

In understanding community patterns it is important to classify the timing of disturbance but this cannot be done by imaging methods unless the disturbance event is directly observed. The date of each disturbance event has to be approximated using information on the life histories of benthic organisms, relating to growth rates (Brey and Clarke 1993), life strategy (MacArthur 1960; Clarke 1979) and community successional patterns (Gutt and Starmans 2001). Gutt and Starmans (2001) assigned disturbance categories to the benthos based principally on the faunal composition, from heavily disturbed (R0) through recolonisation stages (R1 and R2) to undisturbed (UD). These categories were used to investigate the impacts of disturbance on benthic diversity (Gutt and Piepenburg 2003). The photographs of the benthos that were obtained at the shallow Fimbul stations bear resemblance to their representative photographs (Gutt and Piepenburg 2003) with most affinities with the highly disturbed R0 category, although small patches <10m were occasionally observed resembling R1 or R2. Hexactinellids such as *Rossella* spp., which are an indicator of a long term undisturbed benthos, were seen in these patches.

There were very high levels of iceberg disturbance in our study sites particularly sites A and B. The bathymetry observed at Fimbul resembles the "large iceberg bank" which Gutt and Starmans (2001) showed was the most likely to receive large-scale disturbance from icebergs. Several icebergs were observed grounded in this region during the study period. The levels of disturbance at Fimbul are very high, particularly in the shallower stations, where many ploughs were observed, with extensive damage to the seabed visible in photographs. They are comparable with those of the similar Austasen bank, approximately 150nm west of Fimbul, on which 70% of seabed was disturbed of which 30% was in the recently disturbed R0 category (Gutt and Starmans 1998).

Faunal density

Megafaunal density was found to decrease with depth at Fimbul, which has also been observed in other Antarctic and Sub-Antarctic megafaunal studies (Arntz et al. 1994; Thatje and Mutschke 1999) and is most likely related to reductions in organic matter available to the benthos with depth (Lampitt et al. 2001). The trend in faunal density with depth is difficult to compare between regions or even stations as there appears to be a highly heterogeneous nature of habitats and benthic community types (Gutt and Schickan 1998; Gutt and Starmans 1998), which have important effects on measures of community density (and diversity as discussed later).

The maximum faunal densities found in the Weddell Sea from photographic studies (Gutt and Starmans 1998) are higher than found here by over an order of magnitude. This was most likely a result of higher optical resolution from a combination of a reduced imaging area and increased film size in their study. The lowest values found in their 'deposit feeder poor' assemblage were lower than the low densities found in the deepest station suggesting the fauna sampled in this study was not in this assemblage.

Density was found to vary with disturbance intensity. At the shallow station A, the high numbers of sabellids suspension feeding on fine sediment increased the densities of visible megafauna in fine sediment to over that of the less disturbed area. In the less disturbed areas many of the fauna were small colonial forms such as cheilostomatous bryozoans or small sponges that are difficult to enumerate from photographs. In the deeper stations trends in density appeared to be controlled by changes in substratum as a result of past disturbance and not a result of recent direct disturbance from icebergs.

Density was generally higher in areas of coarse sediment associated with the edges of past iceberg ploughing. On the coarse substrata the fauna generally consisted of suspension feeding, sessile forms. Suspension feeders are dominant elsewhere in the Weddell Sea (Gutt and Starmans 1998). Density was lower in fine sediment, which had a deposit feeder dominated community. These trends may reflect a general increase in food availability for suspension feeders over deposit feeders in the Weddell Sea. The density of buried infauna in fine sediments, although not visible in photographs, is thought to be low in the Weddell Sea (Arntz et al. 1994).

Diversity

At Fimbul, diversity was relatively constant between sites, apart from low evenness (and related reduction in diversity measures) at site A (from high densities of sabellids) and a slight decrease in species density with depth. Diversity typically is found to increase with depth in many areas (Rex 1981; Rex et al. 1997). However, in Antarctic species it is postulated that this is not often the case. During Cenozoic glacial periods much of the Antarctic continental shelf was heavily impacted by ice, resulting in mass-wasting of benthic communities. Subsequently, it is thought that the continental shelf was predominantly recolonised by deep-water organisms with wide bathymetric tolerances (Thatje et al. 2005) which are still evident (Dayton et al. 1982). Large scale changes in diversity have been found in the Antarctic associated with the transition between shelf and slope, but not with depth in a specific area of the shelf (Arntz et al. 1997; Gutt and Starmans 1998). The reductions in species density with depth are related to reductions in faunal density leading to fewer individuals present to be sampled (Gotelli and Colwell 2001).

At the shallowest site (A) diversity reduced with disturbance, in undisturbed areas communities had been allowed to develop a high diversity. The structure of these communities resembles the ‘multistoried assemblages’ found elsewhere in the Weddell Sea (Gutt and Schickan 1998) where structuring species such as sponges, gorgonians or bryozoans serve as a substratum for other species, creating a complex habitat with high diversity. Many of the species associated with these habitats were too small to be enumerated from WASP photographs, thus reducing observed diversity compared to Gutt and Starmans (1998). Diversity of larger fauna at the shallow sites at Fimbul was slightly reduced from that found in similar communities elsewhere (Gutt and Starmans 1998). The small size of undisturbed patches may reduce supply of potential re-colonisers (Underwood and Chapman 1996), particularly with the common Antarctic life history pattern of direct development or short-lived larvae with limited dispersal (Thorson 1950; Mileikovsky 1971). In areas of iceberg disturbance communities were less diverse, being dominated by sabellids and a motile fauna consisting predominantly of ophiuroids, asteroids and holothurians. Classification into substratum type was not as effective in delineating disturbance regimes in this habitat as in the deeper sites.

Disturbance in the deeper sites at Fimbul causes changes in community composition. However, unlike the shallow sites, it seems that changes in substratum are the cause for changes in diversity. In this study I found that diversity was highest at intermediate sediments; these sediments had considerably higher substratum heterogeneity and hence had taxa characteristic of both fine and coarse sediment. Coarse substrata were found to be more diverse than fine, a possible result of the relatively high diversity of suspension feeding taxa in the Antarctic (Gutt and Starmans 1998), many of which prefer hard substrata.

Community composition

The findings of this study are an extension of the studies based on data obtained from R.V. *Polarstern* expeditions ANT XIII/3 and ANT XV/3 to the eastern Weddell Sea (Gutt et al. 1996; Gutt and Starmans 2001; Teixido et al. 2002; Gutt and Piepenburg 2003; Gutt and Starmans 2003; Teixido et al. 2004), which represent the most major recent work on megabenthos in this area. The present study extends their work, with overlapping communities at stations A (and to an extent B) and extending deeper into a different community.

The seabed communities at site A were significantly different from those at the other stations, as revealed from the megafaunal results and particularly from the fauna visible in the photographs but too small to quantify. These are most likely the expansive three-dimensional habitats formed of a complex of small suspension feeders including, for example, bryozoans and small sponges (Gutt and Schickan 1998; Gutt and Starmans 1998). The fauna in these patches at Fimbul is less diverse than those in similar communities observed elsewhere in the Weddell Sea (Gutt and Starmans 1998). Additionally, owing to the very high levels of disturbance at the shallow Fimbul sites, the patches of undisturbed fauna are small. At a landscape scale, the complex of iceberg ploughing at Fimbul has left only small areas undisturbed for long enough to allow communities to reach a late successional stage or community equilibrium. At Fimbul, the successional stages appear to be similar to those presented by Gutt and Piepenburg

(2003) with a similar community at the early successional stages (their R0, R1 and R2) which were dominated by sabellids at Fimbul but the area investigated was lacking some dominant large fauna including compound ascidians. Many of the smaller fauna they observed were not visible in WASP photographs and hence density and diversity measured in this study may be lower than that measured elsewhere.

At the stations deeper than 250m (B-G) the communities do not resemble the rich suspension feeder communities identified in Gutt and Starmans (1998) instead having a higher affinities with a combination of their ‘suspension feeders poor’ community and ‘suspension and detritus feeders’ community. The deeper communities at Fimbul were clearly driven by changes in substratum brought about by past iceberg ploughing. It appears that, particularly in the deeper sites, the substratum changes are more important than direct disturbance to the communities from the plough event. The disturbance events probably occurred sufficiently long ago, as indicated by the presence of large hexactinellids, that a climax community has developed within each habitat type. Only the shallow, rich suspension feeder communities have been previously analysed in relation to iceberg disturbance (Gutt and Piepenburg 2003) and the effects observed in deeper water in this study are clearly different and more difficult to detect.

In the waters deeper than 250m, the results of this study suggest that there is a gradient of taxa between sites. This appears to be related to individual taxon bathymetric and habitat preferences. There were no obvious faunal discontinuities observed at Fimbul apart from the separation of shallow (sites A and B) and deep faunas (sites C, D, E, F and G). Megafaunal community structure was found to vary with substratum as a result of individual taxon habitat requirements. The coarse substrata was preferential for most suspension or filter feeders such as anemones, demosponges, corals and crinoids, providing hard substrata for attachment and an elevated position which may enhance the capture success rate of suspension and filter feeders (Muschenheim 1987; Wildish and Kristmanson 1997). The deposit feeders, particularly holothurians for example *Bathyplotes bongraini (*previously *Bathyplotes fuscivinculum)*, were found preferentially on fine substrata (Gutt 1990) owing to their preference for fine particles to feed on (Billett 1991).

The effects of the iceshelf on benthic communities are poorly known. The study sites investigated are all within 8 km of the Fimbul iceshelf. Reduced taxon richness has been found to occur in the southeastern Weddell Sea close to the iceshelf (Arntz et al. 1994) but in the Ross Sea benthic life in the vicinity of the ice edge was rich and varied (Oliver et al. 1976; Oliver and Slattery 1985). Sites at the same depth but at different distances from the ice edge have been shown to have a similar fauna in other studies (Galéron et al. 1992). Dayton and Oliver (1977) show that sea floor current patterns are much more important than proximity to the ice shelf in governing faunal densities and community structure. At Fimbul the seafloor currents are predominantly from the direction of the open ocean, so it is unlikely that the presence of the ice shelf will reduce food supply to the benthic fauna.

The polar conditions of Antarctica result in generally lowered overall metabolism of benthic organisms through reductions in energy intake related to reductions in food supply owing to seasonal ice cover (Clarke 1983). Lowered metabolic rates cause lower rates of growth and reproduction in Antarctic invertebrates (Clarke 1983) and hence reduce the speed at which disturbed areas can be recolonised. For example an Antarctic echinoid has much lower growth and reproductive production than a temperate confamilial (*Sterechinus antarcticus*: individual somatic production $P_S = 0.01$, gonad production $P_G = 0.02$; *Parechinus angulosus*: $P_S = 0.39$, $P_G = 0.09$; all as gAFDM)(Brey et al. 1995). There is also a general trend in Antarctic invertebrate reproduction towards lecithotrophic larval development (Thorson 1950; Pearse 1994), limiting dispersal of recolonising cohorts. Deep-water communities on the Antarctic shelf, as well as being amongst the most heavily disturbed deep-water communities in the worlds oceans (Gutt and Starmans 2001) are also among the slowest to recover (Thatje et al. 2005).

NOTE

As part of this thesis an investigation into the effects of reducing flux of organic matter was planned using the Autosub Autonomous Underwater Vehicle to quantify megafaunal density, diversity and community patterns under the Fimbul Ice Shelf. A campaign of several photography missions was planned extending up to 50km under the ice shelf.

Autosub mission 382 was successfully carried out under Fimbul ice shelf (70°00S 1°25W), penetrating 25 km into the under ice cavity. This first mission was run with cautious off-seabed and off-ice ranges and so afforded no opportunities for photography. Unfortunately, on the following mission (383), Autosub suffered a failure that immobilised the vehicle some 17km under ice and therefore beyond recovery.

CHAPTER 7A: BIOLOGICAL CONCLUSIONS

INTRODUCTION

In the concluding section of this study it is important to compare the physical controls on benthic communities at a within-region scale (β) in areas with different physical controls on the benthic communities and then at the regional (γ) scale between the polar regions. Although this is based on a relatively small sample covering only a small area of these vast regions there are still justifications for this approach:

- The samples in this study use identical methodologies – while there have been several attempts to compare the polar regions, many of these are based on potentially biased data as a result of differences in scale and methodology of the investigations. Through the use of consistent methodologies in this study it is possible to compare these polar regions and different areas within each region without potential sampling bias.
- The WASP vehicle allows comparatively wide areas of the benthic environment to be compared quantitatively. This is likely to scale up to the regional scales more effectively than smaller or less quantitative samples. The visualisation of wide areas of the seabed environment also allows the assessment of heterogeneity within and between samples that may aid interpretation of regional scale applicability.
- The comparisons are based on essentially randomly chosen areas within each region.

These results should be interpreted as an important step in characterisation of polar differences although they should be interpreted with caution, as they are based on sampling only a very small fraction of either region.

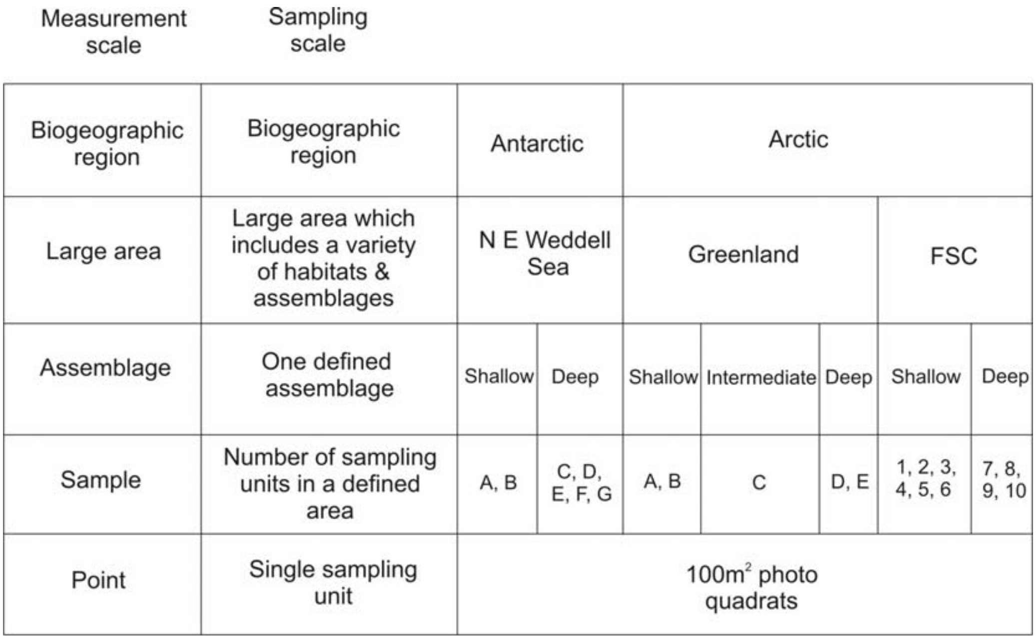
The differences and similarities of benthic communities in the Antarctic and Arctic have been discussed in the literature (Dunbar 1968; Hedgpeth 1971; Dunbar 1977a; Dunbar 1982; Dayton 1990; Dayton et al. 1994; Starmans 1997; Starmans and Gutt 2002). Despite some environmental similarities, for example, high latitude, low temperatures and strong seasonality (in light, ice cover and primary productivity), the benthos of Arctic and Antarctic waters differs considerably in certain ecological aspects, including higher species richness and diversity in the Antarctic (Dunbar 1977b; White 1984; Dayton 1990; Starmans 1997; Starmans and Gutt 2002). These large changes are generally explained in the context of major differences in geological history, recent interchange with adjacent oceans, degree of zoogeographic isolation, impact from land and freshwater as well as the age and variability of sea ice (Hempel 1985; Dayton et al. 1994; Starmans and Gutt 2002). Within the Arctic region there are more comparable studies, particularly in recent times (Piepenburg et al. 2001). However, the benthic fauna of high Arctic areas has never been compared with an area as unique as the Faroe-Shetland Channel where Arctic communities exist undisturbed by ice and in deep-water that is overlain and supplied by temperate waters with their associated differences in primary production. The polar areas have obvious similarities: as high latitude, cold environments with strong seasonality and heavy ice impact. They do, however, have a number of differences outlined in table 7a.1.

Table 7a.1: Some physical parameters of Kangerdlugssuaq, East Greenland; Fimbul, north eastern Weddell Sea, Antarctic and the Faroe-Shetland Channel study sites. Compared by seabed temperature (°C) and salinity measured at seabed for Kangerdlugssuaq and Fimbul in FSC from Turrell et al. (1999); ice cover as averaged yearly concentration for 10° longitude block (30-40°W for Arctic and 0-10°W for Antarctic) for latitudes greater than 50° (Ropelewski 1995); biogeographic provinces after (Longhurst 1998); productivity values from SeaWiFS global primary productivity estimates (Holm-Hansen et al. 1977; Clarke 2003); Predicted flux estimated using equations linking measured depth and surface productivity (Suess 1980; Berger et al. 1988; Herguera 1992); terrigenous input (Paul and Menzies 1974; Arntz et al. 1994; Masson 2001); sediment from observation; current as measured during field campaigns using ADCP over period of study (2-4 weeks; Iceberg disturbance calculated from swath bathymetry; and Latitude.

Physical factor	East Greenland, Arctic	Fimbul area, Antarctic	Faroe-Shetland Channel
Temperature (seabed)	0.5 to 1.5°C	-1.9°C	-0.5 to 0.5 °C
Salinity	34.7	34.3	34.9
Ice cover	Average 46.3 %	Average 39.6 %	None
Biogeographic province	Boreal Polar	Atlantic Subarctic	Austral Polar
Surface productivity	5 to 500g C m^{-2} y^{-1}	Average 16g C m^{-2} y^{-1}	150 to 300 g C m^{-2} yr^{-1}
Ave. predicted flux at average depth	19.5 C m^{-2} y^{-1}	1.6 C m^{-2} y^{-1}	8.6 C m^{-2} y^{-1}
Terrigenous input	High	Lowest	Low
Sediment	Heterogeneous ice rafted	Heterogeneous ice rafted	Heterogeneous ice rafted
Current	0.01 to 0.2cm s^{-1}	3 to 8cm s^{-1}	0.5 to 56 cm s^{-1}
Iceberg disturbance	0-9 ploughs km^{-2}	0-18 ploughs km^{-2}	Relic disturbance in <500m water depth
Latitude	68° N	70° S	61°N

METHODS

Scale is very important in ecology (Menge and Olson 1990; Levin 1992; Solan et al. 2002), it is important to clarify the scales of investigation (Figure 7a.1). These partitions follows the terminology of Gray (2000). The evaluation of patterns at the scale of sample and assemblage have been dealt with previously (Chapters 3-6). This section deals specifically with the assessment and explanations of patterns at the scale of large area and between regions.



Measurement scale	Sampling scale							
Biogeographic region	Biogeographic region	Antarctic		Arctic				
Large area	Large area which includes a variety of habitats & assemblages	N E Weddell Sea		Greenland			FSC	
Assemblage	One defined assemblage	Shallow	Deep	Shallow	Intermediate	Deep	Shallow	Deep
Sample	Number of sampling units in a defined area	A, B	C, D, E, F, G	A, B	C	D, E	1, 2, 3, 4, 5, 6	7, 8, 9, 10
Point	Single sampling unit	100m^2 photo quadrats						

Figure 7a.1: Scales of investigation in this study and the relative scales of data investigated. Following the nomenclature of Gray (2000).

Data analysis

The diversity of single samples (within habitat, α diversity) was compared using firstly the number of taxa recorded, and secondly the number of taxa rarefied to the lowest number of individuals found at a station (Hurlbert 1971).

Between-habitat (β) diversity was assessed initially using Bray-Curtis similarities (Bray and Curtis 1957) with square root transformation calculated for the investigation areas (Magurran 2003). The higher the overall similarities are, the lower the β diversity.

Non-parametric Kruskal-Wallis tests and post-hoc multiple comparison (after Miller (1981), see Zar (1999)) were used to test the significance of differences ($p<0.05$, 2 tailed) between the areas of investigation.

ANALYSIS

Common fauna

Between region

Virtually no taxa were found at both the Arctic and Antarctic stations. The only possible exception to this was the demosponge *Stylocordyla borealis*, which appears to be present in all three study sites. A comparison of phyla between regions reveals similarities in the major phyla between both regions (echinoderms, annelids, cnidarians, poriferans and fish) however the proportions of these vary significantly (Figure 7a.2).

The most major difference is that the Antarctic communities have a greater proportion of echinoderms and lesser proportion of annelids. However in the shallow disturbed Antarctic stations this is not the case. Annelids are at proportions similar to those found in the Arctic; in the deeper Antarctic stations the difference in proportional abundances of annelids and echinoderms is more pronounced. At a smaller scale sponges are proportionally more abundant in the Antarctic than the Arctic.

Within region

There were 8 taxa that were observed to be common between the FSC and the Greenland areas. Although impossible to identify to species in the majority of cases, these 8 taxa are morphologically very similar in both areas. The majority of these taxa are morphologically characteristic sponges, but include pycnogonids (*Colossendeis* sp.), asteroids (*Hymenaster pellucidus*) and fish (*Lycodes* sp.). Differences in proportional abundances of major phyla are apparent between the areas (Figure 7a.2), although proportions of the most abundant phylum, Annelida were similar in both areas. Greenland had a much higher proportional abundance of echinoderms than the FSC, which instead has higher abundances of cnidarians and to a lesser extent, sponges, arthropods (pycnogonids), molluscs and fish.

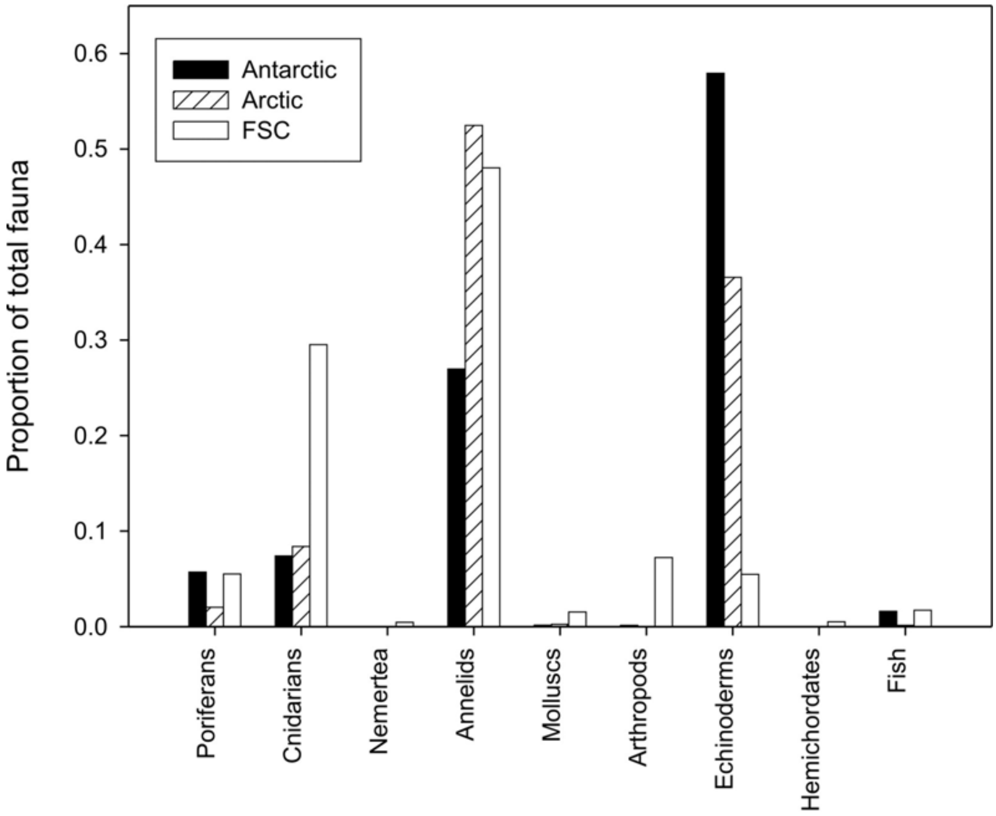


Figure 7a.2: Proportional abundance of megafaunal phyla at Antarctic, Arctic and Faroe-Shetland Channel sample sites.

Changes in faunal densities

Overall faunal densities were not significantly different (Kruskal-Wallis H = 5.09, df = 2, p = 0.08) between the Antarctic, Arctic and FSC (Figure 7a.3). However, there was a large range of megafaunal densities within each site (over an order of magnitude within the Arctic region). Potential causative mechanisms for this variation will be discussed later.

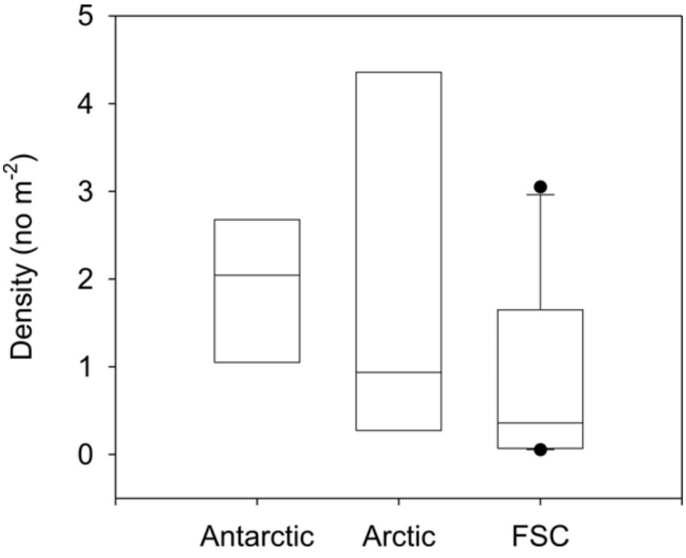


Figure 7a.3: Faunal density comparison between photographic samples at NE Weddell Sea (Antarctic), Kangerdlugssuaq fjord mouth, East Greenland (Arctic) and Faroe-Shetland Channel (FSC). Plotted as box plots: the centre line represents the median, the boxed lines represent the 25th and 75th percentiles and if sufficient sample size the bars represent the 10th and 90th percentiles, circles represent outliers.

Changes in diversity

Within habitat (α) diversity

Rarefied estimates of species richness (Figure 7a.4) do not reveal any significant differences between areas. However as a result of the low abundances of megafauna in the deep FSC, species richness estimates had to be rarefied to a low common sample size for comparison (n = 40). Rarefaction curves are difficult to interpret and may not reveal true patterns in species richness between assemblages at low n (Gray 2000; Magurran 2003). For this reason, the total number of species found (S) was also compared (Figure 7a.4). While this metric does not account for differences in sample size (n = 444 to 3883 in Antarctic, n = 154 to 2859 in Arctic and n = 43 to 1060 in FSC) the ranges of n were similar in each area and a clear significant increase in species richness can be seen in the Antarctic stations. There is no significant difference in number of taxa between the FSC and the Arctic; this trend is echoed in the species accumulation plots (Figure 7a.5). Species accumulation curves do not approach asymptotic values, hence extrapolation to estimate total species richness in each area is not appropriate.

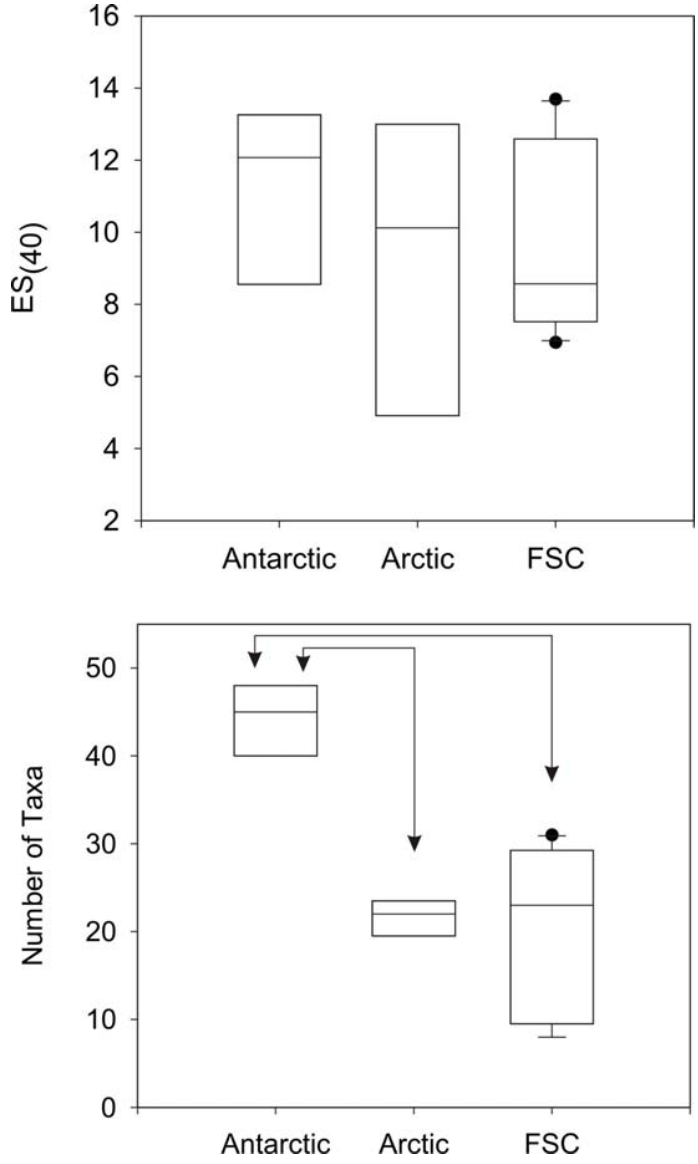


Figure 7a.4: Within habitat diversity (α). (a) Rarefaction richness estimator $ES_{(40)}$; (b) number of taxa in megabenthic assemblages from Antarctic, Arctic and Faroe-Shetland Channel. Plotted as box plots: the centre line represents the median, the boxed lines represent the 25th and 75th percentiles and if sufficient sample size the bars represent the 10th and 90th percentiles, circles represent outliers. Arrows indicate significant differences (post-hoc multiple comparisons after Miller, $p<0.05$) between areas. Sample size (n)=7, 5, 10 for Antarctic, Arctic and FSC respectively.

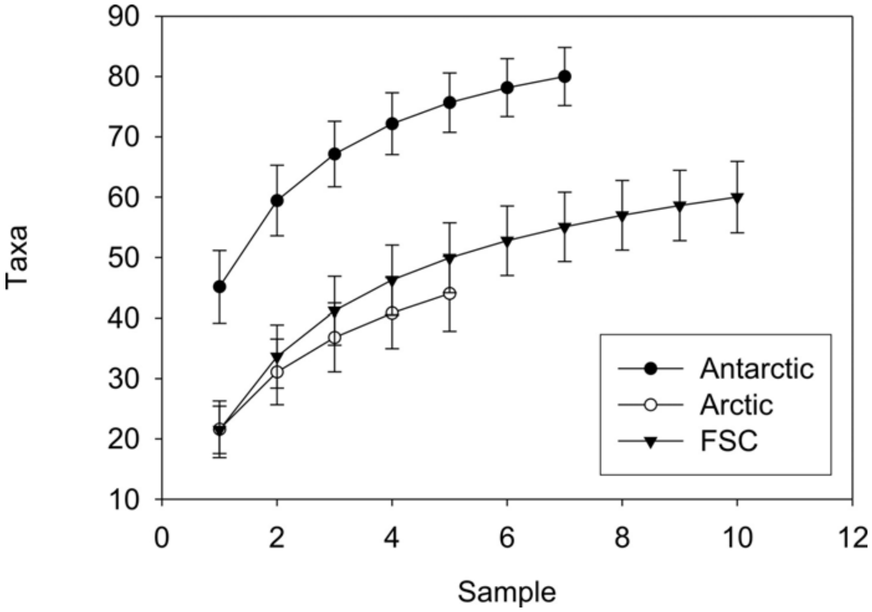


Figure 7a.5: Between habitat species richness. Accumulation curve of number of taxa plotted against number of sampling stations (sample) for random permutations of Antarctic, Arctic and FSC stations. Bars show the 95% confidence interval.

Between habitat (β) diversity

There was a broad range of similarity co-efficients within the areas investigated (Figure 7a.6). The FSC stations had the widest range of values and the lowest median similarity; this indicates high β diversity, as low similarity between spatial units is synonymous with a large difference between units in terms of species composition. Both the FSC and the Arctic areas had significantly larger β diversity than the Antarctic area.

Large area megafaunal species richness ranged from $ES_{(3800)}$ of 72.6 in the Weddell Sea to $ES_{(3800)}$ of 43.1 in East Greenland. On average, local (within assemblage) species richness was greater in Weddell Sea assemblages (mean $ES_{(40)}$ = 11.1) than in the East Greenland (mean $ES_{(40)}$ = 9.2) or FSC (mean $ES_{(40)}$ = 9.6).

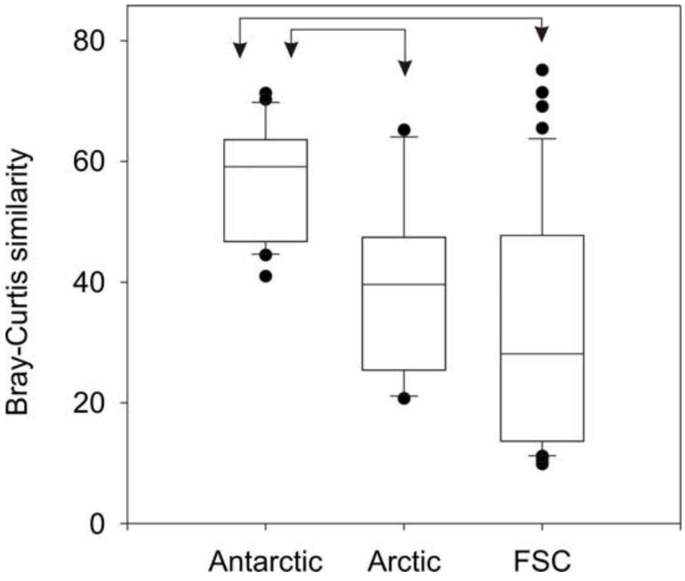


Figure 7a.6: Between habitat diversity (β). Distribution of similarity coefficients between all possible combinations of stations. Sample size (n)=21, 10, 45 for Antarctic, Arctic and FSC respectively. Plotted as box plots: the centre line represents the median, the boxed lines represent the 25th and 75th percentiles and if sufficient sample size the bars represent the 10th and 90th percentiles, circles represent outliers. Arrows indicate significant differences (post-hoc multiple comparisons after Miller, p<0.05) between areas.

Changes in the physical environment between regions and the effects on the communities

Changes with depth

There are few common general trends between the study sites within each polar region (Figure 7a.7). However in both polar regions there is a general trend of reducing density with depth. In the Antarctic there appears to be no trends in species diversity with depth. In the Arctic however species diversity clearly increases with depth.

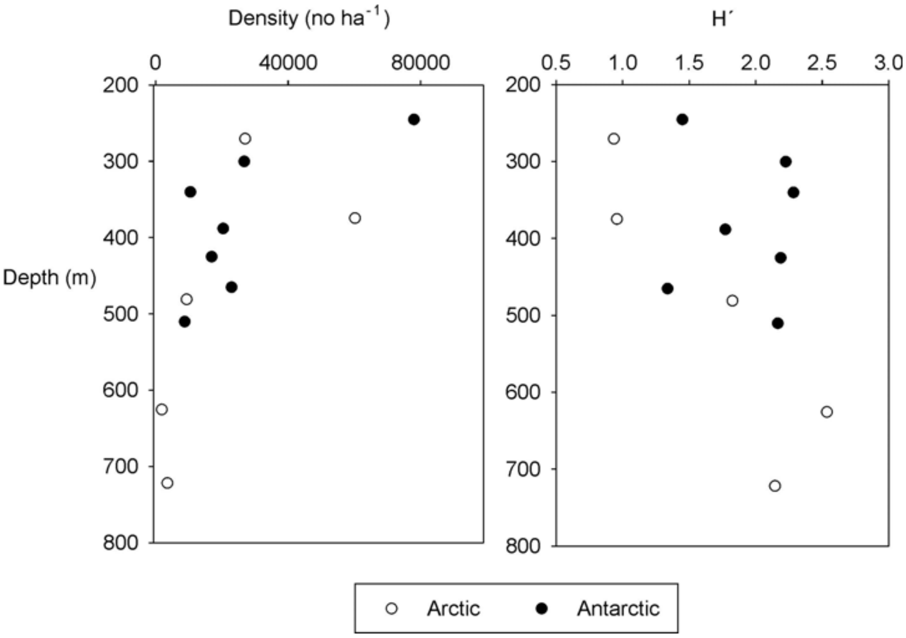


Figure 7a.7: Changes in megafaunal density and diversity with depth in the high Arctic (Greenland) and Antarctic (NE Weddell Sea) sites investigated in this study.

With increasing depth there were variable patterns in species accumulation between large areas (Figure 7a.8). In the Arctic there is uniform species accumulation. In the

Antarctic there is a clear reduction in species accumulation between 300-400m depth. In the FSC there is approximately uniform species accumulation with depth until approx 1150m depth where species virtually cease to accumulate with depth.

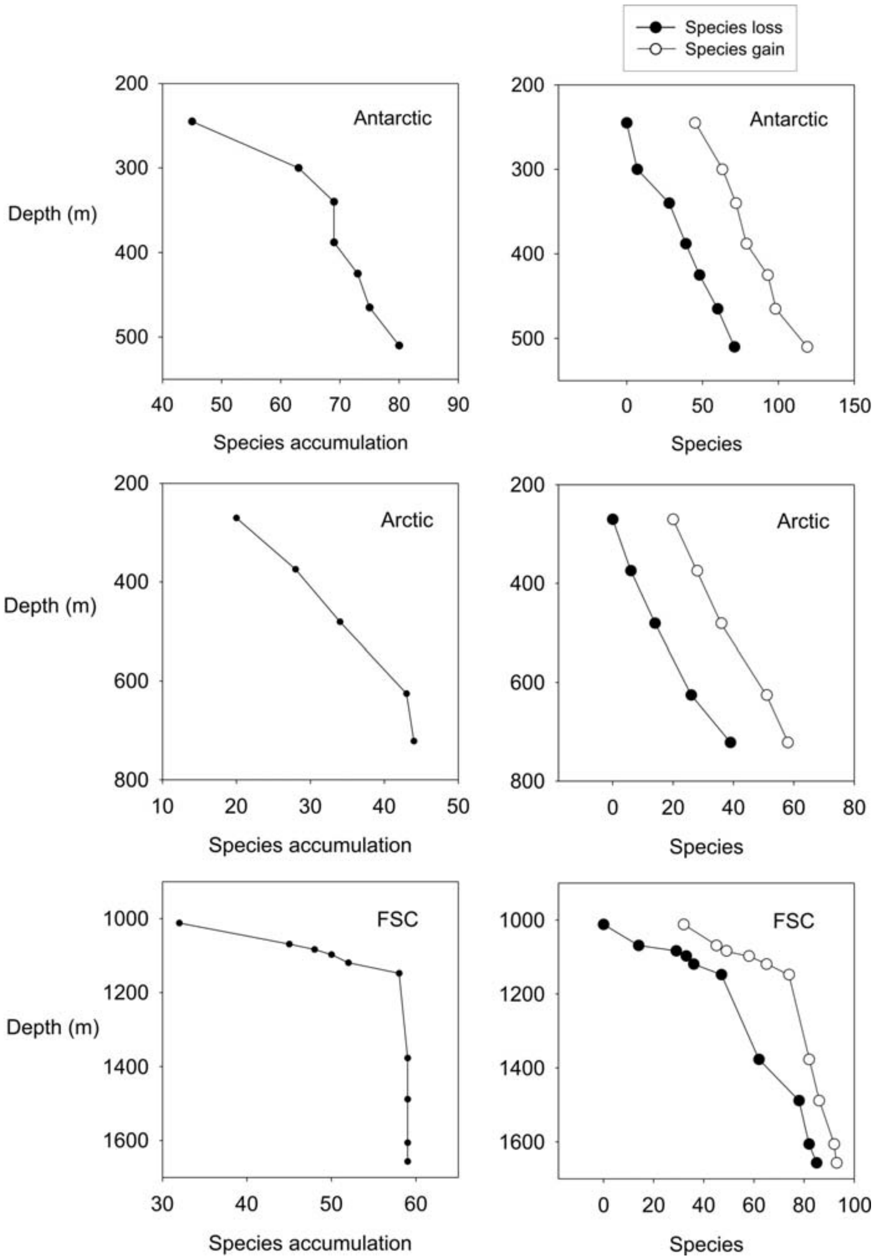


Figure 7a.8: Species accumulation (not randomised; left hand side) and cumulative species gain and loss between samples (right hand side) with depth.

Changes with habitat heterogeneity and disturbance

While it has been shown in the preceding chapters that habitat heterogeneity is important in governing the distribution of fauna, in these investigations it is difficult to distinguish these changes in communities from those associated with disturbance. It is only in the deep FSC (Chapter 3) that disturbance is sufficiently low for habitat to be analysed independently from disturbance. The effects of disturbance in all investigations result in changes to the habitat heterogeneity and therefore these will be discussed together. With the complexities in characterising disturbance there is no common metric by which communities can be compared effectively between regions.

Changes with flux

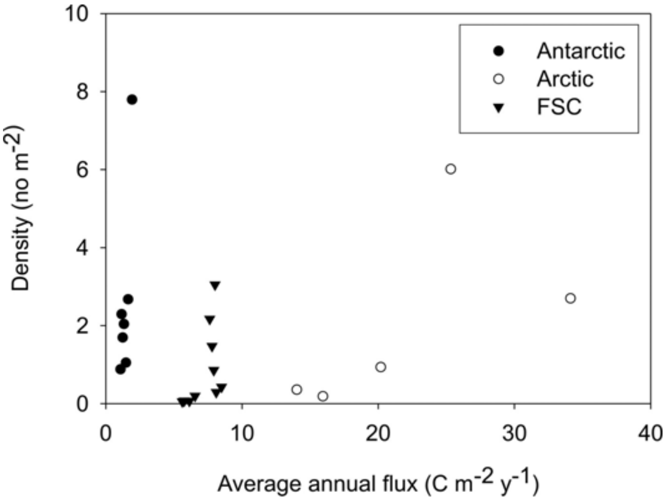


Figure 7a.9: Measured faunal density compared with levels of predicted flux. Average annual flux calculated from depth of sample site, SeaWIFS estimate of average surface primary production for region and average of results obtained from equations in Suess (1980), Herguera (1992) and Berger et al (1988).

Average annual flux estimates show no overall correlation with overall faunal density ($r' = -0.036$ $p = 0.88$; Figure 7a.9), for individual sites there is no significant correlation between flux and density for the Antarctic and Arctic areas ($r'=0.68$ $p=0.09$; $r'=0.8$ $p=0.10$ respectively). A correlation was observed in the FSC ($r'=0.65$ $p<0.05$). Flux estimates are directly proportional to depth and so these correlations echo depth trends.

DISCUSSION

Common fauna between regions

The variation in the faunal composition of the study sites in this thesis is not surprising. Polar invertebrate species have a wide range of distributions from isolated taxa to those with circumpolar or even bi-polar distribution, for example *Stylocordylia borealis* observed here. The number of shared taxa between the Faroe-Shetland Channel and east Greenland is also concurrent with the findings of other studies. Many Arctic invertebrates are found in adjacent boreal or temperate regions (Hayward and Ryland 1995). More widespread distribution is relatively rare although a number of Arctic invertebrates are found throughout the world’s oceans even including the Antarctic (Curtis 1975). For example, Ekman (1953) reveals 75% of fish genera found in the Arctic are present in temperate waters, whereas only 8% are common to both the temperate and tropical-sub tropical Pacific. In the Antarctic there are more circumpolar species than the Arctic (White 1984). For example, Gutt and Koltun (1995) found that 79% of the sponge species that they observed in the Weddell Sea had also been found in other Antarctic sectors. However there appears to be less biogeographic affinities with the adjacent oceans than for the Arctic, reported Antarctic species endemism ranges from 57 to 95% possibly owing to isolation by the hydrological barrier of the Polar Front / Antarctic Convergence (White 1984).

Faunal density between regions

The findings of densities that were not significantly different between sampling sites reflects the large small-scale differences in faunal density common to many benthic ecosystems. The early literature suggests significantly higher densities of fauna in the Antarctic compared with other deep-water areas (White 1984) but this hypothesis has not been confirmed by further investigation (Piepenburg and Schmid 1996; Gutt and Starmans 1998; Starmans et al. 1999; Piepenburg et al. 2001) where highly variable faunal densities have been found in both regions (Figure 7a.10).

Diversity between regions

The main differences in fauna between the polar systems is the increased age and longer isolation of the Antarctic (Brey et al. 1993). During the past 60 million years, the Antarctic experienced a slow and discontinuous transition from a warm water system in the early Tertiary (15°C) to today's cold water system (-1.8 to 2°C) (Kennett 1977). The ice shelves were formed over 36 million years ago in the Oligoscene from glaciation (Zachos et al. 2001). The formation of the circum-Antarctic current about 23 million years ago (Kennett and Barker 1990) isolated the Antarctic fauna from the world ocean (Brey et al. 1993). Most of the present fauna appeared to have evolved within the Southern Ocean (Clarke 1990) as indicated by high levels of endemism (White 1984; Brey et al. 1993). These levels are much greater than in the Arctic which has only had a glacial climate since the end of the Miocene, with ice sheets forming around 8 million years ago and then very extensive glaciation in the Pleistocene (Zachos et al. 2001) with km thick ice sheets during the Pleistocene glaciations (Polyak et al. 2001). It appears likely that the Arctic marine fauna has only developed since the Pleistocene (1.8 – 0.008 million years ago) and may potentially may have been very heavily impacted by ice until 150,000 years ago (Polyak et al. 2001). Levels of endemism are low in the Arctic where boreo-Arctic species dominate (Brey et al. 1993).

Changes between the poles in relation to physical factors

Depth and potential flux

When the results of this study are compared with those available in the literature (Figure 7a.10) it is clear that there is a wide variation in both density and diversity between areas and studies. There is a general reported trend of reducing density with depth in both polar areas, related to reductions in availability of organic matter with depth (Suess 1980). This trend cannot be directly linked to flux estimates here, but this is likely partially a result of estimates being highly approximate. Estimated flux values were based on regional surface primary production and not local (Lampitt et al. 2001), which coupled with widely varying seasonal production and potential underestimates of flux in mass export situations, such as may occur after seasonal blooms (Berger and Wefer 1990), may explain the lack of strong correlations.

Alpha diversity appears to increase predominantly with depth, particularly in the Arctic, although there is no clear trend in the Antarctic. This, in addition to the observed low ß diversity between Antarctic stations (chapter 6), supports the hypothesised wide depth ranges of shelf fauna in the Antarctic relating to past recolonisation of the shelf from deep water following late Cenozoic glacial defaunation (Thatje et al. 2005). It is likely that depth, while very important in controlling diversity, is just one of the many environmental and biological factors that influences diversity and has to be analysed with respect to changes in all these factors.

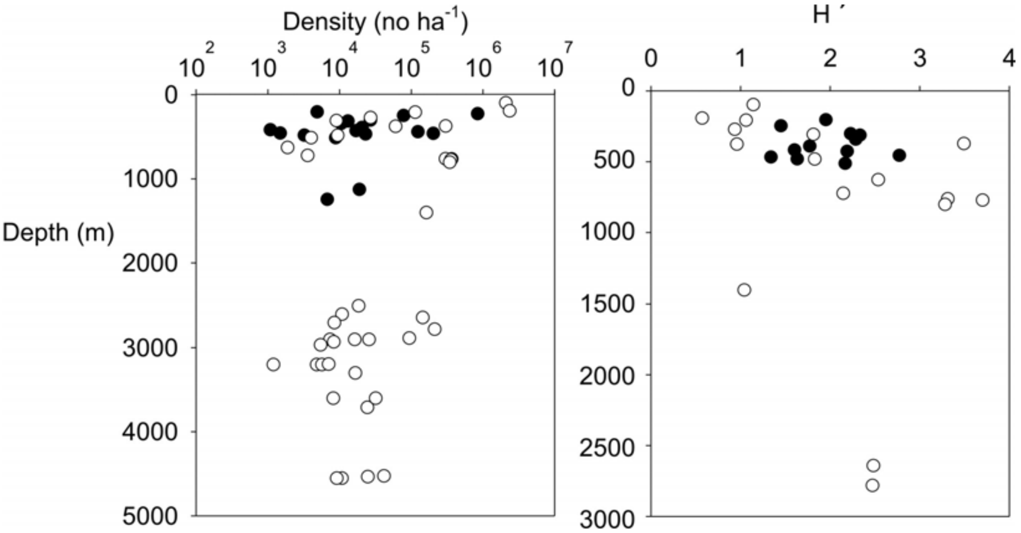


Figure 7a.10: Comparison of megafaunal density and diversity in the high Arctic (white circles) and Antarctic (black circles) investigated in this study and other values from the literature (Piepenburg and Schmid 1996; Gutt and Starmans 1998; Starmans et al. 1999; Piepenburg et al. 2001).

The changes in species accumulation, loss and gain with depth are related to discontinuities between assemblages. In the Arctic, there is uniform species accumulation suggesting a gradient of fauna with depth from one community to another with no major discontinuity. In the Antarctic there is a clear discontinuity between assemblages at 300-400m depth where no new species are accumulating. This appears to be the transition zone between the shallow multi-storeyed fauna identified by Gutt and Starmans (1998) and the deeper fauna found at Fimbul. In the FSC again there is evidence of assemblage partitioning particularly with regard to the lack of species accumulation in the deep, depauperate, very low density assemblage, which may be similar to deep-water communities found throughout the Norwegian Sea (Dahl et al. 1996).

Disturbance

The effects of disturbance have been evaluated in this study within a specific environmental location. From this work it can be seen that there is a large variety of effects of local disturbance on fauna which are summarised in Figure 7a.11. These effects can be divided into two types resulting from initial disturbance: direct changes to the fauna and changes to the environment. Both these effects have important implications for population dynamics and ecosystem function, and these effects, in turn, determine the future recovery of the ecosystem as well as its resistance (ability of the ecosystem to withstand change) and resilience (ability to recover quickly from change) to future disturbances.

The effects of disturbance on ecosystems are somewhat divided temporally into the initial and the long-lasting effects of the disturbance. The initial effects are primarily those that directly affect the fauna and the long-lasting effects are particularly changes to the environment and the ecosystem functioning of the communities affected by the disturbance. In the ROV investigations (Chapter 4), the acute effects of local disturbance on the fauna and the immediate changes to ecosystem functioning were being investigated. However long term changes to the environment and implications of the ecosystem changes were not apparent at this temporal scale. In the assessment of communities in the Faroe-Shetland Channel (Chapter 3), although the seabed environment was shaped by ice related processes, there has been very low natural direct disturbance for at least 10,000 years (Masson 2001). In the investigations of Arctic and Antarctic communities affected by natural disturbance (Chapters 5 and 6), the time since disturbance is not known; however through the changes to the ecosystems observed, and with reference to the growing literature on the effects of disturbance in polar ecosystems (Gutt et al. 1996; Gutt 2001; Gutt and Starmans 2001; Gutt and Piepenburg 2003; Teixido et al. 2004) it is possible to predict approximately the effects on the communities observed.

Of the polar assemblages investigated it appears that it is only the shallow stations that have been impacted by disturbance recently enough for some of the direct impacts of disturbance, such as defaunation (Bluhm 2001; Stronkhorst et al. 2003), and some early evidence of recovery (Gutt and Piepenburg 2003) to be observed. In the Arctic these changes may potentially be visible in the shallow stations through faunal changes but these are more difficult to distinguish owing to a paucity in literature pertaining to ice-related disturbance in the Arctic (Gutt et al. 1996; Conlan et al. 1998). As well as this the dominant fauna in the shallow Arctic are motile organisms, these can quickly recolonise disturbed areas compared with sessile fauna.

In the deeper Antarctic stations the effects of iceberg disturbance are visible but it appears that these effects are entirely a result of large scale changes in the environment. The disturbance has resulted in a partitioning of the habitat into coarse and fine fractions and as a result these habitats have been colonised by separate taxa in response to their individual habitat preferences. It is not clear at what stage the disturbance took place, but with the low sedimentation rates in the Antarctic it may be that these deep-water ploughmarks were caused at the last glacial period where sea levels were lower and the ice sheets were thicker (Berkman 1997).

In the deep Arctic stations it appears that disturbance from ice is not an important structuring force for the communities under investigation. With present ice conditions, icebergs are not generated in East Greenland with sufficient draft to effect directly the seabed at depths greater than 550m (Dowdeswell et al. 1993). The high rate of terrigenous input from the glaciers ensures that the deep benthic environment is homogenised with all relic evidence of ice disturbance covered. The terrigenous inputs in themselves lead to small-scale variation in habitat as a result of the size ranges of particles deposited; this variation appears to be at a scale too small to be readily detected in megafaunal community studies.

In the FSC the situation appears similar to that in the deep Arctic, although the processes that control the communities are different. There are very low sedimentation rates in the FSC and the seabed habitats have remained little changed since the last glacial period when ice rafting of terrigenous material formed the habitat (Masson 2001). For this reason the communities of the FSC have become more specialised to the environment, although again these effects are probably much more pronounced at a smaller scale than investigated (e.g. Klitgaard 1995).

Scale is very important in the understanding of ecological patterns (Levin 1992), particularly those associated with changes in diversity (Menge and Olson 1990; Levin et al. 2001; Gutt and Piepenburg 2003). The studies presented here have focussed on evaluation of pattern at the local scale. Without large sampling programmes, covering wide areas, extrapolation of these local scale changes to the regional scale is rarely possible, particularly in remote polar deep-waters.

The results presented here allow comparison of high and low disturbance regimes in Arctic communities. In the Kangerdlugssuaq sites α and ß diversity was not as high as in the similar habitat of the southern Faroe-Shetland Channel stations (excluding the more deep-sea like stations at the north of the FSC). This may be because local disturbance at Kangerdlugssuaq is sufficiently high throughout the stations investigated (from both ice grounding and increased sedimentation) that succession is limited. The mobile fauna may be transient within the depth boundaries, being displaced by disturbance frequently. An r-selected sessile pioneer epifauna may be all that develops throughout the local system, with slow growth rates, low reproductive output and high disturbance frequency limiting succession (Clarke 1983). In the Faroe-Shetland Channel, large-scale disturbance to fauna does not occur, the high habitat heterogeneity from relic disturbance has resulted in a high α and ß diversity (at the scale investigated here) as more diverse late successional stages are being observed.

At the regional scale local disturbance will act to increase species diversity (Gutt and Piepenburg 2003). This will occur through both the effects of direct impacts to the fauna and the changes to the environment caused by disturbance. At the regional (or landscape) scale temporally varied disturbance will result in a high habitat heterogeneity, with a mosaic of local patches, with different communities, at different stages of succession. While some individual patches may have an impoverished fauna from local disturbance, regional diversity will be high. It would be useful to assess at the large scale, through comparison of high and low disturbance Arctic regions, the relative effects on diversity of direct effects to fauna and habitat changes resulting from disturbance.

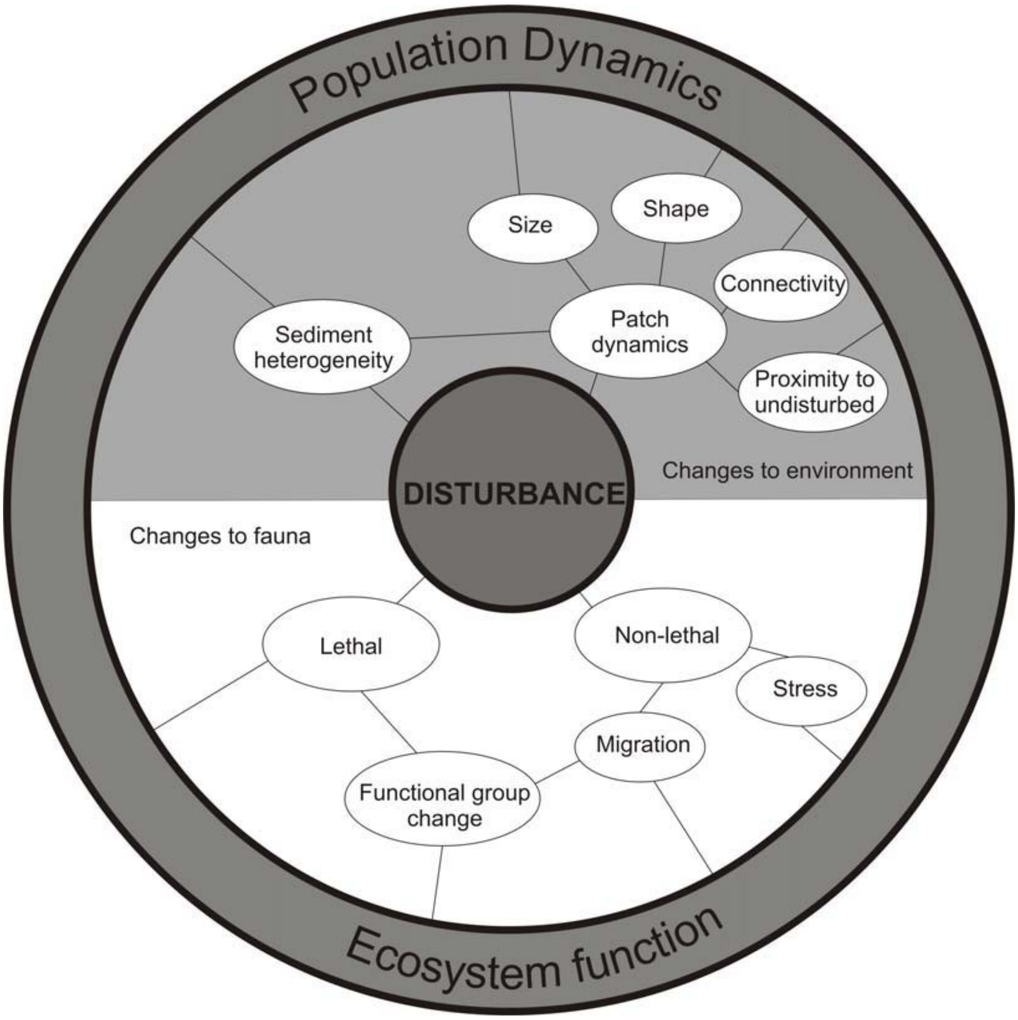


Figure 7a.11: Model of the effects of disturbance on population dynamics and ecosystem function.

Sufficiency of sampling

Species richness

Until an assemblage has been sampled exhaustively, species richness measures will underestimate species richness to an unknown degree (Magurran 2003). An investigator should be relatively confident that the sample is large enough to provide an accurate estimate of the size of the assemblage, but without knowledge of how large the assemblage actually is. Empirical stopping rules are used to indicate the point beyond which further sampling is unnecessary. Colwell and Coddington (1994) suggest that a census can be treated as complete if all species have occurred in at least two samples. In this study, as a result of sampling limitations, this situation was not reached in any sites. Magurran (2003) suggests dividing the total sample into two parts (at random) and estimating the richness of each part separately. If the answers are consistent with that obtained for the whole data set, the investigator can be confident that sufficient data have been collected. In this study again this is not the case with estimates of richness differing between the two parts. For this reason estimates of total species richness as has been done elsewhere (e.g. Colwell et al. 2004) are not appropriate.

Community patterns

The results of this study are important in our understanding of polar ecosystem structure and its controlling factors. There is sufficient coverage of sampling to characterise all but the rare taxa in the epibenthic megafaunal communities investigated within each defined area. It is often the most abundant taxa within an ecosystem that are most important in controlling the biological processes and the ecosystem responses to physical change. The wide coverage of the imaging methods used here provide comparable or greater areal coverage within each study site than most other polar studies. However, owing to the limited number of study sites, caution should be exercised in extrapolation of these results to wider areas, although with our limited understanding of polar systems there is value in this, particularly with inclusion of the additional information found in other studies.

CHAPTER 7B: METHODOLOGICAL CONCLUSIONS

INTRODUCTION

Seabed imaging technology has been in scientific use for a several decades (Hersey 1967; Heezen and Hollister 1971). In recent times the diversity of imaging methods had become huge, with a wide variety of imaging platforms, devices and methodologies. Science is often driven by available technology and this is particularly true for the deep sea. Specific hypotheses remain untested until technology creates the opportunities to conduct *in situ* collection, survey or experimentation to answer these questions. Technology for deep-sea biology is, in some cases science driven, for example deep-water trawls and the WASP camera system. However, in recent years it is commercial applications of subsea technologies that is driving progress, particularly in ROVs and to some extent AUVs and it has been possible for science to benefit from this development. It is very important that, in scientific studies, the methods are carefully assessed, in relation to the strengths and limitations in the data they provide. Throughout the biological observations in this study it has been important to assess the strengths and limitations of each photographic method. From using a range of methods as a result of this study it has been possible to make comparisons between them both in terms of practical and biological values. In some cases this has been possible through direct comparison of produced data and in others comparisons are discussed through extensive use of methods for this study.

Towed camera platforms

Towed camera platforms provide a deep-water equivalent of arial photography although at a smaller spatial scale taking into account the much increased attenuation of the visible light spectrum in water compared to air. Towed camera platforms are used routinely in the investigation of deep-water biology (Machan and Fedra 1975; Hashimoto and Hotta 1985; Christiansen and Thiel 1992; Hecker 1994; Bett et al. 1995; Barker et al. 1999; Cailliet et al. 1999; Bett 2001; Kollmann and Stachowitsch 2001; Cranmer et al. 2003; Mortensen and Buhl-Mortensen 2004) and geology (Hecker 1990; Leybourne and Vanwagoner 1992; Barker et al. 1999; McHugh and Ryan 2000; Fornari 2003), often for the initial assessment of the seabed character before more detailed investigations take place such as in hydrothermal vent research (Lonsdale 1977a; Lonsdale 1977b; McConachy et al. 1986; Klinkhammer et al. 2001).

ROVs

Remotely Operated Vehicles are incredibly versatile tools for deep-water science. With essentially unlimited power and endurance as well as real time control a huge variety of imaging studies and experiments can be carried out. Quantitative imaging of the seafloor with an ROV has been carried out repeatedly in deep-waters for biological observations (Auster et al. 1991; Butler et al. 1991; Adams et al. 1995; Vetter and Dayton 1998; Starmans et al. 1999; Ambrose et al. 2001; Brodeur 2001; Hovland et al. 2002; Gutt and Starmans 2003; Jonsson et al. 2004; Stein et al. 2005). The utility of ROVs has been considered by an number of authors (e.g. Barry and Baxter 1992).

AUVs

Autonomous underwater vehicles are relatively new and have only recently become viable for scientific use. Most of the AUV scientific projects have used acoustics (Stansfield et al. 2001; Millard et al. 2003); direct imaging techniques from AUVs are in their infancy (Jones et al. 2005). At present three AUVs have still camera systems, the NOC Autosub and two Woods Hole Oceanographic Institution Deep Submergence Laboratory (WHOI DSL) vehicles, Autonomous Benthic Explorer (ABE) and SeaBED.

Photographs

Deep-water photography is a long established technique for the investigation of benthic environments. It offers high resolution imaging of reasonably wide areas of seafloor. Practically, a single photograph of the seafloor of use in megafaunal investigation can cover approximately 1-10m^2 of seafloor. In biological investigations it is most practical to measure resolution as the minimal size of repeatedly identifiable organisms, referred to subsequently as 'biological resolution'. Values as low as 1mm have been reported for a 70mm medium format camera operated on a bounce camera system (Gutt and Starmans 1998). These systems tend to photograph only a small area of the seafloor (1.4m^2 in the previous example). An alternative strategy, as adopted by WASP and many other towed camera platforms is to photograph much greater areas of the seafloor at a lower resolution. Typically these systems have a biological resolution of around 5cm. There is generally a trade-off between spatial extent of a survey, film or memory requirements, duration of survey and biological resolution.

The medium for photographic recording is also important in deep-water photography. Traditionally 35mm film is used (Hersey 1967), which provides a reasonably high resolution and, as a standard format, relatively low cost development. Conventional film has some disadvantages, it occupies reasonably large physical spaces particularly in the volumes needed for biological survey, processing usually cannot be done at sea and so image quality and faunal patterns cannot be assessed quickly at a time scale relevant to further sampling and post processing of the film for analysis e.g. scanning can take longer. The resolution of 35mm film conventionally used in deep-water photography (ISO 250 film) is approximately equivalent, in terms of silver crystal density, to a digital resolution of around 10 megapixels, however noise in digital cameras is much lower than grain (its counterpart) in film. Digital camera systems are being increasingly used in deep-water photography (see e.g. Fornari 2003); these systems may have reduced resolution over film but have a number of important advantages: immediate results, low operational cost, virtually unlimited storage and native digital format facilitating presentation and analysis. Computer aided analysis techniques for digital photographs include digital image analysis (for quantification of sizes and areas) and potentially more advanced techniques discussed later. Computer aided analysis techniques are possible by scanning film photographs, however this is costly and time consuming for the volume of photographs required for high quality analyses.

There are several options for camera mounting used in deep-water photography pertaining to the angle of the camera from vertical. A vertical camera angle facilitates scaling, and subsequent measurement as well as maintaining relative size of fauna. Oblique angles provide a greater coverage for a given height as well as a more natural view of the seabed, facilitating identification and observation of fauna; scaling, while possible becomes difficult and perspective effects change relative sizes of fauna depending on their position on the frame (Wakefield and Genin 1987). If photo mosaicing is used a vertical camera angle is necessary. Both methods have been used successfully in deep-water photography (Hersey 1967) although vertical camera angles are more typical.

Video

Underwater video allows a wide swathe of benthos to be recorded quickly with complete coverage. Video resolution if often low, practically around 500 x 500 effective ‘pixels’ (phosphor dots), this figure applies to blacks, greys and whites only, colour resolution is much less, most often between 25x25 and 50x50 (NTSC Broadcast, VHS, S-VHS, Hi-8). Video resolution is continually improving with the state of the art High definition digital video (HD) presently record 1080x1280 effective ‘pixels’. Most existing science video systems, including WASP use lower quality systems although several science-class ROVs have HD video cameras and recording equipment.

METHODS

Photographic technique

Photographs vs video

Using a towed camera platform such as WASP that collects video and photographic data simultaneously, it was possible to compare the biological outcomes for the two techniques directly. This was carried out for an example station in the Faroe-Shetland Channel (FSC1). Photographic and video data were collected as described in chapter 3. Photographic data were analysed as previously described, video data were analysed as ROV video (chapter 4).

Altitude comparisons

Using photographs from the shallow Faroe-Shetland Channel (FSC 1 – 5; Chapter 3) before unrepresentative frames had been removed from analysis, the effect of altitude on mean density of fauna observed was analysed. It was assumed that actual average faunal density was approximately constant and organisms are randomly distributed.

The expected relationship between the mean number of individuals in one photograph and altitude, is:

Where, with WASP camera acceptance angles:

$$\text{Area} = 0.6\, \mathit{altitude}^{2}$$

Therefore:

$$\text{Mean no. individuals} = \mathit{actual\ density}.\ 0.6\, \mathit{altitude}^{2}$$

Actual density was not known, however the “best fit” expected relationship was calculated iteratively to minimise the Chi-squared statistic:

$$\chi^{2} = \sum \frac{(\mathit{observed} - \mathit{expected})^{2}}{\mathit{expected}}$$

The iterative “best fit” occurred when actual density was 0.9 individuals m^{-2}.

Two transects were undertaken using ROV video at the Schiehallion field, UK (420-421m depth, 60°22.95´N 04°05.95´W). The seabed was undisturbed and distant from drilling activity (>1km) but had a small diameter pipeline running across it. Two ROV video transects were conducted running along this pipeline between two conspicuous markings spaced 50m apart on the pipe. One transect was run at 1m altitude and the other at 3m.

Sample size

It was important to provide replication for subsequent analyses. However, the logical sampling unit of individual photographs did not contain enough individuals or species for valid comparisons. Photographs had to be grouped to minimise variance in data between sampling units. As all photographs were taken along a single transect it was important to avoid possible pseudoreplication. All measures were taken to avoid potential sampling biases:

- Transects were undertaken following a stratified random sampling strategy
- direction of the vehicle was random, both with respect to ship track and current conditions driving vehicle track
- photographs to be pooled were selected randomly along the transect.

To pool photographs into a useable sampling unit, photographs within a towed camera platform transect were randomised and then sampled without replacement into pooled groups of a set sample size. It was important to assess correctly the size of the individual sampling units to maximise replication but minimise variance between samples. A Matlab routine was written to assess the effects of differing sample size on the variance of the Shannon-Wiener diversity index between samples. This sampled all photographs within a transect at random without replacement until the area covered was equal to the sample size (± 2 m). It then pooled the numbers of each species for each sample and stored this individual sample array in a species by sample matrix. It continued doing this until there were insufficient photographs left to create a sample. Shannon-Wiener Diversity index (as an example index) was calculated on the values for each sample and the variance calculated between each diversity index measurement. This process was repeated for incrementing sample sizes (incrementing by $10m^2$) between 10 and $200m^2$ which were the practical limitations of the potential replicates as a result of the total photographs taken per station.

Comparison of vehicles

An arctic deployment of Autosub from the RRS *James Clark Ross* allowed comparison of AUV images with seabed photographs from a towed camera platform. The NOC Wide Angle Seabed Photography (WASP) towed camera system was operated in areas clear of ice at a similar depth to the Autosub operations (WASP station D = 625 m depth; Autosub mission 377 = 564m depth; chapter 5). While the exact same area was not covered, the communities within both areas have been shown to be similar (See chapter 5). Unfortunately, owing to the limited number of Autosub photographs (n=19) direct numerical comparison of the communities observed was not possible.

ANALYSIS

Photographs vs video

Despite the greater areal coverage of video as a result of continuous recording (183% coverage of photographs), there were large reductions in faunal densities (38% photographic densities) and all diversity measures when compared with photographic assessment of the same community (Table 7b.1).

Table 7b.1: Photographic vs. video counts of megafauna from WASP vehicle in Faroe-Shetland Channel example station (FSC1). Includes: Total megafaunal number (N), number of taxa observed (S), Rarefied number of taxa ($ES_{(300)}$), Shannon-Wiener diversity index (H'), Margalef diverisy index (d), Pielou evenness (J'), Simpsons diversity index (1-λ'), Total faunal density (no ha^{-1}), and area of seabed covered (m^2) by each method.

	N	S	$ES_{(300)}$	H'	d	J'	1-λ'	Density (no ha^{-1})	Area covered
Photo	437	31	27.59	2.32	4.93	0.67	0.82	4215.44	1036.7
Video	317	18	17.83	1.74	2.95	0.60	0.72	1676.61	1890.7

Importance of altitude

Altitude was found to be very important in photographic investigations. In the WASP investigation tested here, at both high and low camera altitudes there were large departures of observed individuals from expected (Figure 7b.1). Low altitude conditions resulted in the greatest enumeration of organisms, although it was not consistently possible to fly the WASP vehicle at altitudes below 150cm. At high altitudes, while the areal coverage was great, there were significantly lower numbers of visible fauna. Photographs taken between 150 and 350cm altitude revealed consistent average numbers of organisms as well as providing a reasonable range of altitudes for effective operation of the WASP vehicle and hence a reasonable number of photographs for analysis.

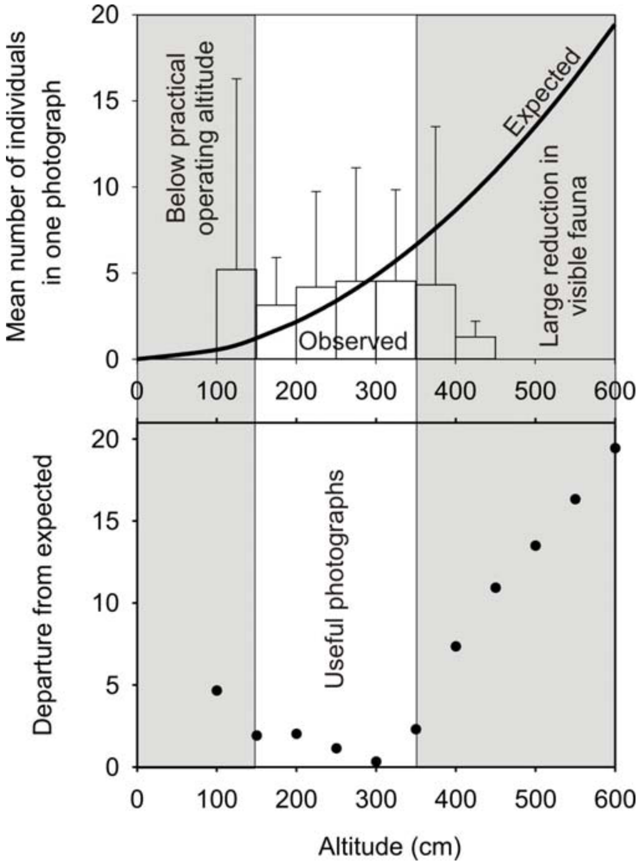


Figure 7b.1: Changes in mean number of individuals in one photograph observed (n = 572) and expected and departure from expected (difference between observed and expected). The data were from the shallow Faroe-Shetland Channel sites (FSC1-5) before high altitude photographs were removed from analysis. Error bars represent the standard deviation.

In video observations at 3m altitude 3 times the areal extent of seabed was investigated to that at 1m altitude. However, only one taxon could be identified at 3m altitude, a brilliant white sponge and even the densities of this species were nearly half that identified from the 1m altitude transect. Overall densities were clearly much reduced in the high altitude video (Table 7b.2).

Table 7b.2: Comparison ROV video transect data from identical length transects (50m) undertaken at low (1m) and high (3m) camera altitude, in the Schiehallion field, UK. Number of species found (S), Estimated number of species (ES(50)), number of individuals (N) and density (no individuals m^{-2}).

	S	ES(50)	N	Density (no m^{-2})
Low	6	5.381	114	2.51
High	1	1	51	0.37

Sample size

Sample size was important in controlling variance in H′ (Figure 7b.2). Variance between individual photographs was very high and as a result pooling of photographs was found to be advisable. Samples were pooled on the basis of area as this allowed comparability of samples between study sites. A sample size of $100m^2$ was taken as this provided at least three replicates at all stations but had minimal associated variance in diversity between samples.

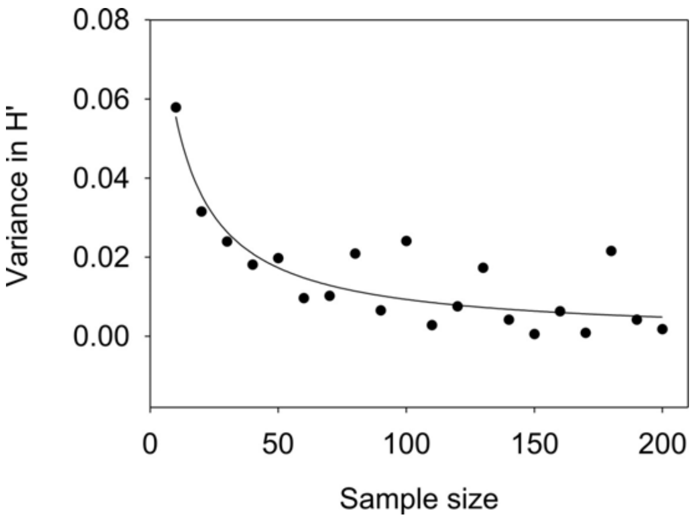


Figure 7b.2: The effect of sample size (m^2) on the variance of Shannon-Wiener diversity index. Points represent the results from one random sample grouping from one transect, the line represents a Monte-Carlo simulation of variance based on 500 random regroupings.

Comparison of vehicles

AUV vs towed camera platform

Images obtained from Autosub were broadly comparable with those taken by the WASP vehicle (Figure 7b.3). Despite the differences in operating altitude, each frame showed a comparable average area of seabed. Unlike Autosub, which holds a relatively constant altitude, WASP ranges in altitude with the ship’s heave, producing useful images from 2m to 4m altitude (area of seabed covered = 2.35m^2 to 9.41m^2). There was a discernibly higher resolution in the WASP images reflecting the increased resolution of conventional film over the CCD imager (1392x1040 pixels). The resolution of the Autosub images is nevertheless satisfactory for scientific characterisation of the seabed.

The colour images from WASP facilitated identification of some species when compared with the monochrome Autosub images.

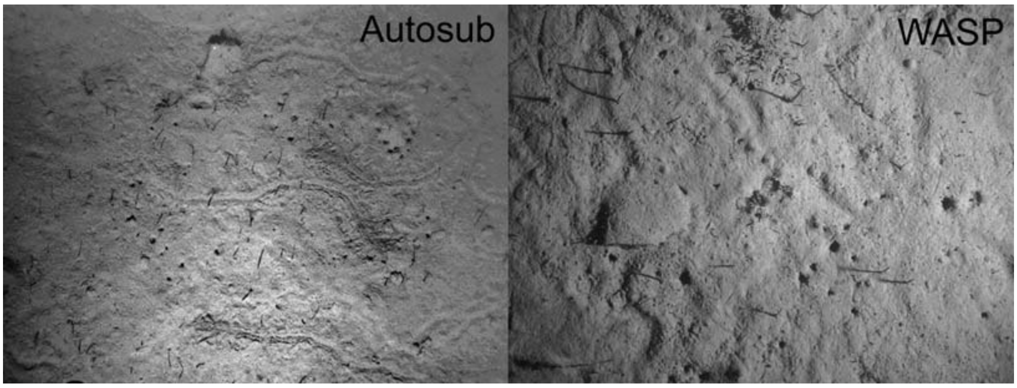


Figure 7b.3: Comparison between Autosub image (left) and WASP image (right) from Arctic Greenland. Autosub image from a water depth of c.600m. The image area is cropped to 2.0 m x 1.6 m. Illumination from the bottom of field. Date: 09/09/04; Time: 04:16:27; Altitude: 10.31 m; Depth 588 m; Position(deg): 68.0336°N, 31.7911°W; Heading /Pitch/ Roll (deg) 36.2, -5.2; -2.45. WASP image from a water depth of 658m. The image area is cropped to 1.4 m x 1.0 m. Illumination from the right of field. Image originally in colour. Date: 03/09/04; Time: 09:46; Altitude: 2.98 m; Depth 658 m; Position(deg): 68.0485°N, 31.7610°W.

DISCUSSION

Imaging investigations

The altitude at which photographs were taken affects the biological resolution of the photographs, which has been shown here to affect the measured density and diversity of the communities under investigation. However increases in altitude result in sampling an increasing area of seabed, particularly important as the area sampled increases proportionally to the square of the altitude.

Photographs

The reduction in faunal numbers observed with increasing altitude was a direct result of the limitations of underwater camera systems. As light dissipates through water much faster than through air; underwater photography over a distance of greater than several metres is challenging. Both absorption by seawater and scattering by suspended particulate matter rapidly reduce light intensity. Additionally, the increased distance results in decreased film grains per area of seabed and hence lower resolution of photographs, making it difficult to distinguish organisms from a heterogeneous substratum.

At low camera altitude there was a high departure of observed individuals from expected. This appears to be a result of greater detection of fauna present from higher resolution of photographs. It was not possible to ‘fly’ the towed camera platform consistently at altitudes of 100cm or less, owing to variations in the bathymetry of the areas investigated.

The biological conclusions of this suggest that when using faunal density values obtained from a platform with variable altitude, caution should be exercised as to the altitude of the vehicle. The optimal altitude depends on the minimum size of fauna that needs to be resolved and the minimum operational altitude of the vehicle. In practical terms for this study with a minimum faunal resolution of 5cm, estimates of faunal density from WASP photographs are likely to be very much reduced from actual values at altitudes greater than 350cm. Only the larger and more conspicuous fauna will be seen at altitudes greater than 350cm.

Video

It is important in ROV studies to minimise the altitude of sampling to identify as many megafaunal organisms as possible. ROVs have a much greater level of control than camera platforms allowing flying altitudes of around 20cm with a resultant camera altitude of around 75cm (or less for systems specifically designed for survey). It has been shown here that video investigations of megafauna should not be conducted at high altitude (>2m).

Comparisons of vehicles

There are a wide variety of vehicles in use for ecological survey in the deep sea. The best method depends strongly on the nature of the survey and facilities available (Table 7b.3). In this section the vehicles will be compared assuming the same camera system is used on each. It should be emphasised that the vehicle is only as good as the imaging sensor it carries.

Table 7b.3: Comparison of platforms for deep-water ecological survey. Including: method of obtaining ecological data, maximum practical resolution (minimum size of organism quantifiable) for photographs and video, comparable coverage of a transect, extent of survey (e.g. area covered per unit time), expense of survey (costs of operating vehicle per unit time), facilities required (additional requirements to vehicle e.g. minimum: standard research ship; maximum: dynamic positioned research ship, fibre optic cables, dedicated control teams and facilities etc.).

Method	method of obtaining ecological data	Max. photo resolution	Video resolution	Coverage	Extent of survey	Reliability	Expense of survey	Facilities required
Bounce Camera	photographs	high	/	low	very low	high	low	low
Towed Camera Platform	photographs and video	medium	medium	high	high	high	medium	low
AUV	photographs	low but increasing	/	high	high	low	high	medium
ROV	photographs, video, samples	high	high	high	medium	medium	high	very high
Submersible	photographs, video, samples	high	high	high	low	high	very high	high
Trawl	samples	/	/	medium qualitative	medium qualitative	high/ medium	low	low

Sensor choice

Sensors have to be chosen carefully with respect to the operational requirements of the vehicle. This is particularly important for AUVs such as Autosub, which will be used as an example to highlight the issues involved and some solutions. The operational limitations of the AUV, particularly with regard to the safe flying altitude (of 10m in Autosub) require solutions for effective photography. Scattering of light by suspended particulate matter can be reduced by minimising the overlap between the illumination and imaging paths. Consequently the camera and flashgun were mounted as far apart as possible, an approach adopted by most imaging vehicles. At a flying altitude of 10m (round trip for light of 20m), very little light except blue and violet returns to the camera lens. Even in pure water very little of the red-orange end of the spectrum returns: 99.5% is attenuated. Hence a colour camera was inappropriate and as only one in four (the blue) pixels would register any light, the sensitivity of a colour system would be at best 25% of a monochrome camera.

If possible maximal resolution should be prioritised in sensor choice. As the most severe limitation of biological analysis of photographs is the detection of species, at whatever scale analysed, resolution is paramount. Without repeatable and accurate identification of species the biological conclusions that can be made from photographs are minimised.

AUV vs towed camera platforms and ROVs

At present AUVs are limited to some degree in terms of power, and hence sensors. The high power requirements of continuous lighting for video as yet have not been met however photography has been shown to be entirely feasible (Jones et al. 2005). Autosub is severely limited, in terms of photography by its flying mechanism (using lift generated by forward motion) and hence minimum safe altitude. One of the more scientifically important alternative approaches is that taken by the Woods Hole Oceanographic Institution Deep Submergence Laboratory's (WHOI DSL) Autonomous Benthic Explorer (ABE) vehicle (Yoerger et al. 1992). This vehicle is unlike Autosub in design and more adapted to precise control over considerably shorter range than Autosub (theoretical range <50km for ABE, 800km for Autosub), ABE has 7 thrusters and is capable of movement in any direction much like an untethered Remotely Operated Vehicle (ROV). It has a camera system currently consisting of stereo, monochrome, downward pointing digital cameras each providing an image resolution of 576x768 pixels with a dynamic range of 8 bits. When updated as planned the ABE camera system will allow colour imaging as the vehicle can operate closer to the seafloor. These vehicles represent different solutions to AUV imaging for science and hence will have different scientific uses. While ABE-like systems may produce 'better' images over a short range they will not be able to sample in the more remote environments or at the long ranges which vehicles such as Autosub are capable of investigating. A development, parallel to ABE, at the WHOI DSL is the SeaBED vehicle (http://www.whoi.edu/DSL/hanu/seabed/index.html), which represents an alternative approach to AUV imaging. It is a readily-available operationally-simple AUV designed to test imaging methods and docking methodologies with the aim of pursuing repeat surveys for change detection and quantification of features. SeaBED is a hover-capable vehicle that performs optical sensing with a 12bit 1280x1024 monochrome CCD camera, combined with acoustic high resolution mapping systems (Singh et al. 2000). The systems and protocols developed with SeaBED will be adopted by larger systems such as Autosub and ABE which will allow these new methods to be carried out in deeper and more remote environments.

The field operations have shown the capacity for AUVs to collect high quality images of the seafloor that are suitable for scientific analysis. Despite reductions in resolution and their monochrome nature, Autosub images were otherwise comparable with those taken with existing towed deep-water imaging systems. While the expense of AUVs will be a consideration in their imaging potential their autonomous nature allows them to be used in remote environments that cannot be sampled with existing technology. In addition, their autonomy from research vessels and ability to work concurrently with other sampling programmes, will make AUVs increasingly important for adding extra data and value to existing research cruises.

AUV photography has a number of novel scientific applications beyond the work in remote environments, predominantly in high resolution surveys over reasonably large areas. Survey work is the most important area of commercial AUV use (Danson 2003), with AUV survey already being explicitly commissioned in deep-water surveys for the oil and gas industry (Knott 2005). While this commercial survey work is principally acoustic, it is inevitable that, with imaging technology becoming available, that this survey will extend to imaging. In many respects these applications could be achieved by other, existing technology such as ROVs or towed camera platforms, but in these cases, the use of AUVs will be justified in terms of time or financial savings. AUVs are particularly suited to high resolution surveys over long distances that can be conducted without the need for human intervention. The AUV can be launched, then left to carry out the scientific task while the mother ship is conducting other work elsewhere. This was proven in the Autosub Arctic field operations where Autosub was deployed and two WASP stations were surveyed (56512#1 and 56513#1) while Autosub was carrying out a photography mission (mission 377). As well as this, the ship requirements of AUVs are potentially low, certainly without the need for the expensive, dynamically-positioned support vessels needed for ROV operations.

One particular aspect of AUV operations, relevant to photography is the unique ability of AUVs to follow terrain closely and maintain a constant altitude. This can be a problem in towed camera studies where only coarse altitude control is possible and as a result, images vary in altitude depending on bathymetry and sea conditions (although typically ±2 m), leading to many unusable images for analysis. Surveys carried out by a large class of imaging platforms, particularly operator-driven ROVs and towed camera platforms, may typically contain large rotational and scale changes between successive images. AUVs, as a stable platform, will avoid these limitations, facilitating photomosaicking of reasonably wide areas of seafloor (Singh et al. 2004). Much current work is going into the design of docking systems, for re-charging and data download, which will allow AUVs to operate for long periods without human intervention (Galletti di Cadilhac and Brighenti 2003). This will expand the scientific uses of AUVs allowing temporally replicated wide-area, high-resolution imaging without human intervention. AUV docking technology may allow high temporal resolution through increased access to deep-water environments and substantial savings in ship time.

While it is perhaps inevitable that AUVs will replace towed camera platforms in the future, at present they are not yet capable of producing images of comparable quality and at a comparable cost. AUVs, as a technology in its infancy, are not yet reliable enough for present survey needs as was shown so graphically by the insufficiency of Autosub image data from Greenland and the loss of the vehicle under the Fimbul Ice Shelf.

ROV vs towed camera platform

The comparison of ROVs and towed camera platforms is difficult as it depends on the sensors that are installed on both systems. Assuming the same sensor, the main differences, in terms of quantitative imaging is in terms of the manoeuvrability and the cost. ROVs can be used effectively as towed camera platforms as has been shown by Starmans and Gutt (2002) but they also have the capacity for much more structured and replicated random sampling. They also can be used consistently at much lower altitudes than towed camera platforms. Another benefit is that ROVs can conduct pre-survey collection or detailed imaging of important organisms facilitating identification. There are numerous other benefits of ROVs in terms of manipulation or monitoring of the environment which will not be discussed. Towed camera platforms are significantly cheaper, more robust (can be taken into more challenging environments) and can potentially cover a wide area of seabed than ROV systems.

Bounce camera vs towed camera platform

As bounce cameras are triggered at a constant altitude it is possible to set the camera in a way that maximises its efficiency as the depth of field, lighting and focus is accurately known in advance. This permits high quality, high resolution images to be obtained consistently. The limitations of this technique are that it only samples a very small area of seabed, while extensive sampling can allow investigation of larger scale patterns, for example over the entire Weddell Sea (Gutt and Starmans 1998). It is only by very extensive survey that landscape level changes in benthic environments become apparent. While towed camera platforms are less able to obtain very high resolution pictures they do allow quantification of a large area of seabed and landscape patterns become more obvious. In deep-sea environments particularly, another limitation of the small scale bounce camera approach is that the number of animals per unit area may be very low (for example in the deeper waters of the Faroe-Shetland Channel investigated in this study) and it is only with a more wide scale approach that sufficient area will be covered to give meaningful faunal density measurements.

THE FUTURE FOR PHOTOGRAPHIC ANALYSIS

Photographic analysis is a technique that is sure to increase in use into the future, with increasing acceptance as a quantitative tool that has minimal environmental impact. Its limitations are widely understood and are comparable with those of other techniques e.g. semi quantitative nature of trawls. Photographs provide a minimum quantitative sample of a known part of the faunal community in a similar manner to a sieve sample of macrofauna. Photographic techniques are continuously in development and the following section provides a speculative account of where I think that photographic techniques will be progressing in the next 10 years.

Investigation of spatial patterns

Conventional studies of megabenthos communities are only partly able to resolve the 2-dimensional distribution of individuals, i.e. trawls lose all spatial information and towed-camera systems provide only a narrow strip of seabed for analysis. With imaging from manoeuvrable ROVs or AUVs, coupled with high-resolution underwater navigation systems, it is possible to create 100% coverage faunal distribution maps through integration with Geographical Information Systems (GIS). Such detailed information on faunal distribution patterns will aid in accurate estimation of population densities and will likely provide insight into the behaviour, reproduction and dispersal of the dominant species present.

Once integrated into GIS spatial pattern in megabenthic communities can be investigated using a variety of integrated approaches:

1. Using statistical approaches to describe organism distribution, such as indices of dispersion (Krebs 1998) to quantify spatial pattern in megafaunal communities.
2. Analysing the environmental causes of organism distribution using the spatial analysis functions of ARCGIS as well as linked programmes (e.g. Biotas) as a powerful

tool for analysis of interrelationships between faunal distribution patterns and available environmental information.

3. Investigation of faunal community dynamics in response to recovery from anthropogenic disturbance along similar lines to the work by Durand et al. (2002) in changing vent communities.

With access to a wide range of spatially referenced data including high resolution bathymetry, ongoing CTD casts, ADCP current data, temperature data, physical and chemical sediment data and pre-drilling environmental and photographic data. The effects of these physical factors on the benthic fauna can be assessed in two dimensions. Spatial pattern is of interest in itself because it is important to understand the ecological processes determining the locations of individuals, which are rarely spread at random over the landscape (Krebs 1998). Ecology at the landscape scale is becoming more and more important in terrestrial and freshwater systems (Forman 1983; Urban et al. 1987; Wiens et al. 1993; Hill et al. 2001; Arbuckle and Downing 2002) and while shown to be important in the marine environment (Levin et al. 2001), the investigation of megafaunal spatial pattern is predominantly limited to those environments easily accessible for sampling namely the intertidal zone (Underwood and Chapman 1998). Although recent work has used photographs to investigate the structure of more remote benthic communities (Garrabou et al. 1998; Garrabou et al. 2002; Parry et al. 2002; Teixido et al. 2002). The spatial structure of deep-sea megabenthic communities has received very little attention due to the limitations of sampling methods and expense of wide area survey.

Three dimensional imaging

Three dimensional photography is not a new technique, stereo imaging and photogrammetry (Wolf 1983) have been used extensively in terrestrial as well as marine settings (Schuldt et al. 1967; Done 1981) to quantify features in three dimensions. This technique appears to be less widely available now than it was in the early days, perhaps as a result of very little actual early work published that made reference to the third dimension (although they had the technology to do it), time pressures (photogrammetric analysis is time consuming), increased camera cost and increased accuracy of camera systems (removing the need for a backup system). It has been shown in recent years that this approach can be very useful in obtaining accurate volume (and hence more accurate biomass) estimates in a non-destructive fashion (Bythell et al. 2001). This is particularly relevant with increased use of digital camera systems which enable quick, easy computer analysis to be carried out through a variety of software packages. This approach is being extended to stereo video systems using software such as Geomsoft's Vision Measurement System to find objects 3d coordinates from video. Quick and accurate quantitative measurement in three dimensions will facilitate species identification (through morphometric analyses), enable faunal volume measurements to be made and assessed over time and improve quantification of features seen in "difficult" video (with variations in vehicle altitude, pitch and roll and camera zoom, pan and tilt) that is very commonly obtained.

Investigation of novel ecological problems

The collection of images, in conjunction with new technologies, enables novel ecological problems to be investigated. These are particularly related to spatial patterns at varying scales, as discussed before for the large scale. These patterns can also be investigated at very small scales if the photographs are taken at low enough altitude and at high enough resolution. This has been shown to be effective in evaluating patch mosaics at the centimetre scale (Garrabou et al. 1998; Teixido et al. 2002) providing a new way of characterising communities with almost complete spatial coverage from photographs. This technique has much potential with regard to the investigation of temporal trends in communities where space is the limiting resource such as the intertidal and shallow sublittoral zone and in deeper waters the Antarctic suspension feeding zone.

CONCLUSIONS

Seabed imaging is a very important technique for quantitative analysis of benthic ecosystems. A wide variety of techniques exist using different sensors and vehicles which are suited to different investigations. There is typically a compromise between area investigated, time and biological resolution. Of these factors biological resolution is the most important, for, without it organisms cannot be distinguished, severely reducing the utility of images. Photography is typically more useful than video investigations particularly for community quantification. All platforms for photography (bounce cameras, towed camera platforms, ROVs and AUVs) have their own specific uses and are all suitable for biological investigation.

Photographic studies have been shown to be very effective in quantifying megabenthic faunal abundances in a variety of habitats (Piepenburg et al. 2001). In photographic studies of the seafloor there are several limitations particularly in the identification of species. Many species can only be identified from small scale morphological variations (Hayward and Ryland 1995) that are not visible in photographs. For many groups, only identification to family or genus is possible. This has consequences of the resolution of results, especially for diversity comparisons and when morphologically similar forms have different life habits. Another limitation found in the use of towed camera platform photographs is in the resolution of small specimens, the minimum size limit of this study (50mm) was large in comparison with the majority of studies, especially as megafauna is typically regarded as >10mm in size (Grassle et al. 1975). As well as this, biomass, an important characteristic of communities, is difficult to assess from photographs, as accurate size-biomass inferences need large associated specimen sample datasets to obtain accurate measurements. Nevertheless, it is clear that photographic studies can provide a valuable insight into the megabenthic ecology of an area such as the Faroe-Shetland Channel. Although there are problems associated with the use of photography it does provide more accurate information on the abundance of this group than other sampling methods. Although megafaunal diversity and biomass estimates may be better in conjunction with trawling techniques (Christiansen and Thiel 1992), these would be impossible in around half of the stations sampled in this study as a result of the rocky substratum (see e.g. Bett et al. 1997). Photography also provides additional ecological information on spatial distribution, size, substratum preference and faunal traces that can not be obtained from trawl samples.

SUMMARY AND CONCLUSIONS

Investigating community scale patterns in polar ecosystems has shown that despite the variation in species complements of these ecosystems, in the areas investigated, the physical controlling factors in both Arctic and Antarctic areas are similar. The effects of ice appear to be the most important in structuring these communities, with past and present ice related impacts on community structure ranging from direct destruction of organisms to long-term habitat changes with associated differentiation of communities between habitat types. Depth is also important in both areas, species-specific bathymetric limits control the overall distribution of organisms. Differences in the physical environment of the study sites changed the duration of the effects of ice mediated disturbance, very high sedimentation rates in Arctic areas removed evidence of disturbance in less impacted areas, homogenising the environment. In the Antarctic where sedimentation rates were very low, iceberg ploughmarks potentially will still have community-structuring effects thousands of years after they were formed. In the Faroe-Shetland Channel, where ice is not present now, much of the existing sediment is of glacial origin, changes in depth and sediment type are responsible for community patterns in this area.

From the results presented here it is clear that disturbance is a very important control on benthic community structure in natural environments. What is not clear, however is the effects of different aspects of the iceberg disturbance. It is clear that those organisms in the middle of the ploughing will be completely destroyed but at the edge the nature of the effects are less obvious. It is not apparent if it is indirect effects (e.g. changes in habitat) or direct effects of disturbance (e.g. sedimentation) that drive densities, diversity and community structure. Through investigation of a known level of disturbance, where Arctic benthic communities were subject to smothering by sediment, as occurs at the edges of ploughmarks, it was possible to quantify the direct effects of this type of disturbance over a short time scale. The effects of disturbance by smothering depended on the extent of disturbance, in general, above a threshold level sessile fauna and some motile fauna are killed, more motile fauna can escape the disturbance event. At low levels of disturbance sessile megafauna can survive the sedimentation and numbers return to typical background levels within a small distance of the disturbance event. This study shows that mobile fauna recolonise disturbed areas within weeks, with elevated density in intermediate disturbance areas. At this small scale diversity increases with distance from disturbance, with no evidence found to support increased diversity at intermediate disturbance. This effect would appear to occur at a larger scale for megafauna. It would seem that changes in community function as a result of habitat changes do not occur at the temporal scale investigated at Laggan.

As methodologically identical studies were carried out in Arctic and Antarctic areas, despite the small scale of investigations, it is possible to draw some general comparisons between these polar areas. Megafaunal density is within the same range in both areas at comparable depths, but small-scale variation is very high in both areas. Diversity is considerably higher in Antarctic stations compared to Arctic with around double the taxa identified. The proportion of taxonomic groups present differed significantly between the regions with higher densities of echinoderms in the Antarctic stations and lower densities of annelids. There were large variations in the proportions of phyla observed with changes in disturbance. Differences in the diversity of the polar regions can only be explained on an evolutionary timescale. It is clear that there has been a much longer evolution of the Antarctic fauna than that in the Arctic, although the specific mechanisms of faunal evolution are not yet fully known.

The use of a range of imaging methods allowed comparison of their uses in deep-water ecology. Photography is generally preferable over video. Different imaging methods have different practical uses, the most versatile vehicles are typically the most expensive. Some vehicles such as AUVs have unique applications in remote environments. From this work it has been possible to investigate experimentally the biological outcomes from these vehicles through a range of potential operations and fine tune to produce the best ecological outcomes.

In many deep-water areas the first basic stages in ecology have not been completed, there is often very little prior knowledge of the densities or diversity of taxa, community structure is generally even less well known. This information is important in understanding the environment and its biological processes as well as being highly valuable for the interpretation of point samples and experimental investigations. Once the controlling factors on these communities can be ascertained, the information gained in studies of community patterns can more readily be extrapolated to other areas. The studies here all bring to light many important questions that can only be answered by experimental investigations into responses to physical factors at scales from the community to individual organisms.

REFERENCES

Abele LG, Walters K (1979a) Marine benthic diversity: a critique and alternative explanation. Journal of Biogeography 6: 115-126

Abele LG, Walters K (1979b) The stability-time hypothesis: re-evaluation of the data. American Naturalist 114: 559-568

Adams PB, Butler JL, Baxter CH, Laidig TE, Dahlin KA, Wakefield WW (1995) Population estimates of Pacific coast groundfishes from video transects and swept-area trawls. Fishery Bulletin 93: 446-455

Aldred RG, Riemann-Zurneck K, Thiel H, Rice AL (1979) Ecological observations on the deep sea anemone *Actinoscyphia aurelia*. Oceanologica Acta 2: 389-395

Ambrose WG, Jr., Clough LM, Tilney PR, Beer L (2001) Role of echinoderms in benthic remineralization in the Chukchi Sea. Marine Biology 139: 937-949

Ambrose WG, Renauld PE (1995) Benthic responses to water column productivity patterns: evidence for benthic-pelagic coupling in the Northeast Water Polynya. Journal of Geophysical Research 100: 4411-4421

Andersen OGN (1989) Primary production, chlorophyll, light and nutrients beneath the Arctic sea ice. In: Hermann Y (ed) The Arctic seas: Climatology, oceanography, geology and biology. Van Nostrand, New York, pp 147-191

Andrews JT, Smith LM, Preston R, Cooper T, Jennings AE (1997) Spatial and temporal patterns of iceberg rafting (IRD) along the East Greenland margin, ca 68 degrees N, over the last 14 cal ka. Journal of Quaternary Science 12: 1-13

Arbuckle KE, Downing JA (2002) Freshwater mussel abundance and species richness: GIS relationships with watershed land use and geology. Canadian Journal of Fisheries and Aquatic Sciences 59: 310-316

Arnaud PM, Hain S (1992) Quantitative distribution of the shelf and slope molluscan fauna (Gastropoda, Bivalvia) of the Eastern Weddell Sea (Antarctica). Polar Biology 12: 103-109

Arnaud PM, Lopez CM, Olaso I, Ramil F, Ramos-Espla AA, Ramos A (1998) Semi-quantitative study of macrobenthic fauna in the region of the South Shetland Islands and the Antarctic Peninsula. Polar Biology 19: 160-166

Arntz W, Brey T, Tarazona J, Robles A (1987) Changes in the structure of a shallow sandy-beach community in Peru during an El Nino event. South African Journal of Marine Sciences 5: 645-658

Arntz WE, Brey T, Gallardo VA (1994) Antarctic zoobenthos. Oceanography and Marine Biology An Annual Review 32: 241-304

Arntz WE, Brey T, Gerdes D, Gorny M, Gutt J, Hain S, Klages M (1992) Patterns of life history and population dynamics of benthic invertebrates under the high Antarctic conditions of the Weddel Sea. In: Colombo G, Ferrari, I., Ceccherelli, V.U., Rossi, R. (ed) Marine eutrophication and population dynamics. Oslen and Oslen, Fredensborg, pp 221-230

Arntz WE, Gallardo VA (1994) Antarctic benthos: present position and future prospects. In: Hempel G (ed) Antarctic science: Global concerns. Springer-Verlag, Berlin, pp 243-277

Arntz WE, Gutt J, Klages M (1997) Antarctic marine biodiversity: an overview. In: Battaglia B, Valencia, J., Walton, D.W.H. (ed) Antarctic communities: species structure and survival. Cambridge University Press, Cambridge, pp 3-14

Aronson RB, Swanson DW (1997) Video surveys of coral reefs: univariate and multivariate applications. Proc. 8th Int. Coral Reef Sym. 2: 1441-1446

Auster PJ, Malatesta RJ, Larosa SC, Cooper RA, Stewart LL (1991) Microhabitat utilization by the megafaunal assemblage at a low relief outer continental shelf site - Middle Atlantic Bight, USA. Journal of Northwest Atlantic Fishery Science 11: 59-69

Axelsson M (2003) The deep seabed of the UK continental margin - integration and interpretation of geological and biological data. PhD Thesis. Southampton Oceanography Centre, Southampton, UK

Babb RJ (1993) Scientific Surveys in the deep ocean using AUVs: the Autosub project. AUVs93, Washington D.C.

Barker BAJ, Helmond I, J. Bax N, Williams A, Davenport S, Wadley VA (1999) A vessel-towed camera platform for surveying seafloor habitats of the continental shelf. Continental Shelf Research 19: 1161-1170

Barnes DKA (1999) The influence of ice on polar nearshore benthos. Journal of the Marine Biological Association of the United Kingdom 79: 401-407

Barnes DKA, Kuklinski P (2003) High polar spatial competition: extreme hierarchies at extreme latitude. Marine Ecology Progress Series 259: 17-28

Barry JP (1988) Hydrographic patterns in McMurdo Sound, Antarctica and their relationship to local benthic communities. Polar Biology 8: 377-391

Barry JP, Baxter CH (1992) Survey Design Considerations for Deep-Sea Benthic Communities Using ROVs. Marine Technology Society Journal 26: 21-26

Barry JP, Dayton PK (1988) Current patterns in McMurdo Sound, Antarctica and their relationship to local biotic communities. Polar Biology 8: 367-376

Barry JP, Grebmeier JM, Smith J, Dunbar RB (2003) Oceanographic versus seafloor-habitat control of benthic megafaunal communities in the S.W. Ross Sea, Antarctica. Antarctic Research Series 78: 327-354

Barthel D (1992) Do hexactinellids structure Antarctic sponge associations? Ophelia 36: 111-118

Barthel D, Gutt J (1992) Sponge associations in the eastern Weddell Sea. Antarctic Science 4: 137-150

Barthel D, Gutt J, Tendal OS (1991) New information on the biology of Antarctic deep-water sponges derived from underwater photography. Marine Ecology Progress Series 69: 303-307

Barthel D, Tendal OS (1993) The sponge association of the abyssal Norwegian-Greenland Sea: Species composition, substrate relationships and distribution. Sarsia 78: 83-96

Begon M, Harper JL, Townsend CR (1990) Ecology: individuals, populations and communities. Blackwell, London

Berelson WM, Anderson RF, Dymond J, DeMaster DJ, Hammond DE (1997) Biogenic budgets of particle rain, benthic remineralization and sediment accumulation in the equatorial Pacific. Deep-Sea Research Part II: Topical Studies in Oceanography 44: 2251-2282

Berger WH, Fischer K, Lai C, Wu G (1988) Ocean carbon flux: global maps of primary production and export production. In: Agegian CR (ed) Biogeochemical cycling and fluxes between the deep euphotic zone and other oceanic realms. National Undersea Research Program, Research Report 88-1, pp 131-176

Berger WH, Parker FL (1970) Diversity of planktonic Foraminifera in deep-sea sediments. Science 168: 1345-1347

Berger WH, Wefer G (1990) Flux of biogenous materials to the seafloor: open questions. In: Hsu KL, Thiede J (eds) Use and misuse of the seafloor. John Wiley, Chichester, pp 285-304

Berkman PA (1990) The population biology of the Antarctic scallop, *Adamussium colbecki* (Smith 1902) at New Harbor, Ross Sea. In: Kerry KR, Hempel G (eds) Antarctic ecosystems. Ecological change and conservation. Springer, Berlin, pp 282-288

Berkman PA (1997) Ecological variability in Antarctic coastal environments: past and present. Cambridge University Press, U.K.

Bertelsen E (1937) Contributions to the animal ecology of the fjords of Angmagssalik and Kangerdlugssuaq in East Greenland. Meddelelser om Gronland 108: 1-58

Bett BJ (2001) UK Atlantic Margin Environmental Survey: introduction and overview of bathyal benthic ecology. Continental Shelf Research 21: 917-956

Bett BJ (2003) Time-lapse Photography in the Deep Sea. Underwater Technology 25: 121-127

Bett BJ, Hughes JA, Masson DG (1997) RRS Charles Darwin Cruise 101C Leg 2, 14 Jul-20 Aug 1996. Atlantic Margin Environmental Survey; seabed survey of the shelf edge and slope west of Shetland. Southampton Oceanography Centre, Southampton, (UK)

Bett BJ, Malzone MG, Narayanaswamy BE, Wigham BD (2001) Temporal variability in phytodetritus and megabenthic activity at the seabed in the deep Northeast Atlantic. Progress in Oceanography 50: 349-368

Bett BJ, Rice AL, Thurston MH (1995) A quantitative photographic survey of "spoke-burrow" type Lebensspuren on the Cape Verde Abyssal Plain. Internationale Revue der gesamten Hydrobiologie 80: 153-170

Billett DSM (1991) Deep-sea holothurians. Oceanography and Marine Biology: An Annual Review 29: 259-317

Billett DSM, Bett BJ, Rice AL, Thurston MH, Galeron J, Sibuet M, Wolff GA (2001) Long-term change in the megabenthos of the Porcupine Abyssal Plain (NE Atlantic). Progress in Oceanography 50: 325-348

Bluhm BA, Piepenburg D, Juterzenka Kv (1998) Distribution, standing stock, growth, mortality and production of Strongylocentrotus pallidus (Echinodermata: Echinoidea) in the northern Barents Sea. Polar Biology 20: 325-334

Bluhm H (2001) Re-establishment of an abyssal megabenthic community after experimental physical disturbance of the seafloor. Deep-Sea Research Part II: Topical Studies in Oceanography 48: 3841-3868

Bluhm H, Schriever G, Thiel H (1995) Megabenthic recolonization in an experimentally disturbed abyssal manganese nodule area. Marine Georesources & Geotechnology 13: 393-416

Bohnsack JA (1979) Photographic quantitative sampling of hard-bottom benthic communities. Bulletin of Marine Science 29: 242-252

Borowski C, Thiel H (1998) Deep-sea macrofaunal impacts of a large-scale physical disturbance experiment in the Southeast Pacific. Deep-Sea Research Part II: Topical Studies in Oceanography 45: 55-81

Boutan L (1893) La photographie sous-marine. Archives de la Zoologie Experimental 3: 281-324

Brandt A (1995) Pericarid fauna (Crustacea, Malacostraca) of the Northeast Water Polyna off Greenland: documenting close benthic-pelagic coupling in the Westwind Trough. Marine Ecology Progress Series 121: 39-51

Brandt A, De Broyer C, Gooday AJ, Hilbig B, Thomson MRA (2004) Introduction to ANDEEP (ANtarctic benthic DEEP-sea biodiversity: colonization history and recent community patterns) - a tribute to Howard L. Sanders. Deep Sea Research Part II: Topical Studies in Oceanography 51: 1457-1465

Bray JR, Curtis JT (1957) An ordination of the upland forest of southern Wisconsin. Ecological Monographs 27: 225-349

Brey T (1999) Growth performance and mortality in aquatic macrobenthic invertebrates. Advances in Marine Biology 35: 153-223

Brey T, Clarke A (1993) Population dynamics of marine benthic invertebrates in Antarctic and subantarctic environments: Are there unique adaptations? Antarctic Science 5: 253-266

Brey T, Gutt J (1991) The genus *Sterechinus* (Echinoderma: Echinoidea) on the Weddell Sea shelf and slope (Antarctica). Polar Biology 11: 227-232

Brey T, Klages M, Dahm C, Gorny M, Gutt J, Hain S, Stiller M, Arntz WE, Wagele JW, Zimmermann A (1993) Antarctic benthic diversity. Nature 368: 297

Brey T, Pearse J, Basch L, McClintock J, Slattery M (1995) Growth and production of Sterechinus neumayeri (Echinoidea: Echinodermata) in McMurdo Sound, Antarctica. Marine Biology 124: 279-292

Brodeur RD (2001) Habitat-specific distribution of Pacific ocean perch (*Sebastes alutus*) in Pribilof Canyon, Bering Sea. Continental Shelf Research 21: 207-224

Brunchhausen PM, Raymond JA, Jacobs SS, DeVries AL, Thorndike EM, DeWitt HH (1984) Fish, Crustaceans, and the Seafloor under the Ross Ice Shelf. In: Ferris-Smith P (ed) Underwater Photography - Scientific and Engineering Applications. Van Nostrand Reinhold, New York, pp 335-341

Bullivant JS (1959) An oceanographic survey of the Ross Sea. Nature 184: 422-423

Bullough LW, Turrell WR, Buchan P, Priede IG (1998) Commercial deep water trawling at sub-zero temperatures - observations from the Faroe-Shetland channel. Fisheries Research 39: 33-41

Bunge J, Fitzpatrick M (1993) Estimating the number of species; a review. Journal of American Statistics Association 88: 364-373

Butler JL, Wakefield WW, Adams PB, Robison BH, Baxter CH (1991) Applications of line transect methods to surveying dermersal communities with ROVs and manned submersibles Oceans '91 Conference Proceedings. Insitiute of Electrical and Electronics Engineers, New York

Bythell JC, Pan P, Lee J (2001) Three-dimensional morphometric measurements of reef corals using underwater photogrammetry techniques. Coral Reefs 20: 193-199

Cailliet GM, Andrews AH, Wakefield WW, Moreno G, Rhodes KL (1999) Fish faunal and habitat analyses using trawls, camera sleds and submersibles in benthic deep-sea habitats off central California. Oceanologica Acta 22: 579-592

Callaway R, Alsvaag J, Boois I, Cotter J, Ford A, Hinz H, Jennings S, Kroencke I, Lancaster J, Piet G, Prince P, Ehrich S (2002) Diversity and community structure of epibenthic invertebrates and fish in the North Sea. ICES Journal of Marine Science 59: 1199-1214

Carey AG (1965) Preliminary studies on animal-sediment interrelationships off the central Oregon coast. Transactions of the Joint Conference of Ocean Scientists and Engineers 1: 100-110

Carey AG (1972) Food sources of sublittoral, bathyal and abyssal asteroids in the northeast Pacific Ocean. Ophelia 10: 35–47

Carey AG (1991) Ecology of the North American Arctic Continental Shelf benthos: a review. Continental Shelf Research 11: 865-883

Carleton JH, Done TJ (1995) Quantitative video sampling of coral reef benthos: large scale application. Coral Reefs 14: 35-46

Carney RS, Haedrich RL, Rowe GT (1983) Zonation of fauna in the deep sea. In: Rowe GT (ed) The Sea, vol. 8: Deep-sea biology. Wiley and sons, New York

Christiansen B (1993) A television and photographic survey of megafaunal abundance in central Sognefjorden, western Norway. Sarsia 78: 1-8

Christiansen B, Thiel H (1992) Deep-sea epibenthic megafauna of the Northeast Atlantic: Abundance and biomass at three mid-oceanic locations estimated from photographic transects. In: Rowe GT, Pariente V (eds) Deep-sea food chains and the global carbon cycle. Kluwer Academic Publishers, Dordrecht (Netherlands), pp 125-138

Clark HES (1963) Fauna of the Ross Sea, Part 3: Asteroidea. Memoirs of the New Zealand Oceanographic Institute 21: 1-84

Clarke A (1979) On living in cold water: K-strategies in Antarctic benthos. Marine Biology 55: 111-119

Clarke A (1983) Life in cold water: the physiological ecology of polar marine ectotherms. Oceanography and Marine Biology: An Annual Review 21: 341-453

Clarke A (1988) Seasonality in the Antarctic marine environment. Comparative Biochemistry and Physiology 90: 461-473

Clarke A (1990) Temperature and evolution: Southern Ocean cooling and the Antarctic marine fauna. In: Kerry KR, Hempel G (eds) Antarctic ecosystems: change and conservation. Springer-Verlag, pp 9-22

Clarke A (1996) Benthic Marine Habitats in Antarctica. In: Ross RM, Hofmann EE, Quetin LB (eds) Foundations for ecological research west of the Antarctic Peninsula. American Geophysical Union, Antarctic Research Series 70, pp 123-133

Clarke A (2003) The Polar deep seas. In: Tyler PA (ed) Ecosystems of the World: Vol. 28. Ecosystems of the deep oceans. Elsevier, Amsterdam, pp 239-260

Clarke A, Crame JA (1989) The Origin of the Southern Ocean Marine Fauna. In: Crame JA (ed) Origins and evolution of the Antarctic biota. Geological Society Special Publication 47, pp 253-268

Clarke A, Johnston NM (2003) Antarctic marine benthic diversity. Oceanography and Marine Biology: An Annual Review 41: 47-114

Clarke KR (1993) Nonparametric Multivariate Analyses of Changes in Community Structure. Australian Journal of Ecology 18: 117-143

Clarke KR, Warwick RM (1994) Changes in marine communities: An approach to statistical analysis and interpretation. Plymouth Marine Laboratory, U.K.

Clarke KR, Warwick RM (2001) Changes in marine communities: An approach to statistical analysis and interpretation. Plymouth Marine Laboratory, U.K.

Coachman LK, Aagaard K (1974) Physical Oceanography of Arctic and Subarctic Seas. In: Herman Y (ed) Marine Geology and Oceanography of the Arctic Seas. Springer - Verlag, New York, pp 1-71

Collins SL, Glenn SM, Gibson DJ (1995) Experimantal analysis of intermediate disturbance and initial floristic composition: decoupling cause and effect. Ecology 76: 486-492

Colwell RK (2005) EstimateS: Statistical estimation of species richness and shared species from samples. Version 7.5. User's Guide and application published at: http://purl.oclc.org/estimates.

Colwell RK, Coddlington JA (1994) Estimating terrestrial biodiversity through extrapolation. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 345: 101-118

Colwell RK, Mao CX, Chang J (2004) Interpolating, extrapolating and comparing incidence-based species accumulation curves. Ecology 85: 2717-2727

Conlan KE, Lenihan HS, Kvitek RG, Oliver JS (1998) Ice scour disturbance to benthic communities in the Canadian High Arctic. Marine Ecology Progress Series 166: 1-16

Conlan KE, Kvitek RG (2005) Recolonization of soft-sediment ice scours on an exposed Arctic coast. Marine Ecology Progress Series 286: 21-42

Connell JH (1972) Community interactions on marine rocky intertidal shores. Annual Review of Ecology and Systematics 3: 169-192

Connell JH (1978) Diversity in tropical rain forests and coral reefs. Science 199: 1302-1310

Connell JH (1979) Tropical rain forests and coral reefs as open nonequilibrium systems. In: Anderson RM, Turner BD, Taylor LR (eds) Population dynamics. Blackwell, Oxford, pp 141-163

Connell JH, Hughes TP, Wallace CC (1997) A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. Ecological Monographs 67: 461–488

Connell JH, Keough MJ (1985) Disturbance and patch dynamics of subtidal marine animals on hard substrata. In: Pickett STA, White PS (eds) The ecology of natural disturbance and patch dynamics. Academic Press, London, pp 125–151

Cornell HV (1999) Unsaturation and regional influences on species richness in ecological communities: a revew of the evidence. Ecoscience 6

Cornell HV, Lawton JH (1992) Species interactions, local and regional processes, and limits to the richness of ecological communities - a theoretical perspective. Journal of Animal Ecology 61: 1-12

Cosson N, Sibuet M, Galeron J (1997) Community structure and spatial hetrogeneity of the deep-sea macrofauna at three contrasting stations in the tropical northeast Atlantic. Deep-Sea Research 44: 247-269

Cosson-Sarradin N, Sibuet M, Paterson GLJ, Vangriesheim A (1998) Polychaete diversity at tropical Atlantic deep-sea sites: environmental effects. Marine Ecology Progress Series 165: 173-185

Cousteau JY, Dugan J (1963) The Living Sea. Harper, New York

Covich AP, Austen MC, Barlocher F, Chauvet E, Cardinale BJ, Biles C, Inchausti P, Dangles O, Solan M, Gessner MO, Statzner B, Moss B (2004) The role of biodiversity in the functioning of freshwater and marine ecosystems. Bioscience 54: 767-775

Cranmer TL, Ruhl HA, Baldwin RJ, Kaufmann RS (2003) Spatial and temporal variation in the abundance, distribution and population structure of epibenthic megafauna in Port Foster, Deception Island. Deep-Sea Research Part II: Topical Studies in Oceanography 50: 1821-1842

Curtis MA (1975) The marine benthos of Arctic and sub-arctic continental shelves. Polar Record 17: 595-626

Dahl E, Laubier L, Sibuet M, Stroemberg JO (1976) Some quantitative results on benthic communities of the deep Norwegian Sea. Astarte 9: 61-79

Danson EFS (2003) AUV tasks in the offshore industry. In: Griffiths G (ed) Technology and applications of Autonomous Underwater Vehicles. Taylor and Francis, London, pp 127-138

Darby DA, Naidu AS, Mowatt TC, Jones G (1989) Sediment composition and sedimentary processes in the Arctic Ocean. In: Hermann Y (ed) The Arctic Seas; climatology, oceanography, geology and biology. Van Nostrand, New York, pp 657-720

Davies JM, Hardy R, McIntyre AD (1981) Environmental effects of North Sea oil operations. Marine Pollution Bulletin 12: 412-416

Davies JM, Kingston PF (1992) Sources of environmental disturbance associated with offshore oil and gas development. In: Cairns WJ (ed) North Sea oil and the environment - developing oil and gas resources, environmental impacts and resources. International Council on Oil and the Environment, Elsevier, London, pp 417-440

Day DS, Pearcy WG (1968) Species associations of benthic fishes on the continental shelf and slope off Oregon. Journal of the Fisheries Research Board of Canada 25: 2665-2675

Dayton PK (1971) Competition, disturbance and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecological Monographs 41: 351-389

Dayton PK (1979) Observations of growth, dispersal and population dynamics of some sponges in McMurdo Sound, Antarctica. In: Levey C, Boury-Esnault N (eds) Biologie des Spongiaries. Colloques Internationaux du Centre National de la Recherche Scientifique, Paris, pp 271-282

Dayton PK (1984) Processes structuring some marine communities: are they general? In: Strong DR, Simberlof D, Lawrence GA, Thistle AB (eds) Ecological communities: conceptual issues and the evidence. Princeton University Press, Princeton, pp 181-197

Dayton PK (1990) Polar Benthos. In: Smith WO (ed) Polar Oceanography. Part B: Chemistry, biology, geology. Academic Press, London, pp 631-685

Dayton PK, Hessler RR (1972) Role of biological disturbance in maintaining diversity in the deep-sea. Deep-Sea Research 19: 199-208

Dayton PK, Newman WA, Oliver J (1982) The vertical zonation of the deep-sea Antarctic acorn barnacle, Bathylasma corolliforme (Hoek): Experimental transplants from the shelf into shallow water. Journal of Biogeography 9: 95-109

Dayton PK, Kooyman GL (1985) Benthic life under thick ice. Antarctic Journal of the United States 19: 128

Dayton PK, Mordida BJ, Bacon F (1994) Polar marine communities. American Zoologist 34: 90-99

Dayton PK, Oliver JS (1977) Antarctic soft-bottom benthos in oligotrophic and eutrophic environments. Science 197: 55-58

Dayton PK, Robilliard GA, Paine RT, Dayton LB (1974) Biological accommodation in the benthic community at McMurdo Sound, Antarctic. Ecological Monographs 44: 105-128

De Ruiter PC, Moore JC, Griffiths B (2002) Biodiversity and Stability in Soil Ecosystems: Patterns, Processes and the Effects of Disturbance. In: Loreau M, Naeem S (eds) Biodiversity and ecosystem functioning: a current synthesis. Oxford University Press, Oxford

Deacon MB (1997) Scientists and the sea 1650-1900: a study of marine science. Ashgate Publishing, Aldershot

Dearborn JH (1968) Benthic invertebrates. Australian Natural History Dec. 1968: 134-139

Dell RK (1972) Antarctic benthos. Advances in Marine Biology 10: 1-216

Dernie KM, Kaiser MJ, Richardson EA, Warwick RM (2003) Recovery of soft sediment communities and habitats following physical disturbance. Journal of Experimental Marine Biology and Ecology 285-286: 415-434

Dial R, Roughgarden J (1998) Theory of marine communities: The intermediate disturbance hypothesis. Ecology 79: 1412-1424

Dolmer P, Kristensen T, Christiansen ML, Petersen MF, Kristensen PS, Hoffmann E (2001) Short-term impact of blue mussel dredging (Mytilus edulis L.) on a benthic community. Hydrobiologia 465: 115-127

Done TJ (1981) Photogrammetry in coral ecology: a technique for the study of change in coral communities. Proc. 4th Int. Coral Reef Sym. 2: 315-319

Dowdeswell JA (2004) Autosub under ice cruise JR106b to the Kangerdlugssuaq Fjord and Shelf, East Greenland. Unpublished cruise report. University of Cambridge, Cambridge, UK

Dowdeswell JA, Elverhoi A, Spielhagen R (1998) Glacimarine sedimentary processes and facies on the Polar North Atlantic margins. Quaternary Science Reviews 17: 243-272

Dowdeswell JA, Forsberg CF (1992) The Size and Frequency of Icebergs and Bergy Bits derived from Tidewater Glaciers in Kongsfjorden, Northwest Spitsbergen. Polar Research 11: 81-91

Dowdeswell JA, Kenyon NH, Laberg JS (1997) The glacier-influenced Scoresby Sund Fan, east Greenland continental margin: evidence from GLORIA and 3.5 kHz records. Marine Geology 143: 207-221

Dowdeswell JA, Villinger H, Whittington RJ, Marienfeld P (1993) Iceberg Scouring in Scoresby Sund and on the East Greenland Continental-Shelf. Marine Geology 111: 37-53

Dowdeswell JA, Whittington RJ, Hodgkins R (1992) The Sizes, Frequencies, and Freeboards of East Greenland Icebergs Observed Using Ship Radar and Sextant. Journal of Geophysical Research-Oceans 97: 3515-3528

Dunbar MJ (1968) Ecological development in polar regions: a study in evolution. Prentice-Hall, Englewood Cliffs, NJ

Dunbar MJ (1977a) The evolution of polar ecosystems. In: Llano GA (ed) Adaptation within the Antarctic ecosystem. Smithsonian Institute, Washington DC, pp 1063-1076

Dunbar MJ (1977b) Polar Oceans. Arctic Institute of North America, Calgary

Dunbar MJ (1982) Arctic Marine Ecosystems. In: Rey L (ed) The Arctic Ocean: The hydrographic environment and the fate of pollutants. MacMillan, London, pp 233-261

Dyer MF, Fry WG, Fry PD, Cranmer GJ (1982) A series of North Sea benthos surveys with trawl and headline camera. Journal of the Marine Biological Association of the United Kingdom 62: 297-313

Ekau W, Gutt J (1991) Notothenioid fishes from the Weddell Sea and their habitat, observed by underwater photography and television. Proceedings of the NIPR Symposium on Polar Biology: 36-49

Ekman S (1953) Zoogeography of the sea. Sidgwick and Jackson, London

Ellett DJ, Roberts DG (1973) The overflow of Norwegian Sea Deep Water across the Wyville-Thomson Ridge. Deep-Sea Research 20: 819-835

Emery WJ, Meincke J (1986) Global water masses: summary and review. Oceanologica Acta 9: 383-391

Emmerson MC, Solan M, Emes C, Paterson DM, Raffaelli D (2001) Consistent patterns and the idiosyncratic effects of biodiversity in marine ecosystems. Nature 411: 73-77

Etter RJ, Grassle JF (1992) Patterns of species diversity in the deep sea as a function of sediment particle size diversity. Nature 360: 576-578

Ewing M, Davis RA (1967) Lebensspuren photographed on the ocean floor. In: Hersey JB (ed) Deep-Sea Photography. John Hopkins Press, Baltimore, pp 256-294

Ewing M, Vine AC, Worzel JL (1946) Photography of the Ocean Bottom. Journal of the Optical Society of America 36: 307-321

Ewing M, Worzel JL, Vine AC (1967) Early development of ocean bottom photography at Woods Hole Oceanographic Institution and Lamont Geological Observatory. In: Hersey JB (ed) Deep-Sea Photography. John Hopkins Press, Baltimore, pp 13-41

Fabricius KE, Dommisse M (2000) Depletion of suspended particulate matter over coastal reef communities dominated by zooxanthellate soft corals. Marine Ecology Progress Series 196: 157–167

Fabricius O (1780) Fauna Groenlandica, Hafniæ et Lipsiæ

Fautin DG, Daly M, Cappola V (2005) Sea anemones (Cnidaria: Actiniaria) of the Faroe Islands: A preliminary list and biogeographic context. Annales Societatis Scientiarum Faroensis Supplementum XXXXI. BIOFAR Proceedings 2005, BIOFAR symposium, Torshavn 4-26 April 2003: 77-87

Fell HB (1962) Fauna of the Ross Sea, Part 1: Ophiuroidea. Memoirs of the New Zealand Oceanographic Inst. 18: 1-79

Fell HB (1967) Biological applications of sea-floor photography. In: Hersey JB (ed) Deep-Sea Photography. John Hopkins Press, Baltimore, pp 207-221

Filatova ZA (1982) On some problems of the quantitative study of deep-sea bottom fauna. Trudy Instituta Okeanologii 117: 5-18 (English translation by Institute of Oceanographic Sciences, Translation No. 179, 1984)

Flach E, Lavaleye M, de Stigter H, Thomsen L (1998) Feeding types of the benthic community and particle transport across the slope of the NW European Continental Margin (Goban Spur). Progress in Oceanography 42: 209-231

Fogg GE (1992) A History of Antarctic Science. Cambridge University Press, Cambridge

Foldvik A, Gammelsrod T, Torresen T (1985) Circulation and water masses on the southern Weddell Sea shelf. In: Jacobs SS (ed) Oceanology of the Antarctic continental shelf. American Geophysical Union. 5-20. (AGU Antarctic Research Series; 43), Washington, DC

Forman RTT (1983) An Ecology of the Landscape. Bioscience 33: 535-535

Fornari DJ (2003) A new deep-sea towed digital camera and multi-rock coring system. EOS, Transactions, American Geophysical Union 84: 69-76

Foster TD (1984) The Marine Environment. In: Laws RM (ed) Antarctic Ecology. Academic Press, London, pp 345-371

Frederiksen R, Jensen A, Westerberg H (1992) The distribution of the Scleractinian coral Lophelia pertusa around the Faroe Islands and the relation to internal tidal mixing. Sarsia 77: 157-171

Gage JD (1972) Community structure of the benthos in Scottish sea-lochs. I. Introduction and species diversity. Marine Biology 14: 281-297

Gage JD (1977) Structure of the abyssal macrobenthic community in the Rockall Trough. In: Keegan BF, O'Ceidigh P, Boaden PJS (eds) Biology of benthic organisms. Pergamon, Oxford, pp 247-260

Gage JD (1986) The benthic fauna of the Rockall Trough: Regional distribution and bathymetric zonation. Proceedings of the Royal Society of Edinburgh 88: 159-174

Gage JD (1996) Why are there so many species in deep-sea sediments? Journal of Experimental Marine Biology and Ecology 200: 257-286

Gage JD (1997) High benthic species diversity in deep-sea sediments: The importance of hydrodynamics. Cambridge University Press, New York

Gage JD, Lamont PA, Kroeger K, Harvey R (1998) Atlantic Margin environmental surveys of the seafloor desktop study of Tranches 19-22. Scottish Association for Marine Sciences, Oban

Gage JD, Lamont PA, Kroeger K, Paterson GL, Gonzalez Vecino JL (2000) Patterns in deep-sea macrobenthos at the continental margin: standing crop, diversity and faunal change on the continental slope off Scotland. Hydrobiologia 440: 261-271

Gage JD, Lamont PA, Tyler PA (1995) Deep-sea macrobenthic communities at contrasting sites off Portugal. Preliminary results: 1. Introduction and diversity comparisons. Internationale Revue der gesamten Hydrobiologie 80: 235-250

Gage JD, Pearson M, Billett DSM, Clark AM, Jensen M, Paterson GLJ, Tyler PA (1985) Echinoderm zonation in the Rockall Trough (NE Atlantic). In: Keegan BF, O'Connor BDS (eds) Echinodermata. A.A. Balkema, Rotterdam, pp 31-36

Gage JD, Tyler PA (1991) Deep Sea Biology. Cambridge University Press, Cambridge

Galeron J, Herman RL, Arnaud PM, Arntz WE, Hain S, Klages M (1992) Macrofaunal communities on the continental shelf and slope of the southeastern Weddell Sea, Antarctica. Polar Biology 12: 283-290

Galéron J, Herman RL, Arnaud PM, Arntz WE, Hain S, Klages M (1992) Macrofaunal communities on the continental shelf and slope of the southeastern Weddell Sea, Antarctica. Polar Biology 12: 283-290

Galletti di Cadilhac R, Brighenti A (2003) Docking systems. In: Griffiths G (ed) Technology and applications of autonomous underwater vehicles. Taylor and Francis, London, pp 93-108

Gambi MC, Lorenti M, Russo GF, Scipione MB, Zupo V (1992) Depth and spatial distribution of some groups of the vagile fauna of the *Posidonia oceania* leaf stratum: structural and trophical analyses. Marine Ecology 13: 17-39

Garrabou J, Ballesteros E, Zabala M (2002) Structure and dynamics of north-western Mediterranean rocky benthic communities along a depth gradient. Estuarine Coastal and Shelf Science 55: 493-508

Garrabou J, Riera J, Zabala M (1998) Landscape pattern indices applied to Mediterranean subtidal rocky benthic communities. Landscape Ecology 13: 225-247

Genin A, Paull CK, Dillon WP (1992) Anomalous abundances of deep-sea fauna on a rocky bottom exposed to strong currents. Deep-Sea Research Part I: Oceanographic Research Papers 39: 293-302

George JD, Lythgoe GI, Lythgoe JN (1985) Underwater photography and television for scientists. Oxford University Press, New York

Gerdes D, Klages M, Arntz WE, Herman RL, Galeron J, Hain S (1992) Quantitative investigations on macrobenthos communities of the southeastern Weddell Sea shelf based on multibox corer samples. Polar Biology 12: 291-391

Gering JC, Crist TO, Veech JA (2003) Additive partitioning of species diversity across multiple spatial scales: implications for regional conservation of biodiversity. Conservation Biology 17: 488-499

Giangrande A, Geraci S, Belmonte G (1994) Life-cycle and life-history diversity in marine invertebrates and the implications in community dynamics. Oceanography and Marine Biology: An Annual Review 32: 305–333

Ginger ML, Billett DSM, Mackenzie KL, Kiriakoulakis K, Neto RR, Boardman DK, Santos V, Horsfall IM, Wolff GA (2001) Organic matter assimilation and selective feeding by holothurians in the deep sea: some observations and comments. Progress in Oceanography 50: 1-4

Gloersen P, Campbell WJ, Cavalieri DJ, Comiso JC, Parkinson CL, Zwally HJ (1992) Arctic and Antarctic sea ice, 1978-1987: satellite passive-microwave observations and analyses. National Aeronautics and Space Administration, Washington D.C.

Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4: 379-391

Gotelli NJ, Graves GR (1996) Null models in ecology. Smithsonian Institution Press, Washington, DC

Graf G (1992) Benthic-pelagic coupling: a benthic view. Oceanography and Marine Biology: An Annual Review 30: 149-190

Grassle JF (1991) Deep-sea benthic biodiversity. Bioscience 41: 464-469

Grassle JF, Grassle JP (1974) Opportunistic life histories and genetic systems in marine benthic polychaetes. Journal of Marine Research 32: 253–284

Grassle JF, Maciolek NJ (1992) Deep-sea species richness: regional and local diversity estimates from quantitative bottom samples. American Naturalist 139: 313-341

Grassle JP, Sanders RR, Hessler GT, Rowe GT, McLellan T (1975) Pattern and zonation: a study of the bathyal megafauna using the research submersible *Alvin*. Deep-Sea Research 22: 457-481

Gray JS (1974) Animal-sediment relationships. Oceanography and Marine Biology - an Annual Review 12: 223-261

Gray JS (1981) The ecology of marine sediments. Cambridge University Press, New York

Gray JS (1994) Is deep-sea species diversity really so high? Species diversity of the Norwegian continental shelf. Marine Ecology Progress Series 112: 205-209

Gray JS (2000) The measurement of marine species diversity, with an application to the benthic fauna of the Norwegian continental shelf. Journal of Experimental Marine Biology and Ecology 250: 23-49

Grime JP (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. Journal of Ecology 86: 902-910

Gutt J (1988) On the distribution and ecology of sea cucumbers (Holothuroidea, Echinodermata) in the Weddel Sea (Antarctica). Berichte zur Polarforschung 41: 1-87

Gutt J (1990) New Antarctic holothurians (Echinodermata). II. Four species of the orders Aspidochirotida, Elasipodida and Apodida. Zoologica Scripta 19: 119-127

Gutt J (1991a) Are Weddell Sea holothurians typical representatives of the Antarctic benthos? Meeresforschung / Reports on Marine Research 33: 312-329

Gutt J (1991b) On the distribution and ecology of holothurians in the Weddell Sea (Antarctica). Polar Biology 11: 145-155

Gutt J (2000) Some "driving forces" structuring communities of the sublittoral Antarctic macrobenthos. Antarctic Science 12: 297-313

Gutt J (2001) On the direct impact of ice on marine benthic communities, a review. Polar Biology 24: 553-564

Gutt J (2002) The Antarctic ice shelf: an extreme habitat for notothenioid fish. Polar biology 25: 320-322

Gutt J, Ekau W (1996) Habitat partitioning of dominant high Antarctic demersal fish in the Weddell Sea and Lazarev Sea. Journal of Experimental Marine Biology and Ecology 206: 25-37

Gutt J, Ekau W, Gorny M (1994) New results on the fish and shrimp fauna of the Weddell Sea and Lazarev Seas (Antarctic). Proceedings of the NIPR Symposium on Polar Biology 7: 91-102

Gutt J, Gorny M, Arntz W (1991) Spatial distribution of Antarctic shrimps (Crustacea: Decapoda) by underwater photography. Antarctic science 3: 371-377

Gutt J, Helsen E, Arntz W, Buschmann A (1999) Biodiversity and community structure of the mega-epibenthos in the Magellan region (South America). Scientia Marina 63: 155-170

Gutt J, Koltun VM (1995) Sponges of the Lazarev and Weddell Sea, Antarctica: Explanations for their patchy occurrence. Antarctic Science 7: 227-234

Gutt J, Piepenburg D (1991) Dense aggregations of three deep sea holothurians in the southern Weddell Sea, Antarctica. Marine Ecology Progress Series 68: 277-285

Gutt J, Piepenburg D (2003) Scale-dependent impact on diversity of Antarctic benthos caused by grounding of icebergs. Marine Ecology Progress Series 253: 77-83

Gutt J, Schickan T (1998) Epibiotic relationships in the Antarctic benthos. Antarctic Science 10: 398-405

Gutt J, Starmans A (1998) Structure and biodiversity of megabenthos in the Weddell and Lazarev Seas (Antarctica): Ecological role of physical parameters and biological interactions. Polar Biology 20: 229-247

Gutt J, Starmans A (2001) Quantification of iceberg impact and benthic recolonisation patterns in the Weddel Sea (Antarctica). Polar Biology 24: 615-619

Gutt J, Starmans A (2003) Patchiness of the megabenthos at small scales: ecological conclusions by examples from polar shelves. Polar Biology 26: 276-278

Gutt J, Starmans A, Dieckmann G (1996) Impact of iceberg scouring on polar benthic habitats. Marine Ecology Progress Series 137: 1-3

Haedrich RL, Rowe GT (1977) Megafaunal biomass in the deep sea. Nature 269: 141-142

Haedrich RL, Rowe GT, Polloni P (1975) Zonation and faunal composition of epibenthic populations on the continental slope south of New England. Journal of Marine Research 33: 191-212

Hain S (1990) The benthic seashells (Gastropoda and Bivalvia) of the Weddell Sea, Antarctica. Berichte zur Polarforschung/Reports on Polar Research 70: 1-181

Hall SJ (1994) Physical disturbance and marine benthic communities: life in unconsolidated sediments. Oceanography and Marine Biology: An Annual Review 32: 179-239

Hall SJ, Raffaelli D, Thrush SF (1994) Patchiness and disturbance in shallow water benthic assemblages. In: Giller PS, Hildrew AG, Raffaelli D (eds) Secondary Patchiness and Disturbance in Shallow Water Benthic Assemblages. Blackwell Science, Oxford, pp 333-375

Hamada E, Numanami H, Naito Y, Taniguchi A (1986) Observation of the marine benthic organisms at Syowa Station in Antarctica using a remotely operated vehicle. Memoirs of National Institute of Polar Research 40: 289-298

Hashimoto J, Hotta H (1985) An attempt of density estimation of megalo-epibenthos by a deep towed TV system and the deep sea research submersible Shinkai 2000. Technical Reports of the Japan Marine Science and Technology Center: 23-36

Hayward PJ, Ryland JS (1995) Handbook of the Marine Fauna of North-West Europe. Oxford University Press, Oxford, U.K.

Hecker B (1990a) Photographic Evidence for the Rapid Flux of Particles to the Sea-Floor and Their Transport Down the Continental-Slope. Deep-Sea Research Part I: Oceanographic Research Papers 37: 1773-1782

Hecker B (1990b) Variation in megafaunal assemblages on the continental-margin south of New England. Deep-Sea Research 37: 37-57

Hecker B (1994) Unusual Megafaunal Assemblages on the Continental-Slope Off Cape-Hatteras. Deep-Sea Research 41: 809-834

Hedgpeth JW (1971) Perspectives of benthic ecology in Antarctica. In: Quam LO (ed) Research in the Antarctic. American Association for the Advancement of Science, Washington D.C., pp 96-136

Heezen BC, Hollister CD (1971) The Face of the Deep. Oxford University Press, London

Hempel G (1985) On the biology of the polar seas, particularly the Southern Ocean. In: Gray JS, Christiansen ME (eds) Marine biology of the polar regions and effects of stress on marine organisms. Wiley, Chichester, pp 3-34

Herguera JC (1992) Deep-sea benthic foraminifera and biogenic opal: glacial to postglacial productivity changes in the western equatorial Pacific. Marine Micropaleontology 19: 79-98

Herring PJ, Gaten E, Shelton PMJ (1999) Are vent shrimps blinded by science? Nature 398: 116-116

Hersey JB (1967) Deep-Sea Photography. John Hopkins Press, Baltimore

Hessler RR, Sanders HL (1967) Faunal diversity in the deep-sea. Deep-Sea Research 14: 65-78

Hewitt JE, Thrush SF, Cummings VJ, Turner SJ (1998) The effect of changing sampling scales on our ability to detect effects of large-scale processes on communities. Journal of Experimental Marine Biology and Ecology 227: 251-264

Hill JK, Collingham YC, Thomas CD, Blakeley DS, Fox R, Moss D, Huntley B (2001) Impacts of landscape structure on butterfly range expansion. Ecology letters 4: 313-321

Hiura T (1995) Gap formation and species diversity in Japanese beech forests: a test of the intermediate disturbance hypothesis on a geographic scale. Oecologia 104: 265-271

Hollister CD, Heezen BC, Nafe KE (1975) Animal traces on the deep sea floor. In: Frey RW (ed) The study of Trace Fossils. Springer, New York, pp 493-510

Holme NA, McIntyre AD (1984) Methods for the study of marine benthos. Blackwell Scientific Publications, Oxford

Holm-Hansen O, El-Sayed SZ, Franceschini GA, Cuhel RL (1977) Primary production and the factors controlling phytoplankton growth in the Southern Ocean. In: Llano GA (ed) Adaptations within Antarctic ecosystems. Smithsonian Institution, Washington D. C.

Holte B, Oug E, Cochrane S (2004) Depth-related benthic macrofaunal biodiversity patterns in three undisturbed north Norwegian fjords. Sarsia 89: 91-101

Hovland M, Vasshus S, Indreeide A, Austdal L, Nilsen O (2002) Mapping and imaging deep-sea coral reefs off Norway, 1982-2000. Hydrobiologia 471: 13-17

Howell KL, Billett DSM, Tyler PA (2002) Depth-related distribution and abundance of seastars (Echinodermata: Asteroidea) in the Porcupine Seabight and Porcupine Abyssal Plain, N.E. Atlantic. Deep-Sea Research Part I: Oceanographic Research Papers 49: 1901-1920

Hudson IR, Wigham BD (2003) *In Situ* Observations Of Predatory Feeding Behaviour Of The Galatheid Squat Lobster Munida Sarsi Using A Remotely Operated Vehicle. Journal of the Marine Biological Association of the United Kingdom 83: 463 - 464

Hudson IR, Wigham BD, Tyler PA (2004) The feeding behaviour of a deep-sea holothurian, *Stichopus tremulus* (Gunnerus) based on *in situ* observations and experiments using a Remotely Operated Vehicle. Journal of Experimental Marine Biology and Ecology 301: 75-91

Huggett O (1987) Mapping of hemipelagic versus turbiditic muds by feeding traces observed in deep-sea photographs. In: Weaver PPE, Thomson J (eds) Geology and Geochemistry of Abyssal Plains. Geological Society Special Publication No. 31, pp 105-112

Hughes JA, Narayanaswamy BE, Bett BJ (2003) SEA 4: An overview of the benthic ecology of the Faroe-Shetland Channel Strategic Environmental Assessment: SEA 4. Consultation Document, London, Department of Trade and Industry, 2003.

Hughes JB, Petchey OL (2001) Merging perspectives on biodiversity and ecosystem functioning. Trends in Ecology & Evolution 16: 222-223

Hunkins KL, Ewing M, Heezen BC, Menzies RJ (1960) Biological and geological observations on the first photographs of the Arctic Ocean deep-sea floor. Limnology and Oceanography 5: 154-161

Hurlbert SH (1971) The nonconcept of species diversity: a critique and alternative parameters. Ecology 52: 577-586

Huston MA (1979) A general hypothesis of species diversity. American Naturalist 113: 81-101

Huston MA (1994) Biological diversity: the coexistence of species on changing landscapes. Cambridge University Press, Cambridge, pp 701

Jahnke R (1996) The global ocean flux of particulate organic carbon, areal distribution and magnitude. Global Biogeochemical Cycles 10: 71-88

Jazdzewski K, Teodorczyk W, Sicinski J, Kontek B (1991) Amphipod crustaceans as an important component of zoobenthos of the shallow Antarctic sublittoral. Hydrobiologia 223: 105-117

Jennings S, Pinnegar JK, Polunin NVC, Warr KJ (2001) Impacts of trawling disturbance on the trophic structure of benthic invertebrate communities. Marine Ecology Progress Series 213: 127-142

Jensen A, Frederiksen R (1992) The fauna associated with the bank forming deepwater coral *Lophelia pertusa* (Scleractinaria) on the Faroe Shelf. Sarsia 77: 53-69

Johnson RK, Goedkoop W, Sandin L (2004) Spatial scale and ecological relationships between the macroinvertebrate communities of stony habitats of streams and lakes. Freshwater Biology 49: 1179-1194

Jones DOB, Bett BJ, Tyler PA (submitted) Megabenthic ecology of the Faroe-Shetland Channel: a photographic study

Jones DOB, McPhail SD, Bett BJ, Flewellen C, Conquer M (2005) Seabed photography from an autonomous underwater vehicle. Journal of Marine Science and Environment C3: 29-36

Jones SE, Jago CF (1993) *In situ* assessment of modification of sediment properties by burrowing invertebrates. Marine Biology 115: 133-142

Jonsson LG, Nilsson PG, Florutta F, Lundalv T (2004) Distributional patterns of macro- and megafauna associated with a reef of the cold water coral *Lophelia pertusa* on the Swedish west coast. Marine Ecology Progress Series 284: 163-171

Kaufmann RS, Smith KL (1997) Activity patterns of mobile epibenthic megafauna at an abyssal site in the eastern North Pacific: Results from a 17-month time-lapse photographic study. Deep-Sea Research 44: 559-579

Kennett JP (1977) Cenozoic evolution of the Antarctic glaciation, the circum-Antarctic ocean and their impact on global paleoceanography. Journal of Geophysical Research 82: 3843-3860

Kennett JP, Barker PF (1990) Latest Cretaceous to Cenozoic climate and oceanographic developments in the Weddell Sea, Antarctica: an ocean-drilling perspective. In: Barker PF, Kennett JP (eds) Proceedings of the Ocean Drilling Program, Scientific Results., Leg 113. ODP. College Station, Texas, pp 937-962

Kenyon NH (1986) Evidence from bedforms for a strong poleward current along the upper continental slope of Northwest Europe. Marine Geology 74: 57-77

Kershaw KA, Looney JHH (1985) Quantitative and dynamic plant ecology. Arnold, London

Kitchell JA, Clark DL (1979) A multivariate approach to biofacies analysis of deep-sea traces from the central Arctic. Journal of Paleontology 53: 1045-1067

Kitchell JA, Kitchell JF, Johnson GL, Hunkins KL (1978) Abyssal traces and megafauna: comparison of productivity, diversity and density in the Arctic and Antarctic. Paleobiology 4: 171-180

Kleinrock MC, Hey RN, Theberge AE (1992) Practical Geological Comparison of Some Sea-Floor Survey Instruments. Geophysical Research Letters 19: 1407-1410

Klinkhammer GP, Chin CS, Keller RA, Dahlmann A, Sahling H, Sarthou G, Petersen S, Smith F (2001) Discovery of new hydrothermal vent sites in Bransfield Strait, Antarctica. Earth and Planetary Science Letters 193: 395-407

Klitgaard AB (1995) The fauna associated with outer shelf and upper slope sponges (Porifera, Demospongiae) at the Faroe Islands, northeastern Atlantic. Sarsia 80: 1-22

Klitgaard AB, Tendal OS, Westerberg H (1997) Mass occurrence of large sponges (Porifera) in Faroe Island (NE Atlantic) shelf and slope areas: characteristics, distribution and possible causes. In: Hawkins LE, Hutchins S (eds) The responses of Marine Organisms to their Environments. Southampton Oceanography Centre, Southampton

Knott T (2005) Delving deeper. Frontiers, the BP magazine of technology and innovation 11: 11-15

Knox GA (1994) The biology of the Southern Ocean. Cambridge University Press, Cambridge

Kollmann H, Stachowitsch M (2001) Long-term changes in the benthos of the northern Adriatic Sea: A phototransect approach. Marine Ecology 22: 135-154

Kramp PL (1963) Summary of the zoological results of the "Godthaab" expedition 1928. Meddelelser om Gronland Bd 81

Krebs CJ (1998) Ecological Methodology. Benjamin Cummings, Menlo Park, California

Krumbein WC, Pettijohn FJ (1938) Manual of Sedimentary Petrography. Appleton-Century-Crofts, New York

Lampitt RS, Antia R (1997) Particle flux in the deep seas: regional characteristics and temporal variability. Deep-Sea Research 44: 1377-1373

Lampitt RS, Bett BJ, Kiriakoulakis K, Popova EE, Ragueneau O, Vangriesheim A, Wolff GA (2001) Material supply to the abyssal seafloor in the Northeast Atlantic. Progress in Oceanography 50: 27-63

Lampitt RS, Billett DSM, Rice AL (1986) Biomass of the invertebrate megabenthos from 500 to 4100 m in the Northeast Atlantic Ocean. Marine Biology 93: 69-81

Lampitt RS, Burnham MP (1983) A free-fall time-lapse camera and current meter system "Bathysnap" with notes on the foraging behaviour of a bathyal decapod shrimp. Deep-Sea Research 30: 1009-1017

Lampitt RS, Merrett NR, Thurston MH (1983) Inter-relations of necrophagous amphipods, a fish predator, and tidal currents in the deep sea. Marine Biology 74: 73-78

Lande R (1996) Statistics and partitioning of species diversity, and similarity among multiple communities. Oikos 76: 5-13

Langton RW, Uzmann JR (1989) A photographic survey of the megafauna of the central Gulf of Maine. Fish. Bull. (U.S.) 87: 945-954

Lauerman LML, Kaufmann RS, Smith Jr KL (1996) Distribution and abundance of epibenthic megafauna at a long time-series station in the abyssal northeast Pacific. Deep-Sea Research 43: 1075-1103

Laughton AS (1963) Microtopography. In: Hill MN (ed) The Sea, Vol. 3. Wiley-Interscience, New York, pp 437-472

Laws RM (1989) Antarctica. The last frontier. Boxtree, London

Leonard GH, Clark RP (1993) Point quadrat versus video transect estimates of the cover of benthic red algae. Marine Ecology Progress Series 101: 203-208

Levin LA, Etter RJ, Rex MA, Gooday AJ, Smith CR, Pineda J, Stuart CT, Hessler RR, Pawson D (2001) Environmental influences on regional deep-sea species diversity. Annual Review of Ecology and Systematics 32: 51-93

Levin LA, Gage JD (1998) Relationships between oxygen, organic matter and the diversity of bathyal macrofauna. Deep-Sea Research Part II: Topical Studies in Oceanography 45: 129-163

Levin S (1992) The problem of pattern and scale in ecology. Ecology 73: 1943–1967

Leybourne MI, Vanwagoner NA (1992) Volcanism, Age, and Hydrothermal Deposits of the West-Valley Segment, Juan-De-Fuca-Ridge. Canadian Journal of Earth Sciences 29: 2346-2352

Lien R, Solheim A, Elverhoi A, Rokoengen K (1989) Iceberg scouring and seabed morphology on the eastern Weddell Sea shelf, Antarctica. Polar Research 7: 43-57

Lipps JH, Hickman CS (1982) Origin, age, and evolution of Antarctic and deep-sea faunas. In: Ernst WG, Morin JG (eds) The environment of the deep sea. Prentice-Hall, Eaglewood Cliffs, NJ, pp 324-356

Lipps JH, Ronan TE, Jr., De Laca TE (1979) Life below the Ross Ice Shelf, Antarctica. Science 203: 447-449

Lohrer AM, Thrush SF, Gibbs MM (2004) Bioturbators enhance ecosystem function through complex biogeochemical interactions. Nature 431: 1092-1095

Longhurst AR (1998) Ecological geography of the sea. Academic Press, San Diego, CA

Lonsdale P (1977a) Clustering of suspension feeding macrobenthos near abyssal hydrothermal vents at oceanic spreading centres. Deep-Sea Research 24: 857-863

Lonsdale P (1977b) Deep-tow observations at the mounds abyssal thermal field, Galapagos Rift. Earth and Planetary Science Letters 36: 67-69

Loreau M, Naeem S, Inchausti P (2002) Biodiversity and ecosystem functioning. Oxford University Press, Oxford

Loreau M, Naeem S, Inchausti P, Bengtsson J, Grime JP, Hector A, Hooper DU, Huston MA, Raffaelli D, Schmid B, Tilman D, Wardle DA (2001) Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294: 804-808

Lunde T (1961) On the snow accumulation in Dronning Maud Land. Norwegian Polarinstitute Skrifter 123: 48

MacArthur RH (1960) On the relative abundance of species. American Naturalist 94: 25-36

MacArthur RH (1965) Patterns of species diversity. Biology Review 40: 510-533

Machan R, Fedra K (1975) A new towed underwater camera system for wide-range benthic surveys. Marine Biology 33: 75-84

Madsen H (1936) Investigations on the shore fauna of East Greenland with a survey of the shores of other arctic regions. Ibidem Bd. 100

Magurran AE (1991) Ecological diversity and its measurement. Chapman and Hall, London

Magurran AE (2003) Measuring Biological Diversity. Blackwell Science, Oxford

Manly BFJ (1998) Randomization, bootstrap and Monte Carlo methods in biology. Chapman and Hall, London

Margalef R (1968) Perspectives in ecological theory. University of Chicago Press, Chicago

Marshall NB, Bourne DW (1964) A photographic survey of benthic fishes in the Red Sea and Gulf of Eden, with observations on their population density, diversity and habitats. Bulletin of the Museum of Comparative Zoology, Harvard University 132: 225-244

Masson DG (2001) Sedimentary processes shaping the eastern slope of the Faroe-Shetland Channel. Continental Shelf Research 21: 825-857

Masson DG, Jacobs CL, Le Bas TP, Huhnerbach V (2000) Section 4.1, Surficial geology, in Environmental Surveys of the Seafloor of the UK Atlantic Margin. Atlantic Frontier Environmental Network (CD Rom). ISBN 09538399-0-7

Mauviel A, Junipers SK, Sibuet M (1987) Discovery of an enteropneust associated with a mound burrow trace in the deep sea: ecological and geochemical implications. Deep-Sea Research 34: 329-335

May RM (1992) Bottoms up for the oceans. Nature 357: 278-279

Mayer M, Piepenburg D (1996) Epibenthic community patterns on the continental slope off East Greenland at 75 degrees N. Marine Ecology Progress Series 143: 151-164

Mazella L, Scipione MB, Gambi MC, Buia MC, Lorenti M, Zupo V, Canceuri G (1993) The Mediterranean sea grass Posidonia oceanica and Cymodocea nodosa. A comparative overview. The first international Conference on the Mediterranean Coastal Environment, MED COAST 93, Antalya, Turkey, pp 103-116

McCabe DJ, Gotelli NJ (2000) Effects of disturbance frequency, intensity and area on assemblages of stream invertebrates. Oecologia 124: 270-279

McConachy TF, Ballard RD, Mottl MJ, Vonherzen RP (1986) Geologic form and setting of a hydrothermal vent field at lat 10-degrees-56'N, East Pacific Rise - A detailed study using ANGUS and ALVIN. Geology 14: 295-298

McCune B, Mefford MJ (1999) Multivariate Analysis of Ecological Data. MjM Software, Gleneden Beach, Oregon, U.S.A.

McGuinness KA (1987) Disturbance and organisms on boulders. I. Patterns in the environment and the community. Oecologia 71: 409-419

McHugh CMG, Ryan WBF (2000) Sedimentary features associated with channel overbank flow: examples from the Monterey Fan. Marine Geology 163: 199-215

McIntosh RP (1967) An index of diversity and the relation of certain concepts to diversity. Ecology 48: 392-404

McIntyre AD (1956) The use of trawl, grab and camera in estimating marine benthos. Journal of the Marine Biological Association of the United Kingdom 35: 419-429

Menge BA, Olson AM (1990) Role of scale and environmental factors in regulation of community structure. Trends in Ecology & Evolution 5: 52-57

Menzies RJ (1962) The abyssal fauna of the sea floor of the Arctic Ocean Proceedings of the Arctic Basin Symposium. Arctic Institute of North America, Hershey, Pa., pp 46-66

Menzies RJ, George RY, Rowe GT (1973) Abyssal environment and ecology of the worlds oceans. Wiley-Interscience, New York

Mileikovsky SA (1971) Types of larval development in marine bottom invertebrates, their distribution and ecological significance: a re-evaluation. Marine Biology 10: 193-213

Millard NW, McPhail SD, Stevenson P, Pebody M, Perrett JR, Webb AT, Squires M, Griffiths G, Thorpe SA, Collins MB, Statham P, German C, Burkill PH, Stansfield K, Smeed DA (2003) Multidisciplinary ocean science applications of an AUV: The Autosub science missions programme. In: Griffiths G (ed) The technology and applications of autonomous underwater vehicles. Taylor and Francis, London, pp 139-159

Miller RG (1981) Simultaneous statistical inference. McGraw-Hill, New York

Mortensen PB, Buhl-Mortensen L (2004) Distribution of deep-water gorgonian corals in relation to benthic habitat features in the Northeast Channel (Atlantic Canada). Marine Biology 144: 1223-1238

Muhlenhardt-Siegel U (1988) Some results on quantitative investigations of macro-zoobenthos in the Scotia Arc (Antarctica). Polar Biology 8: 241-248

Mulder CPH, Bazeley-White E, Dimitrakopoulos PG, Hector A, Scherer-Lorenzen M, Schmid B (2004) Species evenness and productivity in experimental plant communities. Oikos 107: 50-63

Munch-Petersen S, Kristensen PS (2001) On the dynamics of the stocks of blue mussels (Mytilus edulis L.) in the Danish Wadden Sea. Hydrobiologia 465: 1-3

Murphy EJ, Clarke A, Symon C, Priddle J (1995) Temporal variation in Antarctic sea-ice: Analysis of a long term fast-ice record from the South Orkney Islands. Deep-Sea Research Part I: Oceanographic Research Papers 42: 1045-1062

Murray J, Hjort J (1912) The Depths of the Oceans. MacMillan, London

Muschenheim DK (1987) The dynamics of near-bed seston flux and suspension-feeding benthos. Journal of Marine Research 45: 473-496

Naeem S (2002) Ecosystem consequences of biodiversity loss: The evolution of a paradigm. Ecology 83: 1537-1552

Narayanaswamy BE, Bett BJ, Gage JD (2005) Ecology of bathyal polychaete fauna at an Arctic–Atlantic boundary (Faroe–Shetland Channel, North-east Atlantic). Marine Biology Research 1: 20-32

Newell RC, Seiderer LJ, Hitchcock DR (1998) The impact of dredging works in coastal waters: a review of the sensitivity to disturbance and subsequent recovery of biological resources on the sea bed. Oceanography and Marine Biology: An Annual Review 36: 127–178

Nicholls KW (1997) Predicted reduction in basal melt rates of an Antarctic ice shelf in a warmer climate. Nature 388: 460-462

Nicholls KW (2005) Autosub under ice cruise JR97 to the NE Weddell Sea, Antarctica. Unpublished cruise report. British Antarctic Survey, Cambridge, U.K.

Ninio R, Delean S, Osborne K, Sweatman H (2003) Estimating cover of benthic organisms from underwater video images: variability associated with multiple observers. Marine Ecology Progress Series 265: 107-116

Nørrevang A, Brattegard T, Josefson AB, Sneli JA, Tendal OS (1994) List of BIOFAR stations. Sarsia 79: 165-180

Nost OA (2004) Measurements of ice thickness and seabed topography under the Fimbul Ice Shelf, Dronning Maud Land, Antarctica. Journal of Geophysical Research-Oceans 109: art. no.-C10010

Nybakken J (1993) Marine Biology: an ecological approach. HarperCollins, New York

Ohta S (1983) Photographic census of large-sized benthic organisms in the bathyal zone of Suruga Bay, central Japan. Bulletin of the Oceanographic Research Institute 15: 1-244

Oliver JS, Slattery PN (1985) Effects of crustacean predators on species composition and population structure of soft-bodied infauna from McMurdo Sound. Ophelia 24: 155-175

Oliver JS, Watson DJ, O'Connor EF, Dayton PK (1976) Benthic communities of McMurdo Sound. Antarctic Journal of the United States 11: 58-59

Olsgard F, Gray JS (1995) A Comprehensive Analysis of the Effects of Offshore Oil and Gas Exploration and Production on the Benthic Communities of the Norwegian Continental-Shelf. Marine Ecology Progress Series 122: 277-306

Orejas C, Lopez-Gonzalez PJ, Gili JM, Teixido N, Gutt J, Arntz WE (2002) Distribution and reproductive ecology of the Antarctic octocoral *Ainigmaptilon antarcticum* in the Weddell Sea. Marine Ecology Progress Series 231: 101-114

Orheim O (1985) Iceberg discharge and the mass balance of Antarctica. In: Lingle CS (ed) Glaciers, ice sheets and sea level effect of a CO2-induced climatic change. Report of a Workshop held Seattle, Washington, 13-15 Sep 1984,. National Research Council, Washington, D.C., pp 210-215

Owen DM, Sanders HL, Hessler RR (1967) Bottom photography as a tool for estimating benthic populations. In: Hersey JB (ed) Deep-sea photography. John Hopkins Press, Baltimore, pp 95-105

Paine RT, Levin SA (1981) Intertidal landscapes, disturbance, and the dynamics of pattern. Ecological Monographs 51: 145-178

Paine RT, Tegner MJ, Johnson EA (1998) Compounded perturbations yield ecological surprises. Ecosystems 1: 535–545

Palmer MW (1993) Putting things in even better order: the advantages of canonical correspondence analysis. Ecology 74: 2215-2230

Parry DM, Kendall MA, Pilgrim DA, Jones MB (2002) Identification of patch structure within marine benthic landscapes using a remotely operated vehicle. Journal of Experimental Marine Biology and Ecology 285-286: 497-511

Paterson GLJ, Lambshead PJD (1995) Bathymetric patterns of polychaete diversity in the Rockall Trough, northeast Atlantic. Deep Sea Research Part I: Oceanographic Research Papers 42: 1199-1214

Paul AZ, Menzies RJ (1974) Benthic ecology of the high Arctic deep sea. Marine Biology 27: 251-262

Pearse JS (1994) Cold water echinoderms break "Thorson's rule". In: Young CM, Eckelbarger KJ (eds) Reproduction, larval biology and recruitment of the deep-sea benthos. Columbia University Press, New York, pp 26-43

Peck LS, Brockington S, Vanhove S, Beghyn M (1999) Community recovery following catastrophic iceberg impacts in a soft-sediment shallow-water site at Signy Island, Antarctica. Marine Ecology Progress Series 186: 1-8

Peters RH (1991) A critique for ecology. Cambridge University Press, Cambridge, England

Picken GB (1980) The distribution, growth and reproduction of the Antarctic limpet *Nacella (Patinigera) concinna* (Strebel, 1908). Journal of Experimental Marine Biology and Ecology 42: 71-85

Picken GB (1985) Marine habitats - benthos. In: Bonner WN, Walton DWH (eds) Key environments: Antarctica. Pergamon Press, Oxford, pp 154-172

Pickett STA, White PA (1985) The Ecology of Natural Disturbance and Patch Dynamics. New York Academic Press, New York

Pielou EC (1969) An introduction to mathematical ecology. Wiley, New York

Pielou EC (1984) The interpretation of ecological data. Wiley, New York

Piepenburg D, Ambrose WG, Brandt A, Renaud PE, Ahrens MJ, Jensen P (1997a) Benthic community patterns reflect water column processes in the Northeast Water Polynya (Greenland). Journal of Marine Systems 10: 467-482

Piepenburg D, Blackburn TH, Dorrien C, Gutt J, Hall POJ, Hulth S, Kendall MA, Opalinski KW, Rachor E, Schmid MK (1995) Partitioning of benthic community respiration in the Arctic (northwestern Barents Sea). Marine Ecology Progress Series 118: 199-213

Piepenburg D, Brandt A, von Juterzenka K, Mayer M, Schnack K, Seiler D, Witte U, Spindler M (2001) Patterns and determinants of the distribution and structure of benthic faunal assemblages in the northern north Atlantic. In: Schafer P, Ritzrau M, Schluter M, Thiede J (eds) The Northern North Atlantic: A changing environment. Springer, Berlin, pp 179-198

Piepenburg D, Chernova NV, Dorrien C, Gutt J, Neyelov AV, Rachor E, Saldanha L, Schmid MK (1996) Megabenthic communities in the waters around Svalbard. Polar Biology 16: 431-446

Piepenburg D, Schmid MK (1996a) Brittle star fauna (Echinodermata: Ophiuroidea) of the Arctic northwestern Barents Sea: composition, abundance, biomass and spatial distribution. Polar Biology 16: 383-392

Piepenburg D, Schmid MK (1996b) Distribution, abundance, biomass, and mineralization potential of the epibenthic megafauna of the Northeast Greenland Shelf. Marine Biology 125: 185-194

Piepenburg D, Schmid MK (1997) A photographic survey of the epibenthic megafauna of the Arctic Laptev Sea shelf: distribution, abundance and estimates of biomass and organic carbon demand. Marine Ecology Progress Series 147: 63-75

Piepenburg D, von Juterzenka K (1994) Abundance, Biomass and Spatial-Distribution Pattern of Brittle Stars (Echinodermata, Ophiuroidea) on the Kolbeinsey Ridge North of Iceland. Polar Biology 14: 185-194

Piepenburg D, Voss J, Gutt J (1997b) Assemblages of sea stars (Echinodermata: Asteroidea) and brittle stars (Echinodermata: Ophiuroidea) in the Weddell Sea (Antarctica) and off Northeast Greenland (Arctic): A comparison of diversity and abundance. Polar Biology 17: 305-322

Pineda J, Caswell H (1998) Bathymetric species-diversity patterns and boundary constraints on vertical range distributions. Deep-Sea Research 45: 83-101

Pogrebov VB, Goncharova EG, Vakovelv AV (1994) An analysis of the macrozoobenthos distribution on the Novaya Zemlya shelf of the Barents Sea by the method of self-organising simulation based on underwater photography. Oceanology 34: 839-846

Polyak L, Edwards MH, Coakley BJ, Jakobsson M (2001) Ice shelves in the Pleistocene Arctic Ocean inferred from glaciogenic deep-sea bedforms. Nature 410: 453-457

Poore G, Wilson GDF (1993) Marine species richness. Nature 361: 597-598

Priede IG, Merrett NR (1998) The relationship between numbers of fish attracted to baited cameras and population density: studies on demersal grenadiers *Coryphaenoides (Nematonurus) armatus* in the abyssal NE Atlantic Ocean. Fisheries Research 36: 133-137

Probert PK (1984) Disturbance, sediment stability, and trophic structure of soft bottom communities. Journal of Marine Research 42: 893-921

Raffaelli D, Emmerson M, Solan M, Biles C, Paterson D (2002) Biodiversity and ecosystem processes in shallow coastal waters: an experimental approach. Journal of sea research, special issue 49: 133-141

Raghukumar C, Loca Bharathi PA, Ansari ZA, Nair S, Ingole BS, Sheelu G, Mohandass C, Nath BN, Rodrigues N (2001) Bacterial standing stock, meiofauna and sediment nutrient characteristics: indicators of benthic disturbance in the Central Indian Basin. Deep-Sea Research Part II: Topical Studies in Oceanography 48: 3381-3399

Ramsay K, Kaiser MJ, Hughes RN (1998) Responses of benthic scavengers to fishing disturbance by towed gears in different habitats. Journal of Experimental Marine Biology and Ecology 224: 73-89

Rasmussen E (1973) Systematics and ecology of the Isefjord marine fauna (Denmark). Ophelia 11: 1-507

Rex MA (1973) Deep-sea species diversity: Decreased gastropod diversity at abyssal depths. Science 181: 1051-1053

Rex MA (1976) Biological accommodation in the deep-sea benthos: comparative evidence on the importance of predation and productivity. Deep-Sea Research 23: 975-987

Rex MA (1977) Zonation in deep-sea gastropods: the importance of biological interactions to rates of zonation. In: Keegan BF, Ceidigh PO, Boaden PJS (eds) Biology of benthic organisms. Pergamon Press, New York, pp 521-530

Rex MA (1981) Community structure in the deep-sea benthos. Annual Review of Ecology and Systematics 12: 331-353

Rex MA, Etter RJ, Stuart CT (1997) Large-scale patterns of species diversity in the deep-sea benthos. Cambridge University Press, New York

Rex MA, Stuart CT, Coyne G (2000) Latitudinal gradients of species richness in the deep-sea benthos of the North Atlantic. Proceedings of the National Academy of Sciences, USA 97: 4082-4085

Rex MA, Stuart CT, Hessler RR, Allen JA, Sanders HL, Wilson GDF (1993) Global-scale latitudinal patterns of species diversity in the deep-sea benthos. Nature 365: 636-639

Rex MA, Watts MC, Etter RJ, O'Neil S (1988) Character variation in a complex of rissoid gastropods from the upper continental slope of the western North Atlantic. Malacologia 29: 325-339

Rhoads DC (1974) Organism seiment relations on the muddy sea floor. Oceanography and Marine Biology: An Annual Review 12: 263-300

Rice AL, Aldred RG, Darlington E, Wild RA (1982) The Quantitative Estimation of the Deep-Sea Megabenthos - a New Approach to an Old Problem. Oceanologica Acta 5: 63-72

Rice AL, Billett DSM, Thurston MH, Lampitt RS (1991) The Institute of Oceanographic Sciences biology programme in the Porcupine Seabight: Background and general introduction. Journal of the Marine Biological Association of the United Kingdom. Plymouth 71: 281-310

Ricotta C (2004) A Recipe for Unconventional Evenness Measures. Acta Biotheoretica 52: 95-104

Riegman R, Kraay GW (2001) Phytoplankton community structure derived from HPLC analysis of pigments in the Faroe-Shetland Channel during summer 1999: the distribution of taxonomic groups in relation to physical/chemical conditions in the photic zone. Journal of Plankton Research 23: 191-205

Rodrigues N, Sharma R, Nath BN (2001) Impact of benthic disturbance on megafauna in Central Indian Basin. Deep-Sea Research Part II: Topical Studies in Oceanography 48: 3411-3426

Rogers CS (1990) Reponses of coral reefs and reef organisms to sedimentation. Marine Ecology Progress Series 62: 185-202

Romero-Wetzel MB, Gerlach S (1991) Abundance, biomass, size distribution and bioturbation potential of deep-sea macrozoobenthos on the Voring Plateau (1200-1500m, Norwegian Sea). Meeresforsch 33: 247-265

Ropelewski CF (1995) NOAA/NMC/CAC Arctic and Antarctic monthly sea ice extent. National Snow and Ice Data Center. Digital media, Boulder, CO

Rosenberg R (1995) Benthic marine fauna structured by hydrodynamic processes and food availability. Netherlands Journal of Sea Research 34: 303-317

Rosenzweig ML, Abramsky H (1993) How are species diversity and productivity related? In: Ricklefs RE, Schluter D (eds) Species diversity in ecological communities: Historical and changing perspectives. University of Chicago Press, Chicago, pp 53-65

Rowe GT (1983) Biomass and production of the deep-sea macrobenthos. In: Rowe GT (ed) The Sea. Wiley-Interscience, New York, pp 97-121

Rowe GT, Menzies RJ (1969) Zonation of large benthic invertebrates in the deep-sea off the Carolinas. Deep-Sea Research 16: 531-537

Rowe GT, Polloni P, Haedrich RL (1982) The deep-sea macrobenthos on the continental margin of the northwest Atlantic Ocean. Deep-Sea Research 29A: 257-278

Rowe GT, Sibuet M (1983) Recent advances in instrumentation in deep-sea biological research. In: Rowe GT (ed) The Sea. John Wiley, New York, pp 81-95

Rowe GT, Sibuet M, Vangriesheim A (1986) Domains of Occupation of Abyssal Scavengers Inferred from Baited Cameras and Traps on the Demerara Abyssal Plain. Deep-Sea Research 33: 501-522

Rysgaard S, Finster K, Dahlgaard H (1996) Primary production, nutrient dynamics and mineralization in a northeastern Greenland fjord during the summer thaw. Polar Biology 16: 497-506

Sanders HL (1968) Marine benthic diversity: a comparative study. American Naturalist 102: 243-282

Sanders HL, Hessler RR (1969) Diversity and composition of abyssal benthos. Science 163: 1034

Sater JE (1969) The Arctic Basin. Arctic Institute of North America, Washington D.C.

Saunders PM (1990) Cold outflow from the Faeroe Bank Channel. Journal of Physical Oceanography 20: 29-43

Schenck HJ, Kendall H (1954) Underwater photography. Cornell Maritime Press, Cambridge, Maryland

Schuldt MD, Cook CE, Hale BW (1967) Photogrammetry applied to photography at the bottom. In: Hersey JB (ed) Deep Sea Photography. John Hopkins Press, Baltimore, pp 69-74

Schwinghamer P (1981) Characteristic size distribution of integral benthic communities. Canadian Journal of Fisheries and Aquatic Science 38: 1255-1263

Sejr MK, Jensen KT, Rysgaard S (2000) Macrozoobenthic community structure in a high-arctic East Greenland fjord. Polar Biology 23: 792-801

Self RFL, Jumars PA (1988) Cross-phyletic patterns of particle selection by deposit feeders. Journal of Marine Research 46: 119-143

Sharma R, Nath BN, Parthiban G, Sankar SJ (2001) Sediment redistribution during simulated benthic disturbance and its implications on deep seabed mining. Deep-Sea Research Part II: Topical Studies in Oceanography 48: 3363-3380

Sharma R, Rao AS (1992) Geological factors associated with megabenthic activity in the Central Indian Basin. Deep-Sea Research Part I: Oceanographic Research Papers 39: 705-713

Sherwin T (1995) Tidal oscillations of the thermocline in the Faroe-Shetland Channel. Ocean Challenge 6: 33-35

Sibuet M, Lawrence JM (1981) Organic content and biomass of abyssal holothuroids (Echinodermata) from the Bay of Biscay. Marine Biology 65: 143-147

Simmons KL, Landrum BJ (1973) Bottom photographs of Antarctic benthos. Antarctic Journal of the United States 8: 41-43

Simpson EH (1949) Measurement of diversity. Nature 163: 688

Singh H, Howland J, Pizarro O (2004) Advances in Large-Area Photomosaicking

Underwater. IEEE Journal of Oceanic Engineering 29: 872-886

Singh H, Whitcomb L, Yoerger D, Pizarro O (2000) Microbathymetric Mapping from Underwater

Vehicles in the Deep Ocean. Computer Vision and Image Understanding 79: 143-161

Smith CR (1985) Food for the deep sea: utilisation, dispersal and flux of necton falls at the Santa Catalina Basin floor. Deep-Sea Research 32: 417-442

Smith CR, Hamilton SC (1983) Epibenthic megafauna of a bathyal basin off southern California: patterns of abundance, biomass, and dispersion. Deep-Sea Research 30: 907-928

Smith CR, Levin LA, Mullineaux LS (1998) Deep-sea biodiversity: a tribute to Robert R. Hessler. Deep-Sea Research 45: 1-11

Smith KL (1992) Benthic boundary layer communities and carbon cycling at abyssal depths in the central North Pacific. Limnology and Oceanography 37: 1034-1056

Smith KL, Kaufmann RS, Wakefield WW (1993) Mobile megafaunal activity monitored with a time-lapse camera in the abyssal North Pacific. Deep-Sea Research 40: 2307-2324

Smith LM, Andrews JT (2000) Sediment characteristics in iceberg dominated fjords, Kangerlussuaq region, East Greenland. Sedimentary Geology 130: 11-25

Smith WO, Walsh ID, Booth BC, Deming JW (1995) Particulate matter and phytoplankton and bacterial biomass distributions in the Northeast Polynya during summer 1992. Journal of Geophysical Research 100: 4357-4370

Snelgrove PVR, Butman CN (1994) Animal sediment relationships revisited: cause versus effect. Oceanography and Marine Biology: An Annual Review 32: 111-117

Snelgrove PVR, Grassle JP, Grassle JF, Petrecca RF, Ma HG (1999) *In situ* habitat selection by settling larvae of marine soft- sediment invertebrates. Limnology and Oceanography 44: 1341-1347

Solan M, Cardinale BJ, Downing AL, Engelhardt KAM, Ruesink JL, Srivastava DS (2004) Extinction and ecosystem function in the marine benthos. Science 306: 1177-1180

Solan M, Germano JD, Rhoads DC, Smith C, Michaud E, Parry D, Wenzhofer F, Kennedy B, Henriques C, Battle E (2002) Towards a greater understanding of pattern, scale and process in marine benthic systems: a picture is worth a thousand worms. Journal of Experimental Marine Biology and Ecology 285-286: 313-338

Sousa WP (1980) The responses of a community to disturbances: the importance of successional age and species' life histories. Oecologia 45: 72–81

Sousa WP (1984) The role of disturbance in natural communities. Annual Review of Ecology and Systematics 15: 353-391

Sousa WP (1985) Disturbance and patch dynamics on rocky intertidal shores. In: Pickett STA, White PS (eds) The ecology of natural disturbance and patch dynamics. Academic Press, San Diego, pp 101-124

Sousa WP (2001) Natural disturbance and the dynamics of marine benthic communities. In: Bertness MD, Gaines SD, Hay ME (eds) Marine community ecology. Sinauer Associates, Sunderland, pp 85–130

Southward TRE (1978) Ecological Methods. Chapman and Hall, London

Sparck R (1933) Contributions to the animal ecology of Franz Joseph Fjord and adjacent East Greenland waters. Meddelelser om Gronland 100: 1-38

Spindler M (1990) A comparison of Arctic and Antarctic sea ice and the effects of different properties on the sea ice biota. In: Bleil U, Thiede, J. (ed) Geological History of the Polar Oceans: Arctic versus Antarctic. Kluwer Academic Publishing

Stansfield K, Smeed D, Gasparini G, McPhail SD, Millard N, Stevenson P, Webb A, Vetrano A, Rabe B (2001) Deep Sea, high resolution, hydrography and current measurements using an AUV: The overflow from the Strait of Sicily. Geophysical Research Letters 28: 2645-2648

Starmans A (1997) Comparative studies on the ecology and biodiversity of the Arctic and Antarctic mega-epibenthos. Berichte zur Polarforschung 250: 1-150

Starmans A, Gutt J (2002) Mega-epibenthic diversity: a polar comparison. Marine Ecology Progress Series 225: 45-52

Starmans A, Gutt J, Arntz WE (1999) Mega-epibenthic communities in Arctic and Antarctic shelf areas. Marine Biology 135: 269-280

Stein DL, Felley JD, Vecchione M (2005) ROV observations of benthic fishes in the Northwind and Canada Basins, Arctic Ocean. Polar Biology 28: 232-237

Stein M (2000) Hydrographic and atmospheric conditions off east Greenland -Their potential effect on the distribution of shrimp (Pandalus borealis). Journal of Northwestern Atlantic Fisheries Society 27: 63-67

Stendera SES, Johnson RK (2005) Additive partitioning of aquatic invertebrate species diversity across multiple spatial scales. Freshwater Biology 50: 1360-1375

Stockton WL (1982) Scavenging amphipods from under the Ross ice shelf, Antarctica. Deep-Sea Research 29: 171-178

Stride AH (1982) Offshore tidal sands: processes and deposits. Chapman & Hall, London

Stronkhorst J, Ariese F, Van Hattum B, Postma JF, De Kluijver M, Besten PJD, Bergman MJN, Daan R, Murk AJ, Vethaak AD (2003) Environmental impact and recovery at two dumping sites for dredged material in the North Sea. Environmental Pollution 124: 17-31

Stuart CT, Rex MA, Etter RJ (2003) Large-scale spatial and temporal patterns of deep-sea benthic species diversity. In: Tyler PA (ed) Ecosystems of the World: Vol. 28. Ecosystems of Deep Oceans. Elsevier, Amsterdam, pp 295-311

Suess E (1980) Particulate organic carbon flux in the oceans - surface productivity and oxygen utilisation. Nature 288: 260-263

Svedrup HU, Johnson MW, Fleming RH (1942) The Oceans. Prentice-Hall, New Jersey

Swithinbank C (1957) The morphology of the ice shelves of western Dronning Maud Land. In: Swithinbank C (ed) Norwegian-British-Swedish Antarctic Expedition, 1942-51. Norwegian Polarinstitute, Tromso, Norway, pp 3 – 36

Syvitski JPM, Andrews JT, Dowdeswell JA (1996) Sediment deposition in an iceberg-dominated glacimarine environment, East Greenland: basin fill implications. Global and Planetary Change 12: 251-270

Teixido N, Garrabou J, Arntz W (2002) Spatial pattern quantification of Antarctic benthic communities using landscape indices. Marine Ecology Progress Series 242: 1-14

Teixido N, Garrabou J, Gutt J, Arntz WE (2004) Recovery in Antarctic benthos after iceberg disturbance: trends in benthic composition, abundance and growth forms. Marine Ecology Progress Series 278: 1-16

Tendal OS, Barthel D (1997) Composition and distribution of the Eastern Weddell Sea Scleractinian coral fauna. Berichte zur Polarforschung 249: 53-54

ter Braak CJF (1986) Canonical Correspondence Analysis: A New Eigenvector Technique for Multivariate Direct Gradient Analysis. Ecology 67: 1167-1179

Thatje S, Mutschke E (1999) Distribution of abundance, biomass, production and productivity of macrozoobenthos in the sub Antarctic Magellan Province (South America). Polar Biology 22: 31-37

Thatje S, Hillenbrand CD, Larter R (2005) On the origin of Antarctic marine benthic community structure. Trends in Ecology & Evolution 20: 534-540

Thistle D (1983a) The role of biologically produced habitat heterogeneity in deep sea diversity maintainance. Deep-Sea Research 30: 1235-1245

Thistle D (1983b) The stability-time hypothesis as a predictor of diversity in deep-sea soft-bottom communities: a test. Deep-Sea Research 30: 267-277

Thistle D (1988) A temporal difference in harpacticoid-copepod abundance at a deep-sea site: caused by benthic storms? Deep-Sea Research 35: 1015-1020

Thistle D (2001) The deep-sea floor: an overview. In: Tyler PA (ed) Ecosystems of the world: Vol. 28. Ecosystems of Deep Oceans. Elsevier, Amsterdam

Thistle D, Levin LA (1998) The effect of experimentally increased near-bottom flow on metazoan meiofauna at a deep-sea site, with comparison data on macrofauna. Deep-Sea Research 45: 625-638

Thistle D, Sherman KM (1985) The nematode fauna of a deep-sea site exposed to strong near-bottom currents. Deep-Sea Research 32A: 1077-1088

Thomson CW (1872a) On the Crinoids of the 'Porcupine' deep-sea dredging expedition. Proceedings of the Royal Society of Edinburgh 1871-1872: 764-773

Thomson CW (1872b) On the Echinoidea of the 'Porcupine' deep-sea dredging expedition. Proceedings of the Royal Society of Edinburgh 1872: 491-497

Thomson CW (1873) The Depths of the Sea. MacMillan and Co., London

Thorndike EM (1959) Deep-sea cameras of the Lamont Observatory. Deep-Sea Research 5: 234-237

Thorson G (1934) Contributions to the animal ecology of the Scoresby Sound fjord complex. Meddelelser om Gronland 100: 1-68

Thorson G (1950) Reproductive and larval ecology of marine bottom invertebrates. Biology Review 25: 1-45

Thorson G (1957) Bottom communities. Geological Society of America Memoir 67: 461-534

Thrush SF, Hewitt JE, Cummings VJ, Dayton PK (1995) The impact of scallop dredging on marine benthic communities: what can be predicted from the results of experiments? Marine Ecology Progress Series 129: 141-150

Thrush SF, Pridmore RD, Hewitt JE, Cummings VJ (1991) Impact of ray feeding disturbances on sandflat macrobenthos: do communities dominated by polychaetes or shellfish respond differently. Marine Ecology Progress Series 69: 245-252

Thrush SF, Pridmore RD, Hewitt JE, Cummings VJ (1992) Adult infauna as facilitators of colonisation on intertidal sandflats. Journal of Experimental Marine Biology and Ecology 159: 253-265

Thrush SF, Whitlach RB, Pridmore RD, Hewitt JE, Cummings VJ (1996) Scale-dependent recolonisation: the role of sediment stability in a dynamic sandflat habitat. Ecology 77: 2472-2487

Thurston MH, Bett BJ, Rice AL, Jackson PAB (1994) Variations in the invertebrate abyssal megafauna in the North Atlantic Ocean. Deep-Sea Research 41: 1321-1348

Thurston MH, Rice AL, Bett BJ (1998) Latitudinal variation in invertebrate megafaunal abundance and biomass in the North Atlantic Ocean Abyss. Deep-Sea Research 45: 203-224

Tipper JC (1979) Rarefaction and rarefiction - the use and abuse of a method in paleoecology. Paleobiology 5: 423-434

TOTAL E & P UK Plc (2004) Laggan appraisal well 206/1a-ABC1 Environmental Statement. Statement prepared by TOTAL E & P UK Ltd and AURORA Environmental Ltd

Toudal L (1999) Ice extent in the Greenland Sea 1978-1995. Deep-Sea Research 46: 1237-1254

Tuck I, Hall SJ, Robertson M, Armstrong E, Basford D (1998) Effects of physical trawling disturbance in a previously unfished sheltered Scottish sea loch. Marine Ecology Progress Series 162: 227-242

Turnewitsch R, Witte U, Graf G (2000) Bioturbation in the abyssal Arabian Sea: influence of fauna and food supply. Deep-Sea Research 47: 2877-2911

Turrell WR, Slesser G, Adams RD, Payne R, Gillibrand PA (1999) Decadal variability in the composition of Faroe Shetland Channel bottom water. Deep-Sea Research Part I: Oceanographic Research Papers 46: 1-25

Tweddle JF, Simpson JH, Janzen CD (2005) Physical controls of food supply to benthic filter feeders in the Menai Strait, UK. Marine Ecology Progress Series 289: 79–88

Tyler PA (1980) Deep-sea ophiuroids. Oceanography and Marine Biology: An Annual Review 153

Tyler PA (1995) Conditions for the existence of life at the deep sea floor: An update. Oceanography and Marine Biology: An Annual Review 33: 221-244

Tyler PA, Emson RH, Sumida PYG, Howell KL (2005) Ophiuroid distribution at sublittoral and bathyal depths round the Faroe Islands, NE Atlantic Ocean. Annales Societatis Scientiarum Faroensis Supplementum XXXXI. BIOFAR Proceedings 2005, BIOFAR symposium, Torshavn 4-26 April 2003: 175-194

Tyler PA, Zibrowius H (1992) Submersible Observations of the Invertebrate Fauna on the Continental-Slope Southwest of Ireland (Ne Atlantic-Ocean). Oceanologica Acta 15: 211-226

Underwood AJ (1994) On Beyond BACI - Sampling Designs That Might Reliably Detect Environmental Disturbances. Ecological Applications 4: 3-15

Underwood AJ, Chapman MG (1996) Scales of spatial patterns of distribution of intertidal invertebrates. Oecologia 107: 212-224

Underwood AJ, Chapman MG (1998a) A method for analysing spatial scales of variation in composition of assemblages. Oecologia 117: 570-578

Underwood AJ, Chapman MG (1998b) Spatial analyses of intertidal assemblages on sheltered rocky shores. Australian Journal of Ecology 23: 138-157

Urban DL, O'Neill RV, Shugart HH (1987) Landscape ecology. Bioscience 37: 119-127

Vale FK, Rex MA (1988) Repaired shell damage in deep-sea prosobranch gastropods from the western North Atlantic. Malacologia 28: 65-79

Van Dover CL (2000) The ecology of deep-sea hydrothermal vents. Princeton University Press, Princeton N. J.

Vetter EW, Dayton PK (1998) Macrofaunal communities within and adjacent to a detritus-rich submarine canyon system. Deep-Sea Research 45: 25-54

Vevers HG (1951) Photography of the sea floor. Journal of the Marine Biological Association of the United Kingdom 30: 101-111

Vinogradova NG (1997) Zoogeography of the Abyssal and Hadal Zones. Advances in Marine Biology 32: 325-388

Voss J (1988) Zoogeography and community analysis of macrozoobenthos of the Weddell Sea (Antarctica). Berichte zur Polarforschung 45: 1-145

Waide RB, Willig MR, Steiner CF, Mittelbach G, Gough L (1999) The relationship between productivity and species richness. Annual Review of Ecology and Systematics 30: 257-300

Wakefield WW, Genin A (1987) The use of a Canadian (perspective) grid in deep-sea photography. Deep-Sea Research 34: 469-478

Wakefield WW, Smithey W (1989) Two camera sleds for quantitative study of deep-sea megafauna. Vol. 89-14, Scripps Institution of Oceanography Refereence Series

Walker M, Tyler PA, Billett DSM (1987) Organic and calorific content of the body tissues of deep sea elasipodid holothurians in the northeast Atlantic Ocean. Marine Biology 96: 277-282

Warwick RM (1984) Species size distributions in marine benthic communities. Oecologia 61: 32-41

Warwick RM, Clarke KR (1993) Increased variability as a symptom of stress in marine communities. Journal of Experimental Marine Biology and Ecology 172: 215-226

Wassmann P (1991) Dynamics of primary production and sedimentation in shallow fjords and polls of Western Norway. Oceanography and Marine Biology: An Annual Review 29: 87-154

Weaver PP, Wynn RB, Kenyon HN, Evans J (2000) Continental margin sedimentation, with special reference to the north-east Atlantic margin. Sedimentology 47: 239-256

Wentworth CK (1922) A scale of grade and class terms for clastic sediments. Journal of Geology 30: 377-392

Wheatcroft RA, Jumars PA (1987) Statistical re-analysis for size dependency in deep-sea mixing. Marine Geology 77: 157-163

Wheatcroft RA, Smith CR, Jumars PA (1989) Dynamics of surficial trace assemblages in the deep sea. Deep-Sea Research 36: 71-91

White MG (1984) Marine benthos. In: Laws RM (ed) Antarctic Ecology. Academic Press, London, pp 421-463

Whittaker RH (1960) Vegetation of the Siskiyou Mountains, Oregon and California. Ecological Monographs 30: 279-338

Whittaker RH (1977) Evolution of species diversity in land communities. In: Hecht MK, Steere WC, Wallace B (eds) Evolutionary Biology. Plenum, New York, pp 1-67

Widdicombe S, Austen MC (1998) Experimental evidence for the role of *Brissopsis lyrifera* (Forbes, 1841) as a critical species in the maintenance of benthic diversity and the modification of sediment chemistry. Journal of Experimental Marine Biology and Ecology 228: 241-255

Wiens JA, Stenseth NC, Vanhorne B, Ims RA (1993) Ecological Mechanisms and Landscape Ecology. Oikos 66: 369-380

Wildish D, Kristmanson D (1997) Benthic suspension feeders and flow. Cambridge University Press, Cambridge

Wilsey BJ, Potvin C (2000) Biodiversity and ecosystem functioning: importance of species evenness in an old field. Ecology 81: 887-892

Wilson MV, Mohler CL (1983) Measuring compositional change along gradients. Vegetatio 54: 129-141

Winston JE (1992) Systematics and marine conservation. In: Eldredge N (ed) Systematics, ecology, and the biodiversity crisis. Columbia University Press, New York, pp 114-168

Witte U (1999) Consumption of large carcasses by scavenger assemblages in the deep Arabian Sea: observations by baited camera. Marine Ecology Progress Series 183: 139-147

Wlodarska-Kowalczuk M, Pearson TH, Kendall MA (2005) Benthic response to chronic natural physical disturbance by glacial sedimentation in an Arctic fiord. Marine Ecology Progress Series 303: 31-41

Wolf PR (1983) Elements of Photogrammetry. McGraw-Hill, New York

Yoerger DR, Bradley AM, Walden BB (1992) Autonomous benthic explorer. Sea Technology 33: 50-54

Zachos J, Pagani M, Sloan L, Thomas E, Billups K (2001) Trends, rhythms, and aberrations in global climate 65 Ma to Present. Science 292: 686-693

Zar J (1999) Biostatistical analysis. Prentice-Hall, Upper Saddle River, New Jersey

Zwally HJ, Comiso JC, Gordon AL (1985) Antarctic offshore leads and polynyas and oceanographic effects. In: Jacobs SS (ed) Oceanology of the Antarctic continental shelf. American Geophysical Union Antarctic Research Series; 43, Washington, DC, pp 203-226

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Deep water observations of *Lophius piscatorius* in the north-eastern Atlantic Ocean by means of a remotely operated vehicle

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In situ behaviour of anglerfish *Lophius piscatorius* was observed by a remotely operated vehicle (ROV) in the vicinity of the Schiehallion oil field to the west of the Shetland Isles, Scotland at water depths *c.* 350 m. Several behaviour patterns associated with the 'sit-and-wait' feeding strategy of *L. piscatorius* were identified and are described. Concealment behaviour was characterized by recess creation using pectoral and pelvic fins. Sit-and-wait and resting behaviour was typified by relaxed dorsal fin rays and a 34 s exhalation rate. Prey detection responses had a range of *c.* 5 m and were identified by erection of the fin rays and a reduction in the exhalation rate to once every 65 s. Prey attraction was characterized by lure (illicia) casting, erect dorsal rays and was dependant on both the proximity and position of potential prey. An opportunistic feeding attack is also described. Walking behaviour was also recorded and is described.

Key words: anglerfish; feeding; *in situ* behaviour; *Lophius*; monkfish; remotely operated vehicle.

INTRODUCTION

Two species of the genus *Lophius* occur in the north-eastern Atlantic: *Lophius piscatorius* L. (anglerfish also known as monkfish) and *Lophius budegassa* (Spinola) (black-bellied anglerfish). Both occur from the Mediterranean and northwards to waters around Britain (Caruso, 1989). *Lophius piscatorius* dominates in waters around Britain and its range extends to waters around Norway, Faroe and Iceland. It occurs from the shoreline to a depth of at least 1000 m (Afonso-Dias & Hislop, 1996). The Lophiidae are distinctive in appearance, with their depressed body form and wide mouth. Teeth are slender and recurved (Caruso, 1989) and a fleshy flap (esca) on the distal end of the first dorsal fin ray (illicium), situated on the snout, is used to lure prey towards the mouth (Field, 1966).

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In waters around Britain, the biology of *L. piscatorius* is less well understood than that of the more traditionally exploited species. Recent publications have concentrated on the reproduction and early life history of the species (Afonso-Dias & Hislop, 1996; Afonso-Dias, 1997; Hislop *et al.*, 2000, 2001; Wright *et al.*, 2002). It has been found that, in general, juvenile fish are distributed inshore and move offshore into deeper water as they grow (Laurenson, 2003). Females have been found to mature at a greater size than males. Total length at maturity ($L_{T50\%}$) values for Scottish waters varies between 73 and 98 cm for females and 48 and 58 cm for males (Afonso-Dias & Hislop, 1996; Laurenson, 2003; J.D.M. Gordon, pers. comm.). Large sexually mature females appear to be rare, with few being caught in fishery surveys, but they are presumed to live in deep water.

Dietary analyses have found *L. piscatorius* to be mainly ichthyophagous (Smith, 1891; Fulton, 1903), but Crozier (1985) reported that *Nephrops norvegicus* (L.) could form an important part of its diet. Although the mode of life of *L. piscatorius* has been described as well known (Field, 1966), this appears to be based on inferences made from their morphology, or from tank based observation studies, such as those by Chadwick (1929), when feeding behaviour was described. The behaviour of *L. piscatorius* is described as the individual lying on the sea bed patiently flicking the lure to attract prey to the mouth (Field, 1966). To date there is, however, no published information on the *in situ* feeding behaviour of *L. piscatorius*.

Obtaining good quality *in situ* recordings of fish behaviour, particularly in deep waters, is both difficult and expensive. Remotely operated vehicles (ROV) are routinely deployed for oilrig maintenance and inspection work. Collaboration between ROV operators and scientists and recent technological developments in the cameras that can be used, has made it possible to obtain good quality recordings of marine life in the vicinity of oilrigs. The ROVs used are ideally suited as they provide a non-invasive means of obtaining detailed *in situ* observations in the location of deployment. During such recording deployments success depends on the ROV pilots happening on an organism that is of interest when a specific behaviour is being performed. Such opportunities can, however, be infrequent.

In this paper *in situ* observations of specific behaviour patterns of anglerfish are reported for the first time. From these observations, the authors suggest that the behaviour patterns and mode of life of *L. piscatorius* are more complex than the generally held preconception that an individual merely rests on the sea bed 'flicking' the lure to attract prey.

MATERIALS AND METHODS

Centurion HD work-class ROVs equipped with a full pan tilt zoom video camera system and a 3·3 mega pixel digital stills camera were deployed from the MSV Regalia operated by SUBSEA 7 and BP. Video sequences were recorded at the Schiehallion and Foinaven oil fields west of Shetland during July 2002. Water depth at the site (60°06′ N; 04°04′ W) was 380 m. Sediment in the area was mainly sand, *c.* 60 µm. Video recordings were obtained in the SVHS format *via* live video feed. Analysis from SVHS was completed using Final Cut Pro and Quicktime 5. Sequences to be analysed were captured and split into frame-by-frame format (two frames s^{-1} and 25 frames s^{-1}). Images were formatted from colour into 16-bit greyscale in TIFF format. Images were edited using Paint Shop Pro v7.04. Video footage was recorded as part of the BP-SOC ROV Collaboration Scheme.

ESTIMATION OF FISH LENGTHS

Where possible, L_T of individual fish: anglerfish, cod *Gadus morhua* L., ling *Molva molva* (L.) and redfish *Sebastes* spp. were estimated in relation to structures of known dimensions. From sequences of feeding behaviour by cod next to a pipe marked with bands of known width, the lengths of three dominant size classes were identified. Lengths of anglerfish could also be estimated in relation to these three dominant size classes of cod.

FOOTAGE OF ANGLERFISH

Video footage of five anglerfish, that was >2 h in duration was analysed. Details are given in Table I.

RESULTS

The most abundant fish species observed were cod, ling and redfish. Three main size classes of cod were identified in the area. These were estimated to be *c*. 45, 60 and 90 cm, with those *c*. 60 cm dominating. Lengths of ling ranged from an estimated 50 to 110 cm. All the redfish were estimated to be between 30 and 40 cm. Additionally, dense swarms of unidentified crustaceans were observed in association with some of the structures. From the video recording, one or more types of behaviour were identified from each of five individual anglerfish. In total, five distinct behaviour patterns were identified and are described. Anglerfish L_T were estimated to be 50–60 cm (one fish), *c*. 60 cm (three fish) and >100 cm (one fish).

RESTING AND SIT-AND-WAIT BEHAVIOUR

Resting and sit-and-wait behaviour was typified by an individual lying motionless and often recessed into the sediment. Individuals appeared to be

TABLE I. Summary of the video footage obtained of five anglerfish and the displayed behaviours that were analysed

Fish	Estimated L_T (cm)	Date and start time of recording (hours)		Duration of recording (min)	Behaviour analysed
1	>100	23/07/02	0910	75	Concealment, cough response, resting exhalation rates, prey detection and attraction
2	50–60	24/07/02	1433	17	Walking, resting exhalation rates
3	60	24/07/02	1451	28	Sediment scooping, attack
4	60	24/07/02	1544	5	Resting exhalation rates
5	60	25/07/02	2239	7	Attack

well camouflaged, with dorsal fin rays held flat to the body, pectoral fins extended and touching the sea bed and the caudal fin often lying to one side. The only visible movement was the periodic exhalation of water through the gill opening behind the pectoral fins. During exhalation the skin that covers the gill opening formed a funnel with a circular or oval opening, through which a current of exhaled water was passed. From a rear view and during exhalations the white of the inside and underside of the gill opening could be seen. Between exhalations the gill opening closed. Periods between each exhalation were recorded from three resting individuals (Fish 1, 2 and 4; see Table I). The mean ± S.D. period between exhalations and numbers of observations were as follows: Fish 1, $34 \pm 1{\cdot}65$ s, $n = 37$; Fish 2, $34 \pm 1{\cdot}14$ s, $n = 15$ and Fish 4, $34 \pm 1{\cdot}65$ s, $n = 8$.

CONCEALMENT BEHAVIOUR

Two of the anglerfish were observed to use digging, scraping and scooping actions to create recesses in the seafloor. Both Fish 1 and 3 were observed to use the pectoral fins to scoop sediment out from underneath their bodies. An example of the digging, scraping and scooping behaviours exhibited by Fish 1 was sequenced frame by frame and is illustrated in Fig. 1 where simultaneous scooping of sediment using the pectoral fins and scraping of sediment using the anal fin and undulations of the tail are shown.

During the behaviour sequence in which sediment was moved from underneath the body, Fish 1 had first employed a digging behaviour using the pelvic fins. This appeared to loosen and 'fluidise' the sediment. The pectoral fins were then used to scoop the loosened sediment from underneath the body. This behaviour was alternated between each pectoral fin. It involved each pectoral fin in turn being used to reach backwards and underneath the body. The fin was then formed into an arc with the posterior edge (furthest underneath the fish) being pushed into the loosened sediment. Bringing the fin (still in its arc shape) away from under the body completed the scooping action.

Fish 1 was also observed to undertake several episodes of scraping behaviour using the anal fin. This scraping behaviour was characterized by the tail being lifted slightly above the sediment. The outer margin of the anal fin was then pushed into the sediment. The lateral undulations of the tail that followed resulted in the anal fin scraping then flicking sediment to either side of the tail. During the process substantial sediment clouds were visible on either side of the tail. The scraping behaviour had the effect of creating a recess in which the tail would lie and was observed to occur both simultaneously to, and following, bouts of scooping behaviour.

Fish 1 used a considerable amount of effort to conceal itself. When it later moved from its recess, the recess was distinct on the sea bed. As it swam from the recess it lifted itself from the sea bed by *c.* 10–20 cm. At this time it was noted that the abdomen of this fish was visibly distended. The distended abdomen had effectively been concealed when the individual had been laying in the recess that it had created. Fish 3 was also observed to use a scooping behaviour to move sediment from under its body. The recording was, however, over a shorter time period and that individual was in the early stages of recess creation.

FIG. 1. An anglerfish (Fish 1), scooping sediment using the left pectoral fin and scraping sediment using the anal fin with the right pectoral fin pushed into sediment. (a) Left pectoral fin underneath body and pushed into sediment, tail stationary with anal fin pushing into sediment, sediment cloud emerging from left side of fish (0 s). (b) Left pectoral fin is formed into arc and emerges from under the body; the tail is lifted to the right clear of the sediment (1·5 s). (c) Left pectoral fin emerges further as tail is moved further to the right and the anal fin is pushed into the sediment (3 s). (d) Left pectoral fin is lifted up and out, still in arc shape; tail twists then pushes sediment to the left creating a sediment cloud (7 s). (e) Anal fin flicks sediment then is lifted from the sediment as the left pectoral fin starts to reach under the body (10·5 s). (f) Left pectoral fin reaches further under the body and down into the sediment as the tail is brought to the right (12 s).

After digging, scooping and scraping, or during a prolonged bout of this activity, Fish 1 was observed to exhibit ‘cough responses’, presumably to clear the gills of any disturbed sediment. The ‘cough response’ was characterized by a change from the resting exhalation rate, the head was lifted and the mouth partially opened to take in water, the mouth was then closed and the expanded buccal cavity contracted. A plume of water was forcibly exhaled through the gill opening; on several occasions the plume appeared to be cloudy with sediment. Sequences of two to three cough responses usually occurred in succession, mean ± S.D. time between coughs was 14 ± 4 s ($n = 10$) and each cough sequence was 6–20 s in duration.

When the anglerfish had settled after a period of digging and scraping, cod often approached, on occasion to within several centimetres of the tail. It appeared that the sediment disturbance caused by the anglerfish attracted the cod that were searching for invertebrate prey items in the benthos.

PREY DETECTION AND ATTRACTION RESPONSES

When potential prey, for example cod, approached to within a range of *c.* 5 m a 'prey detection' response was frequently initiated. This was characterized by an alteration of the exhalation rate and erection of the dorsal fin rays. The exhalation rate halved from the resting rate to once every 65 s (16 observations averaged over three fish). During prey detection the 4th–6th cephalic dorsal rays were raised to an angle of *c.* 45° and if the potential prey approached to within *c.* 2–3 m these rays would generally become erect (*c.* 90° to the body). If a potential prey was within a range of *c.* 1–2 m and was in front of, or above the anglerfish, then the eyes could on occasion be observed to move, apparently tracking the potential prey.

During the 'prey attraction' response lure casting was always associated with the rays being erect. Raising and casting the lure forwards took *c.* 1 s. From being in the forward position, to returning to the lowered position took 1–2 s. Casting was only observed when potential prey were within close proximity and occurred in bouts of one to three casts. If the potential prey was not in a position suitable for a successful attack, for example behind the anglerfish, then lure casting was usually not initiated.

ATTACK BEHAVIOUR

Two instances of attack behaviour were observed. One was an attack where no obvious potential prey was present (Fish 3), although there were krill and other crustaceans in the area that may have initiated the response. This attack served to illustrate the speed of the action, which was <1 s in duration. The sequence was separated frame by frame at 25 frames per second and is illustrated in Fig. 2.

The other attack resulted in the capture of a cod and illustrated the opportunistic nature of the anglerfish as the attack occurred without prior attraction behaviour being displayed. The anglerfish (Fish 5) was lying beside a piece of equipment, the sediment in front of it had been disturbed and there was activity by disturbed invertebrates. As the anglerfish had not raised or flicked the lure in an attempt to attract the cod it is assumed that the cod was attracted by the activity of the invertebrates. The cod was estimated to be 50 cm L_T. As the cod approached, the eyes of the anglerfish moved and appeared to focus on the cod prior to the strike. During the strike it appeared that the pelvic fins were used to propel the anglerfish upwards and forwards. The initial strike is illustrated in

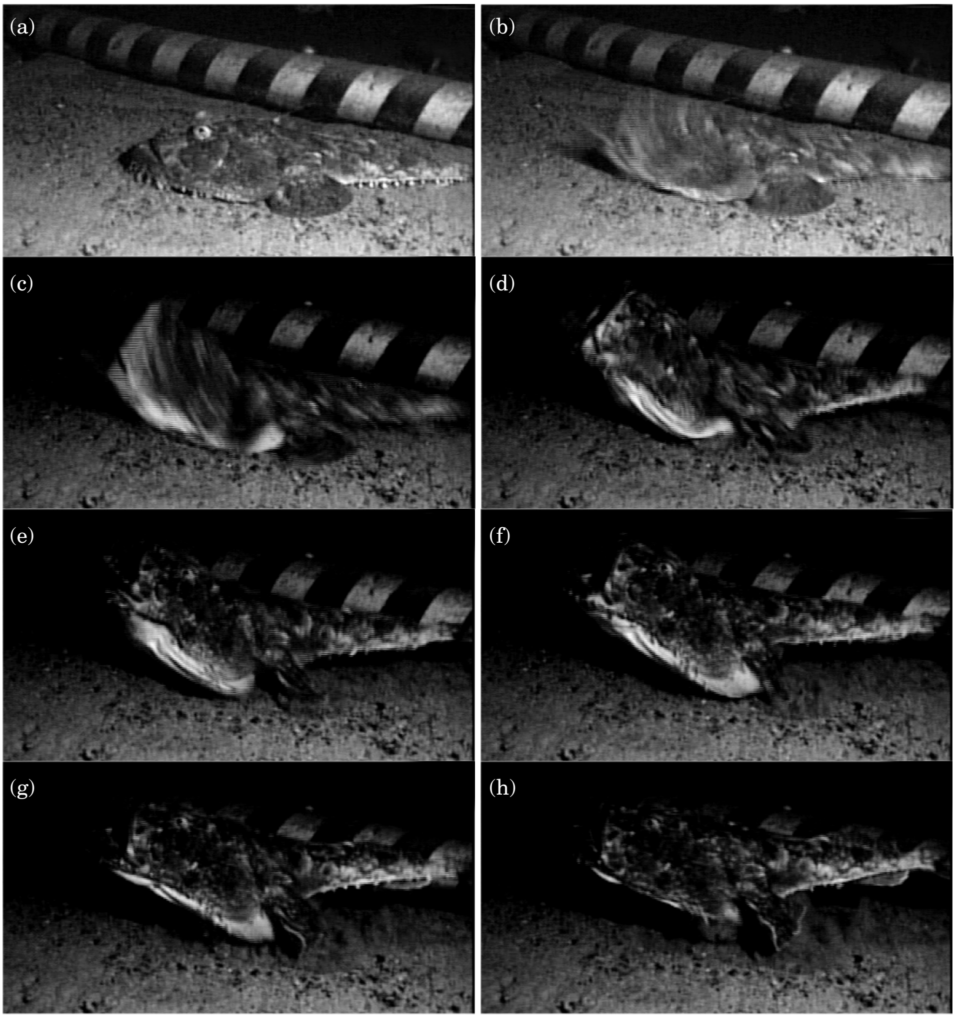

FIG. 2. Frames illustrating the 'fake attack' by an anglerfish (Fish 3); (for scale each band on the pipe was 7·5 cm). (a) Fish lying flat on sea bed, dorsal rays at 45° (0·00 s). (b) The mouth and anterior part of the head starts to move upwards, anterior part of pectoral fin angled down (0·16 s). (c) Head lifted higher as mouth opens (0·20 s). (d) Head at highest position and mouth with widest gape; posterior part of tail lifting (0·28 s). (e) Mouth closing, buccal cavity expanded; tail lifted and pectoral fin lifting (0·36 s). (f) Body lifted from sea bed, buccal cavity retracting as brachial cavity expands (0·48 s). (g) Body straightening, mouth closing (0·60 s). (h) Mouth almost to closed position, water being exhaled, fish still above sea bed (0·72 s).

Fig. 3. As the strike was initiated, the cod started an escape response. This resulted in the anglerfish catching the cod by gripping it across the left side and over the back. The anglerfish held onto the cod for 3 min 17 s before it was released. During this period the cod initially appeared to be stunned holding its body in a rigid posture. The anglerfish made several attempts to reposition or get a better grip on the cod by altering its bite. The cod was eventually released after it started 'thrashing around' as is illustrated in Fig. 4.

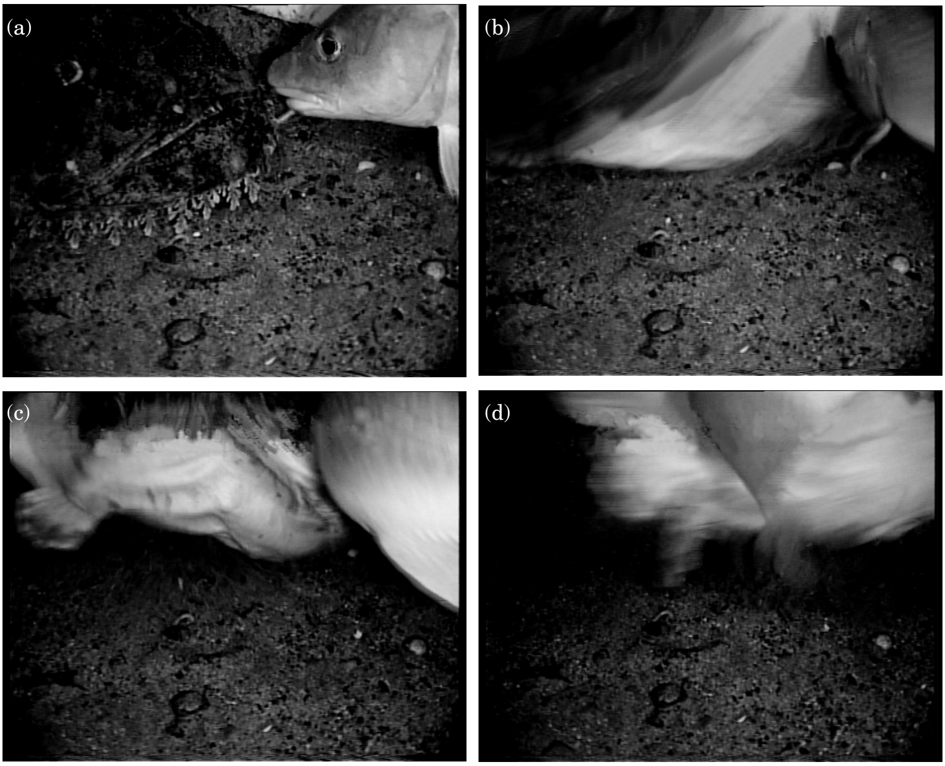

FIG. 3. Frames showing strike sequence by an anglerfish (Fish 5) on a prey cod. (a) Anglerfish poised to attack (0·00 s). (b) As the anglerfish moves forwards and upwards, the cod initiates an escape response (0·24 s). (c) After propelling the anglerfish forwards and upwards the pelvic fins lift off the sea bed, the buccal cavity is expanded and the anglerfish bites the cod (0·40 s). (d) The anglerfish lifts from the sea bed, turning to the left (0·64 s).

WALKING BEHAVIOUR

Fish 2 was observed to undertake several episodes of walking behaviour. During each episode both the pelvic and pectoral fins were involved. To illustrate the sequence of movement along one side of the body, one of the episodes was sequenced frame by frame and is shown in Fig. 5. It appeared that the pelvic fins were used to lift the body up from the sea bed and those were the main weight bearing fins. The tail was slightly raised from the sea bed and although it was moved back and forth the impression was given that the main propulsion was due to a combination of the pelvic and pectoral fins.

The gait observed was such that as the right pelvic fin bore the weight of the fish and was in a forward position, the right pectoral fin was angled backwards. The left pectoral was also observed to be in the forward position at this time. The left pelvic fin was obscured, but from the movement of the fish and from the obvious weight bearing role of the right pelvic fin it is believed that the left pelvic fin was in the backwards position. As the fish moved forward over the right pelvic fin it also moved forwards in relation to the position of the left pectoral fin. This resulted in both fins being in the backwards position. As this

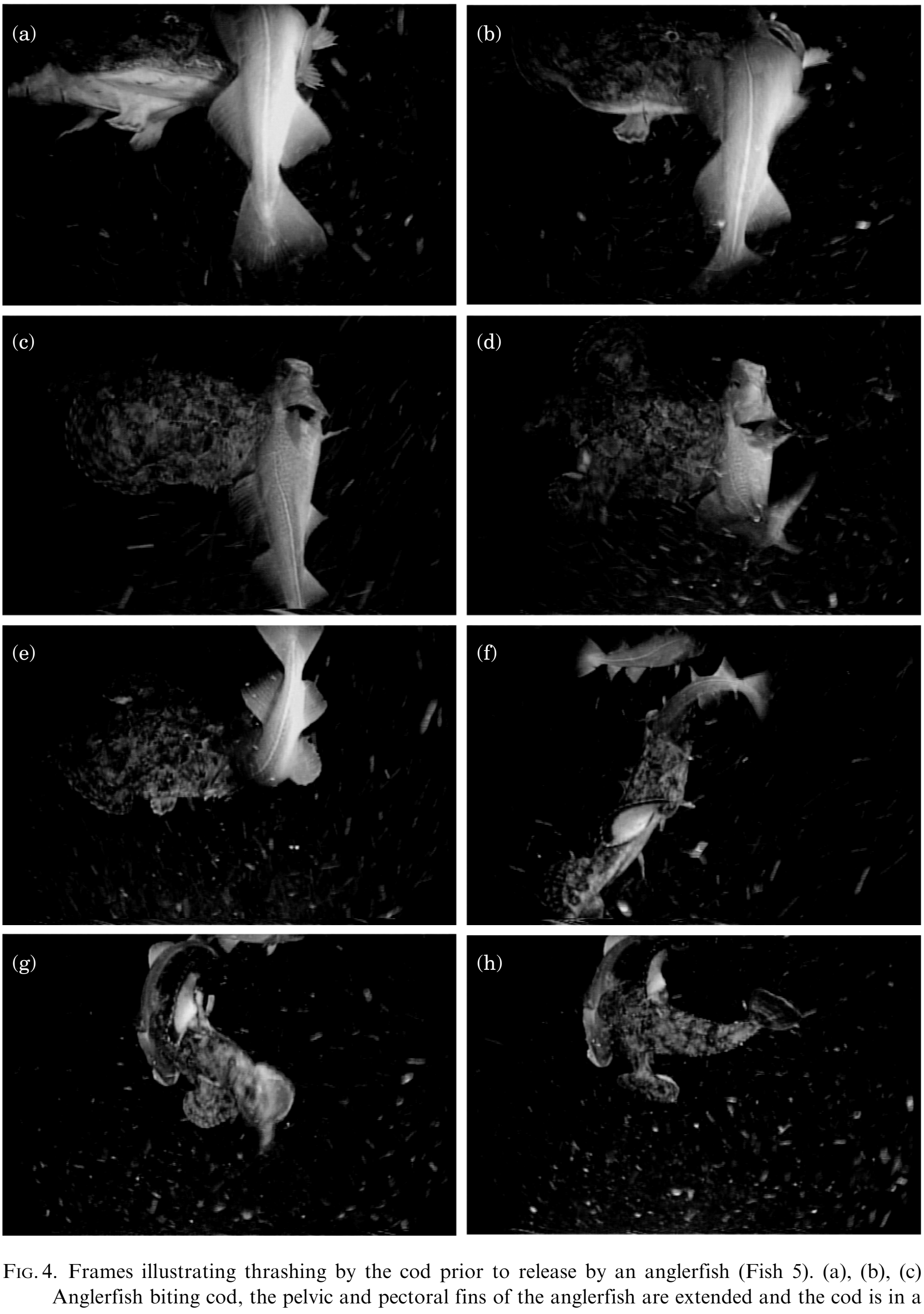

FIG. 4. Frames illustrating thrashing by the cod prior to release by an anglerfish (Fish 5). (a), (b), (c) Anglerfish biting cod, the pelvic and pectoral fins of the anglerfish are extended and the cod is in a rigid posture with opercula open (0, 1·5 and 5 s). (d) The cod starts thrashing, the tail is brought to the right and this starts to twist the body of the anglerfish in a clockwise rotation (2·5 s). (e) The movement of the anglerfish tail and pectoral fins appears to reverse the rotation; the cod is twisted further up as the anglerfish rights itself (5 s). (f) The cod bends towards the left, as this happens the anglerfish becomes more vertical and its tail twists to the left (l0 s). (g) The anglerfish twists around so that the cod is facing downward (11·5 s). (h) The anglerfish starts to right itself (12·5 s).

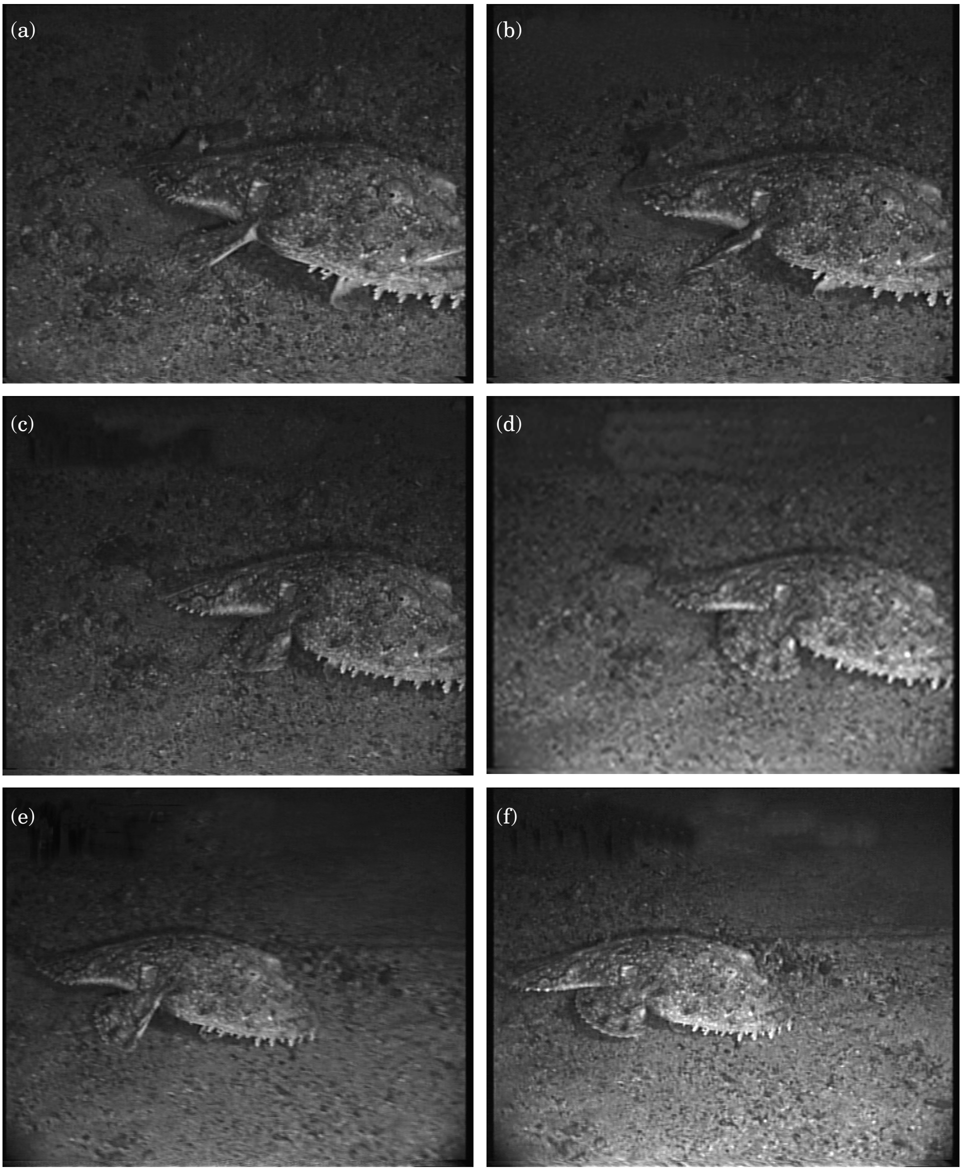

FIG. 5. Sequence illustrating an anglerfish (Fish 2) walking across the sea bed using the pectoral and pelvic fins. (a) Right pelvic fin forward, bearing weight, right pectoral fin backward position (0·0 s). (b) Moving over right pelvic fin, right pectoral fin further back, anterior edge starting to lift (0·5 s). (c) Right pelvic fin backwards; right pectoral fin being brought forward (1·0 s). (d) Right pectoral fin forwards; right pelvic fin not visible (1·5 s). (e) Right pelvic fin returned to forward position, right pectoral fin moving backwards (2·0 s). (f) Moving over right pelvic fin, right pectoral fin further back and lifting from sea bed (2·5 s).

occurred, the right pectoral fin was brought forward. As the fish continued to move forward it appeared that the right pectoral fin bore some of the weight of the fish. As the forwards movement continued it resulted in the right pectoral fin returning to the backwards position and at this time the right pelvic fin was observed to have returned to the forward position. From the spread of the pectoral fins it appeared that they provided stability during the walking behaviour.

DISCUSSION

For a sit-and-wait feeding strategy to be effective it seems logical that an individual would benefit from increasing the effectiveness of its camouflage. It appears that the creation of a recess assists in the concealment of individuals, in particular, individuals with a distended abdomen, due to either a large meal or due to the presence of ripe gonads. This is because the recess allows the dorsal surface of the fish to be more level with the sea bed. From the video recording obtained, it is evident that a significant investment can be made in recess creation. The use of the pelvic fins as a digging tool to loosen sediment explains their morphology. The pelvic fins are well developed in that they are thick, fleshy and stout and the skin appears more robust than skin elsewhere on the body. Similarly the well developed fan-like pectoral fins allows them to reach underneath the body and their flexibility enables the arc shape to be formed and this plays a key role in scooping the loosened sediment out from underneath the body.

During recess creation substantial amounts of sediment were disturbed. After bouts of sediment excavation cough responses were usually initiated. These were presumed to have the effect of clearing the gills of sediment. Similar coughing responses have previously been observed after periods of burrow excavation by the snake blenny *Lumpenus lampretaeformis* (Walbaum) (Atkinson *et al*., 1987). Once the anglerfish had settled into a resting behaviour, after a period of sediment excavation, potential bottom feeding prey such as cod were observed to approach and investigate the newly disturbed sediment. Cod attracted in this manner appeared unaware of, or unperturbed by, the presence of the anglerfish.

The prey detection responses by the anglerfish were clearly initiated by the approach, from any direction, of potential prey. The distance at which a response was triggered was estimated to be *c*. 5 m. The halving of the exhalation rate would assist in continuing the concealment. The purpose of the 3rd–6th rays being raised to an angle of *c*. 45° and then becoming erect upon a closer approach by potential prey may be part of the prey attraction behaviour. Equally, the erection of the rays could be important in the detection of vibrations in the water caused by the swimming motion of the potential prey. The neuromasts that all fishes have over their body surface, and in the lateral lines of teleosts and elasmobranchs, are mechano-receptors that detect water movements (Moyle & Cech, 2000). The swimming motion of fishes creates hydrodynamic trails and recently it has been shown that fishes are capable of tracking other fishes on this basis (Montgomery *et al*., 2002). The halving of the exhalation rate at this time would reduce any water movements created by the anglerfish and this may increase the sensitivity of the anglerfish to movements produced by potential prey. In anthropomorphic terms, it appears analogous to holding one's breath and listening intently.

In the observed cases, lure casting was used economically. No more than three individual casts were observed to occur in succession and casting appeared to occur only when a potential prey fish was towards the front of the anglerfish, *i.e.* close to striking distance. On the occasions when cod were investigating sediment, just centimetres from the anglerfish tail, casting was not initiated although the other dorsal rays were erect. If a strategy of sustained lure casting was undertaken it could result in the mechanism becoming less effective, for example through loss of concealment or by habituation of the potential prey.

The attack on the cod that was recorded confirms that anglerfish can be opportunistic in nature. Studies on the diet of anglerfish have shown that they are unselective and that stomach contents largely reflect prey availability (Crozier, 1985; Laurenson, 2003). In waters off Shetland gadoids can form an important part of the diet (seasonally up to 80% by mass) with cod representing 40%, although this may be reduced during the summer (Laurenson, 2003). The opportunistic attack also demonstrated that anglerfish may attempt to take prey items that are quite large in relation to their own body size. Diet studies have also noted that anglerfish can consume large meals, of one or more prey items, to the point where the stomach walls are thin and stretched, and the abdomen visibly distended (Laurenson, 2003).

Incidences of net feeding, the opportunistic feeding during capture by trawl, was recently found to occur in up to 15% of individuals captured during demersal trawling around Shetland (Laurenson, 2003). During that study, cod up to two-thirds L_T of an individual anglerfish were recorded as having been taken in this manner (C.H. Laurenson, unpubl. data). The L_T of the cod involved in the opportunistic attack recorded in this study was somewhat larger (50 cm) in relation to the attacking anglerfish (60 cm). Although the attack that was recorded was not successful, it does serve to highlight that the species will attempt to take prey items almost as large as themselves. The largest anglerfish observed in this study would certainly have been capable of preying on the dominant size class of cod, estimated to be *c.* 60 cm L_T. The remaining anglerfish, themselves at *c.* 60 cm L_T, may have been more limited to the smallest of the cod and ling observed, and possibly the redfish (all estimated as 30–40 cm L_T).

The other main behaviour described was the walking behaviour. This behaviour has not previously been reported in *Lophius* species. The gait observed for *L. piscatorius* involved a combination of movements using both the pelvic and pectoral fins. The pelvic fins, which, as previously discussed, are quite well developed and stout in appearance, appeared to be the primary weight bearing fins during walking and provides another explanation as to the functional role in relation to the morphology of these fins. The pectoral fins, which when extended appeared to act as wings, were more important for stability during walking. The gait recorded is different to that described by Pietsch & Grobecker (1990) for frogfishes *Antennarius* spp. when two different gaits were reported. The first was described as 'crutching', when the pelvic and pectoral fin pairs alternate in bearing weight. The second gait was described as 'walking' and was characterized by use of only the pectoral fins.

The walking behaviour appeared to be adopted for moving short distances, *i.e.* several metres at a time, across the sea bed. The function of walking, as opposed to swimming, was not clear but it may be related to the selection of particular sediment characteristics, which it would presumably determine from contact by the pelvic fins. The use of walking to allow the stalking of potential prey was not recorded but the distances walked did, on occasion, appear to bring the anglerfish into areas where potential prey were more densely congregated.

Catch rates of anglerfish in the region are typically lower than those for species such as cod or haddock *Melanogrammus aeglefinus* (L.) (C.H. Laurenson, unpubl. data). During this study it was not possible to determine whether densities of the fish species were higher in the immediate vicinity of the underwater structures compared to the surrounding area. The numbers of fish, and the feeding activity that was observed as a result of sediment disturbance, however, have led to the believe that the observed fish were aggregated around the structures, at least on a temporary basis when work causing minor sediment disturbance was being undertaken. Previous studies have also found significant aggregations of fishes close to oil platforms (Caselle *et al.*, 2002; Løkkeborg *et al.*, 2002; Soldal *et al.*, 2002). Common reasons for fishes aggregating at artificial reefs such as oil platforms include an improved food supply, shelter from currents and possibly reduced risk of predation. In the current study it would appear that the presence of the observed fishes could be related to food supply. In addition, due to the 500 m fisheries exclusion zones around platforms in U.K. waters the platforms may act, on a small scale, as refuges or protected areas allowing aggregations of fishes to form.

The video footage analysed in this paper serves to highlight the potential wealth of *in situ* behavioural information that could be generated through the use of ROVs, particularly through collaborative projects where ROVs are already routinely deployed. This is of particular importance for commercially exploited species such as anglerfish where relatively little is known of their biology. From footage of just >2 h duration *in situ* feeding behaviour and the associated behaviours of recess creation, prey detection and attraction responses exhibited by anglerfish have been described for the first time. Walking behaviour has also been described for the first time and the functional morphology of the pectoral and pelvic fins has been related to the behaviours described. The behaviours described for *L. piscatorius* in this paper indicate that the investment in concealment behaviour by a sit-and-wait strategist can be substantial.

We wish to thank the ROV pilots, offshore supervisors and onshore staff of Subsea 7 for their support, expertise and enthusiasm, without which this footage would not have been taken, and to BP for their continued efforts in ROV collaboration projects. We also wish to thank S. Marrs for comments on early versions of this manuscript.

References

Afonso-Dias, I. (1997). Aspects of the biology and ecology of anglerfish (*Lophius piscatorius*, L.) off the west-coast of Scotland (I.C.E.S. Sub-area VIa). PhD Thesis, University of Aberdeen.

Afonso-Dias, I. & Hislop, J. R. G. (1996). The reproduction of anglerfish *Lophius piscatorius* Linnaeus from the north-west coast of Scotland. *Journal of Fish Biology* **49,** 18–39.

Atkinson, R. J. A., Pelster, B., Bridges, C. R., Taylor, A. C. & Morris, S. (1987). Behavioural and physiological adaptations to a burrowing lifestyle in the snake blenny, *Lumpenus lampretaeformis*, and the red band-fish, *Cepola rubescens*. *Journal of Fish Biology* **31,** 639–659.

Caruso, J. H. (1989). Lophiidae. In *Fishes of the North-eastern Atlantic and the Mediterranean* (Whitehead, P. J. P., Bauchot, J.-C., Nielsen, J. & Tortonese, E., eds), pp. 1362–1363. Paris: UNESCO.

Caselle, J. E., Love, M. S., Fusaro, C. & Schroeder, D. (2002). Trash or habitat? Fish assemblages on offshore oilfield seafloor debris in the Santa Barbara Channel, California. *ICES Journal of Marine Science* **59** (Suppl. 1), S258–S265. doi: 10.1006/jmsc.2002.1264

Chadwick, H. C. (1929). Feeding habits of the angler-fish *Lophius piscatorius*. *Nature* **124,** 337.

Crozier, W. W. (1985). Observations on the food and feeding of the angler-fish, *Lophius piscatorius* L. in the northern Irish Sea. *Journal of Fish Biology* **27,** 655–665.

Field, J. G. (1966). Part II. The feeding mechanism of the angler-fish, *Lophius piscatorius* Linnaeus. *Zoologica Africana* **2,** 45–67.

Fulton, T. W. (1903). The distribution, growth, and food of the angler, *Lophius piscatorius*. *Twenty-first Annual Report of the Fishery Board for Scotland*, pp. 186–217.

Hislop, J. R. G., Holst, J. C. & Skagen, D. (2000). Near-surface captures of post-juvenile anglerfish in the North-east Atlantic - an unsolved mystery. *Journal of Fish Biology* **57,** 1083–1087. doi: 10.1006/jfbi.2000.1364

Hislop, J. R. G., Gallego, A., Heath, M. R., Kennedy, F. M., Reeves, S. A. & Wright, P. J. (2001). A synthesis of the early life history of the anglerfish, *Lophius piscatorius* (Linnaeus, 1758) in northern British waters. *ICES Journal of Marine Science* **58,** 70–86. doi: 10.1006/jmsc.2000.0991

Laurenson, C. H. (2003). Aspects of the biology and fishery for monkfish *Lophius piscatorius* Linneaus 1758, in waters around the Shetland Isles, Northeastern Atlantic. PhD Thesis, University of Aberdeen.

Løkkeborg, S., Humborstad, O.-B., Jørgensen, T. & Soldal, A. V. (2002). Spatio-temporal variations in gillnet catch rates in the vicinity of North Sea oil platforms. *ICES Journal of Marine Science* **59** (Suppl. 1), S294–S299. doi: 10.1006/jmsc.2002.1218

Montgomery, J. C., Macdonald, F., Baker, C. F. & Carton, A. G. (2002). Hydrodynamic contributions to multimodal guidance of prey capture behavior in fish. *Brain Behaviour and Evolution* **59,** 190–198.

Moyle, P. B. & Cech, J. J. J. (2000). *Fishes - In Introduction to Ichthyology*, 4th edn. Upper Saddle River, NJ: Prentice Hall.

Pietsch, T. W. & Grobecker, D. B. (1990). Frogfishes. *Scientific American* **262,** 96–103.

Smith, W. R. (1891). On the food of fishes. *Eighth Annual Report of the Fishery Board for Scotland*, (Section B), pp. 230–245.

Soldal, A. V., Svellingen, I., Jørgensen, T. & Løkkeborg, S. (2002). Rigs-to-reefs in the North Sea: hydroacoustic quantification of fish in the vicinity of a "semi-cold" platform. *ICES Journal of Marine Science* **59** (Suppl. 1), S281–S287. doi: 10.1006/jmsc.2002.1279

Wright, P. J., Woodroffe, D. A., Gibb, F. M. & Gordon, J. M. D. (2002). Verification of first annulus formation in the illicia and otoliths of white anglerfish, *Lophius piscatorius* using otolith microstructure. *ICES Journal of Marine Science* **59,** 587–593. doi: 10.1006/jmsc.2002.1179

Seabed photography from an autonomous underwater vehicle

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This paper details the development and integration of a digital stills camera system for the *Autosub* autonomous underwater vehicle (AUV). A monochrome Charge Coupled Device (CCD) imager (for amateur astronomy) and a zoom flash (for conventional amateur photography) were selected and prepared for deepwater operation. The system was successfully trialled in the Western Approaches (May 2004) and its first science missionwas carried out in East Greenland (September 2004).

AUTHORS' BIOGRAPHIES

Daniel Jones has a BSc (Hons) in marine biology and an MSc in marine resource management. He is currently studying for a PhD in marine ecology supervised by Brian Bett and Paul Tyler at Southampton Oceanography Centre. His specialist area is in the use of underwater images from towed cameras, remotely operated vehicles and autonomous underwater vehicles to assess seabed ecology in polar deep waters.

Steve McPhail manages the software and electronics development team for the *Autosub* AUV project, with a particular personal interest in the dynamic control, navigation and collision avoidance systems. He has been deeply involved with the *Autosub* project since the outset and has participated in the majority of the *Autosub Science* and *Autosub Under Ice* campaigns, recently heading the *Autosub* technical team in the Arctic 2004 campaign. He also leads the development of the new 6000m depth rated AUV *Autosub6000*.

Brian Bett is a deepsea biologist and leads the DEEPSEAS benthic biology group of the George Deacon Division at Southampton Oceanography Centre. He has a particular interest in the use of photography in the quantitative study of deepsea biology.

Chris Flewellen joined the National Institute of Oceanography, from Bath University in 1969. He worked initially on the design and testing of underwater acoustic transducers. As computers came on the scene he got involved in the development of software for a number of instruments based on microprocessors. After moving with the Institute to Southampton Oceanography Centre, he developed the software for a new deepsea stills camera and then the *Autosub* digital camera.

Mike Conquer trained as a technical photographer and works at Southampton Oceanography Centre. He has assisted with the design of several camera systems including the *Autosub* camera and flash.

INTRODUCTION

Autonomous Underwater Vehicles (AUV) are unmanned, untethered, self-powered submersibles that can be used for a variety of undersea tasks. They are programmed to carry out missions without communication from the surface. The potential of AUVs to gather oceanographic and geophysical data from the world's oceans is large and their operation greatly increases the amount and quality of data that can be obtained from scientific cruises. The Institute of Oceanographic Science Deacon Laboratory (IOSDL), now part of the Southampton Oceanography Centre (SOC), began the development of a scientific AUV called *Autosub*, a 6.7m streamlined, torpedo-shaped vehicle with a free-flooding hull, large payload space and sufficient battery capacity for long range missions. *Autosub* can carry a wide variety of physical, biological, geophysical and chemical sensors to provide scientists with the ability to monitor the oceans in ways not possible with conventional research ships. These sensors can be tailored to the science requirements of the mission. For investigations close to the seabed a camera system can provide very important information on seabed geology and biology, although there are many inherent problems in integrating seabed camera systems into AUVs.

Photography of the seafloor has been very important in the development of marine science particularly in deeper waters.[1, 2] These direct observations of the oceanfloor are critical to understanding the physical, chemical and biological processes occurring there. Photography is a very effective tool for obtaining high resolution quantitative data about geological and biological features of the seafloor over a relatively large area. Deepwater photography is typically carried out using towed camera platforms[3] or Remotely Operated Vehicles (ROV)[4] but these approaches require physical communication with a research vessel. Using an AUV for underwater photography allows the imaging of remote environments that cannot be accessed by standard methods and opens up new possibilities for marine science.

The *Autosub Under Ice* (AUI) programme (http://www.soc.soton.ac.uk/aui) is a UK Natural Environment Research Council (NERC)-funded thematic programme to utilise the *Autosub* AUV to investigate the nature of physical and biological processes beneath polar ice. These high-latitude environments are among the most remote and least known on Earth, but are of considerable significance with far-reaching implications for the global system. This project showcases the unique scientific capabilities of AUVs in an area where sampling by other methods is impossible. For the AUI missions a camera system is very important, and this represents the first opportunity for scientists to see this unstudied environment and gather quantitative ecological and geological data. The camera system needs to take and store regular high resolution photographs of the seabed that show the greatest amount of scientific information and that are of known physical scale to allow the quantification of the data obtained.

ENGINEERING AN AUV FOR SCIENCE

Autosub AUV

The *Autosub2* AUV is 6.7m long, 0.9m max diameter and has a $3.6m^3$ form displacement.[5] Over the last six years it has been used for a wide variety of scientific missions in the fields of ocean physics[6], biology[7], chemistry[8] and more recently geophysics and glaciology in the Arctic and Antarctic.

The vehicle (Fig 1) splits into three sections: rear, central and front. The central section comprises seven, 3m long carbonfibre reinforced plastic (CFRP) pressure vessels, with interstitial spaces filled with syntactic foam. Four of the tubes house the battery system (3900 'D type' primary manganese alkaline cells, total weight = 540 kg) which provided up to 60kWh of energy (depending upon usage rate and temperature). The three other tubes house control and sensor electronics. The CFRP pressure vessels limited the safe operating depth of *Autosub2* to 1600m.

The *rear section* is mainly free-flooding with some extra buoyancy (syntactic foam). It houses essential sub-systems, (eg, navigation, control actuation and propulsion systems) and scientific sensors (eg, digital camera, upward-looking 300kHz RDI Acoustic Doppler Current Profiler (ADCP) and multibeam receiver).

The navigation housing consists of a 150kHz RDI ADCP and Ixsea PHINS fibreoptic gyro-based inertial navigation system (INS). For best accuracy, the navigation system needs bottom locked velocity data aiding from the ADCP, requiring a range to the seabed of less than 500m. With bottom tracked aiding, operational results with *Autosub2* demonstrated accuracy of better than 0.1% of distance travelled, even at high latitudes (as high as 80deg north), where INS systems are generally less accurate. This is of vital importance in under-ice operations, where *Autosub* may need to return to a small area of clear water after a long run under sea-ice or ice shelf. A single brushless direct-drive (no gearbox) dc motor and five-bladed propeller propels the vehicle with a speed range of 1 to 2m/s. A rear mounted rudder and sternplane provides control in yaw, pitch and depth.

The front section is free-flooding and houses other essential sub-systems (eg, forward looking collision sensor and emergency abort system) and science sensors (eg, the Conductivity Temperature Depth (CTD) system and the multibeam transmitter). The control system for *Autosub* was based upon a distributed, networked control architecture.[9] One of the major advantages of such a modular approach is that new sensors can be integrated into the system with relative ease.

Three small hydrophones on the base of the nose section act as receivers for the homing system which guides the *Autosub* back to the mother ship. This facility is particularly useful when the vehicle is operated under mobile sea-ice and it is not possible to predict in advance where there might be an opening in the ice cover suitable for its recovery. The homing system was used to effect safe recovery of *Autosub* in several of the missions during the AUI campaign in August 2004.

Collision avoidance and flight constraints

The *Autosub2* mission control system executes a pre-programmed list (the mission script) of position waypoints, depth, altitude and speed demands. For depth control, at any segment of the mission, the vehicle can be programmed to run at a specific depth, an altitude off the seabed or a distance below an ice-shelf. Safety limits for depths and altitude were set independently of, and override, the mission script demands. For camera work, the constant altitude mode was used. Altitude feedback was provided by range measurements by two of the four downward-looking beams of the ADCP.

The forward-looking echosounder provides a simple measurement of the range to any target ahead of the vehicle.

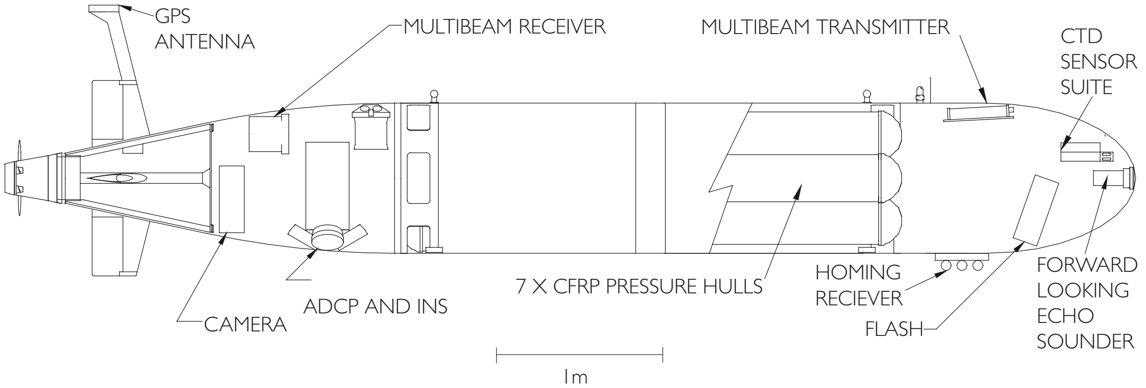

Fig 1: *Autosub2* schematic. The camera is mounted vertically in the tail section and the flash gun is mounted in the nose section, angled back at 27 deg to the vertical (optimum for a flying altitude of 10m)

The collision avoidance system triggers a 'collision imminent' event if the following condition is true:

Collision Imminent Set if (and only if):

1. The range rate was greater than 1m/s for 10sec (the target is approaching continuously)
2. AND the range is less than 100m.

In a collision imminent event, the collision avoidance control system temporarily assumes command of the vehicle. It sets the minimum altitude limit to a safer value (40m). It commands the vehicle to execute a reciprocal course for a set distance (reciprocal course is assumed safe) and then it commands the vehicle to attempt to go around the obstacle. If this fails (a further collision imminent event occurs), then the vehicle repeats the procedure, but with a new, randomly chosen heading offset to the original track. Once clear of the obstacle, the original course and safety limits are restored.

The minimum safe altitude for *Autosub* to fly at depends upon the type of terrain. In smooth, sedimented, well-know terrain it could be flown at altitudes of about 3m, but in areas with rougher terrain or where the terrain is less well know, then a practical minimum safe altitude is 10m.

Camera system

Successful operation of a camera in *Autosub* had a number of implications for the camera system. Integration of a camera system into an AUV brought about limitations on size, to fit into the limited scientific payload space on the vehicle and power consumption of flash and camera. The camera system required autonomy in operation as well as links to the onboard computer systems on the AUV.

The operational limitations of the AUV, particularly with regard to the safe flying altitude of 10m, required solutions for effective photography. Light dissipates through water much faster than through air; underwater photography over a distance of 10m is challenging. Both absorption by seawater and scattering by suspended particulate matter rapidly reduce light intensity. The latter effect can be reduced by minimising the overlap between the illumination and imaging paths. Consequently the camera and flashgun were mounted as far apart as possible, separated by the centre section of *Autosub*. At a flying altitude of 10m (round trip for light of 20m), very little light except blue and violet returns to the camera lens. Even in pure water very little of the red-orange end of the spectrum returns: 99.5% is attenuated. Hence a colour camera was inappropriate and as only one in four (the blue) pixels would register any light, the sensitivity of a colour system would be at best 25% of a monochrome camera. Research during the Antares underwater neutrino experiment[10] measured a blue light (450nm) attenuation length of 60m at 2400m water depth in the Mediterranean. Based on this (most likely best case, the result was close to that of pure water) for our 20m round trip, then only 29% of the blue light would have been attenuated.

The camera system chosen was a Starlight SXV-H9, a black and white CCD imager intended for use by amateur astronomers. The imager used a Sony ICX285AL Exview HAD CCD with square pixels size of 6.45x6.45µm and an imaging area of 1392 x 1040 pixels. This imager was selected for its good photon efficiency in the blue part of the spectrum and low readout noise (about 20 photons rms equivalent). It was mounted on a peltier effect device that lowered the chip temperature as much as 30°K below ambient, giving much reduced sensor dark current. The imager signal was digitised to 16 bit resolution, allowing the high dynamic range of the sensor to be exploited. This high dynamic range allowed useful images to be extracted from data with high levels of back scatter, by subtraction of the backscatter field. This technique has been used in astronomy to good effect to remove the effects of light pollution and it was equally applicable in the underwater, backscatter environment. The camera was fitted with a 25mm focal length cine lens, which with the water/air interface magnification factor of 1.33, gave a field size of 2.7m x 2.0m with *Autosub* flying at 10m altitude (pixel resolution on the seafloor of 2mm square). The camera was installed pointing vertically downwards in the tail section of *Autosub* within a 150mm dia, 400mm long aluminium housing, with a plane glass window.

An efficient flash system was needed to get a good signal to noise ratio. A Minolta 3600HS zoom flash was selected, modified with a fixed zoom setting of 85mm (for a 35mm camera). Tests with a photodiode indicated that 50% of the energy was output within 1000 microseconds (1 millisecond). Given a vehicle forward speed of 1.6 ms^{-1}, then some image smearing (~1.6mm) was expected along the direction of vehicle travel (although this was not apparent in field results). With a well focussed flash, narrow camera field of view and a good (4.5m) separation between camera and flash, the problems of back-scatter from particulates were minimised, as a result of the small intersection volumes of the camera field of view and flash illuminated cone. The flash was mounted in a 100mm dia enclosure, with a glass window and installed in the nose section of vehicle, angled back at 27 deg to match the 10m flying altitude.

Field of view calculations

One of the performance limiting factors for use of such an imaging arrangement was the depth of field (DOF) required. A trade-off must be made between the DOF and amount of light entering the imager as a large DOF required a small aperture (high f-number). In-focus images were required for a flying altitude between 9.5 and 10.5m. The field of view for a camera system, with focal length: f, numerical aperture: N, acceptable circle of confusion: c, range to object: R, is shown in equation 1.

$$\text{DOF}=\frac{2\cdot f^{2}\cdot R\cdot c\cdot(f-R)}{(R\cdot N\cdot c-f\cdot N\cdot c-f^{2})\cdot(R\cdot N\cdot c-f\cdot N\cdot c+f^{2})} \tag{1}$$

With f = 25 x 1.33mm (focal length corrected for water/air magnification factor), N=2.8, c=6.45µm (pixel side), R=10m, the DOF was 3m (±1.5m). This was acceptable and allowed the use of a reasonably large aperture.

Data logging

The camera data logger was a PC104 format personal computer running Labview under Windows 98. It communicated with the camera via a USB port. The raw 16 bit images were written to an 80 Gb hard disc, which could be accessed via the *Autosub* Ethernet link and IEEE802.11b radio link. The ability to download the images from the *Autosub* via radio was operationally very useful. With a radio operating range of 500m, in many cases the images could be downloaded before the vehicle was recovered onto the support ship.

System integration of camera and flash on *Autosub*

A control node microcomputer, connected into the vehicle LonWorks control network, was used to co-ordinate the synchronisation of the camera and flash. The connection of the node into the vehicle control network, with access to the vehicle sensor data, facilitated its programming to fire the camera and flash only when the vehicle was within range (15m) of the seabed. The node also sent the serial number of the flash taken to the vehicle engineering data logger, so that the digital photographs could be referenced to vehicle position, depth and attitude at the instant of the frame. This node triggered the camera 140 milliseconds before it triggered the flash, as the camera took this time to initialise before opening its (electronic) shutter. The shutter was left open for 10 milliseconds. The maximum photo rate was limited by the slow USB-1 interface between the camera and the data logger to one frame every 8 sec.

FIELD OPERATIONS

Trials cruise

The first opportunity to test the camera system was during *Autosub* systems trials in the general area of the Western Approaches in May 2004. The first images proved the viability of the general approach. Images showed good signal to noise ratio (rms noise for a black field is 20 counts: rms signal is 1500 counts). The main technical issue was uneven illumination, owing in part to shading of the flash gun within its enclosure. This can be remedied partially by image post processing to even out the apparent illumination, although the less well illuminated areas at the image edges have lower signal to noise ratio. Raw data from the camera was processed using Matlab and the image files produced using a high pass filter and dynamic range compensation.

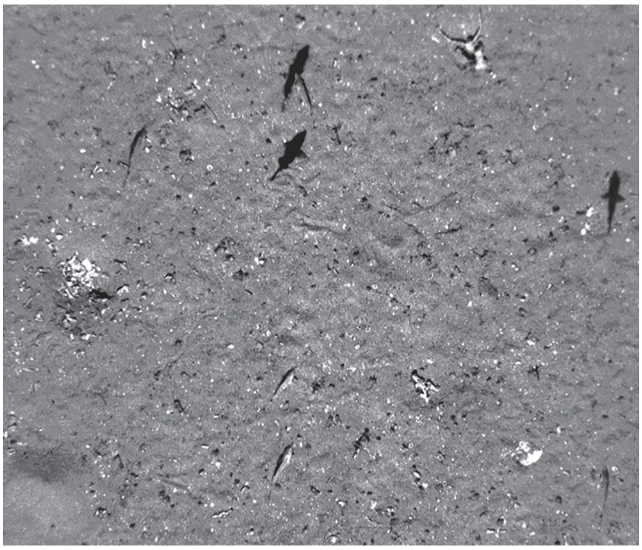

Fig 2: One of the first images obtained by the *Autosub* digital camera in a water depth of 230m. The image area is cropped to 2.0m × 1.6m. Illumination from the bottom of field. Notice the fish shallows, which are more distinct than the fish images. Date: 05/19/04; Time: 19:22:23; Altitude: 10.1m; Depth 229.4m; Position (deg): 48.25321N, 9.5942W; Heading/Pitch/Roll (deg) 271.5, -2.84; -2.77

Arctic deployment of *Autosub*

An arctic deployment of *Autosub* from the RRS *James Clark Ross* was the second of three scientific voyages in the AUI programme. The work was carried out in the Kangerdlugssuaq Fjord system in east Greenland. This is a deep fjordic system impacted by seasonal ice cover and with permanent areas of floating ice from the many glaciers that drain into this area. *Autosub* conducted many successful missions in this area carrying out a suite of different operations, seabed photographs were obtained from two stations at the entrance to the fjord system (Fig 2). Concurrent with the *Autosub* investigations, the SOC Wide Angle Seabed Photography (WASP) towed camera system was operated in areas clear of ice to take photographs of the seabed. This was carried out to provide images, from a conventional towed camera system, that could be compared with the images acquired by *Autosub*. WASP is an off-bottom (2-6m) towed camera platform, operated using an acoustic telemetry system, carrying a vertically mounted still camera and a vertically mounted video camera. This vehicle is typically operated for one hour at the seabed, yielding some 250 still photographs (35mm Kodak Vision 250D colour negative) and continuous video footage (mini digital video cassette).

Comparisons with existing technology

Images obtained from *Autosub* (Fig 3) were broadly comparable with those taken by the WASP vehicle (Fig 4). Despite the differences in operating altitude, each frame showed a comparable average area of seabed. Unlike *Autosub* which holds a relatively constant altitude, WASP ranges in altitude with the ships heave, producing useful images from 2m to 4m altitude (area of seabed covered = 2.35m^2 to 9.41m^2). There was a discernibly higher resolution in the WASP images reflecting the increased resolution of conventional film over

Fig 3: *Autosub* image from arctic Greenland in a water depth of c.600m. The image area is cropped to 2.0m × 1.6m. Illumination from the bottom of field. Date: 09/09/04; Time: 04:16:27; Altitude: 10.31m; Depth 587.8m; Position (deg): 68.03364 N, 31.79108 W; Heading/Pitch/Roll (deg) 36.2, -5.2; -2.45

the CCD imager (1392x1040 pixels). The resolution of the *Autosub* images is nevertheless highly satisfactory for scientific characterisation of the seabed. The monochrome nature of the *Autosub* images did not reduce the scientific value of the image although in some cases identification of some species is aided by colour information.

Generation of scientific data from photographs

The aim of the biological analysis of the arctic *Autosub* mission was to generate scientific data from the photographs. For quantitative investigation it is first necessary to scale the images and calculate the area of seabed shown in each frame, this was achieved using trigonometry from the camera acceptance angles and the altitude of the camera from the seabed using the methods of Wakefield and Genin.[11] Vertically shot images obtained from *Autosub* facilitated such scaling. The fraction of the biological community identifiable in photographs is typically referred to as megafauna.[12] The megafauna in each frame were identified as far as possible, which was greatly aided by concurrent trawl sampling, and numbers of each taxon counted. These values were converted to numbers per unit area. It was often also possible to identify faunal traces or lebensspuren, such as tracks, trails, imprints and burrows in the sediment. These traces were identified and their area measured as a proxy for megafaunal activity in an area. Faunal body size was also measured for abundant or important taxa. The seabed fabric observed was also characterised. In the case of Kangerdlugssuaq, where the seabed was highly heterogeneous as a result of glacially derived material, seabed sediments were classified by particle size following the scheme of Wentworth.[13] To classify seabed type in each frame, 100 random points were projected onto the image and the composition of the seabed at each point noted to give percentage cover of each sediment size class. Geological features were also noted and their presence was assessed in relation to geophysical data (eg, swath bathymetry) obtained concurrently by *Autosub*.

While the scientific results of the arctic fieldwork will be presented in full elsewhere, it is appropriate to present some preliminary observations on the benthic megafauna generated from both the *Autosub* and WASP images of the Kangerdlugssuaq fjord mouth area as an example. Photographs revealed a highly heterogeneous seabed characteristic of iceberg rafting, with sediments ranging from fine sand to large boulders, often over small spatial scales. Multivariate similarity analysis of megafauna revealed three distinct communities in shallow (270-375m depth), intermediate (480m depth) and deep waters (625-720m depth). Faunal abundance was found to decline with depth (from abundances of >60 000 individuals ha^{-1} in the shallow stations to <2000 individuals ha^{-1} in the deeper stations) while diversity increased (Shannon-Wiener diversity index, H' increased from 0.96 at the shallow stations to 2.76 at the deeper stations). Faunal trace area (0.04% total area sampled disturbed by traces in shallow and 1.01% in deep waters) and number (2980 traces ha^{-1} in shallow, 77 440 traces ha^{-1} in deep waters) increased with depth, reflecting a change in dominant feeding strategy from suspension feeders at shallow sites to deposit feeders in deeper waters. There was high within site patchiness of some fauna which may be related to iceberg disturbance.

DISCUSSION

The field operations have shown the capacity for *Autosub* to collect high quality images of the seafloor that are suitable for scientific analysis. Despite reductions in resolution and their monochrome nature, *Autosub* images were otherwise comparable with those taken with existing towed deepwater imaging

Fig 4: WASP image from arctic Greenland in a water depth of 658m. The image area is cropped to 1.4m x 1.0m. Illumination from the right of field. Image originally in colour. Date: 03/09/04; Time: 09:46; Altitude: 2.98m; Depth 658m; Position (deg): 68.0485 N, 31.7610W

systems. While the expense of AUVs will be a consideration in their imaging potential their autonomous nature allows them to be used in remote environments that cannot be sampled with existing technology. In addition, their autonomy from research vessels and ability to work concurrently with other sampling programmes, will make AUVs increasingly important for adding extra data and value to existing research cruises.

As part of the continuing *Autosub Under Ice* programme, *Autosub* will be used to take photographs under the Filchner Ronne ice shelf in Antarctica. The Filchner Ronne ice shelf is one of the biggest on earth, fed by several ice streams draining the West Antarctic Ice Sheet. It is a very challenging environment with permanent ice cover up to 600m thick and seabed depths of up to 1400m under the ice. At the seaward edge of the ice shelf there is a shallow sill, rising from 1000 to 400m deep, which may leave as little as 100m water column thickness in some areas at the ice front.[14] This area will pose some interesting challenges for *Autosub* but may provide the first pictures of this unique environment and some insights into the hitherto unknown benthic biology and geology of the area.

Deploying an AUV in the deep ocean is expensive. Hence it is desirable to maximise the data rate from any sensor system. The two ways of achieving this for a camera system are to use an image sensor with more pixels and to increase the frame rate. The average power needed by the flash system is proportional to the number of pixels and the frame rate. However, the power drain by the camera system from an AUV the size of *Autosub* would not be an issue, even for a multi-mega pixel camera and frame rates up to 1Hz. The present digital camera system produces an image of an area of 2.7x2m at 10m altitude. With the present image rate of one per ten seconds and a 1.5m/s vehicle speed, then the system is under sampling the seabed by a factor of about ten. Although the image rate could easily be doubled, simply by providing a USB-2 rather than USB-1 interface for the data logger, this would represent the maximum for this camera and flash. An example of a sensor with good efficiency and higher number of pixels is the Kodak KAF-16801E(LE), which has a 16 mega pixel monochrome sensor, with good quantum efficiency in the blue region. Given suitable optics, this in itself would increase the data rate by a factor of 11, with options of either better resolution or a larger image area. Its maximum read rate places a limit of one image every 1.6 sec.

Autosub was among the first AUVs to have a camera system. One of the more scientifically important alternative approaches is that taken by the Woods Hole Oceanographic Institution Deep Submergence Laboratory's (WHOI DSL) *Autonomous Benthic Explorer* (ABE) vehicle.[15] This vehicle is unlike *Autosub* in design and more adapted to precise control over considerably shorter range than *Autosub* (theoretical range <50km for ABE, 800km for *Autosub*), ABE has seven thrusters and is capable of movement in any direction much like an untethered ROV. It has a camera system currently consisting of stereo, monochrome, downward pointing digital cameras each providing an image resolution of 576x768 pixels with a dynamic range of 8 bits. When updated as planned the ABE camera system will allow colour imaging as the vehicle can operate closer to the seafloor. These vehicles represent different solutions to AUV imaging for science and hence will have different scientific uses. While ABE-like systems may produce 'better' images over a short range they will not be able to sample in the more remote environments or at the long ranges which vehicles such as *Autosub* are capable of investigating.

A development, parallel to ABE, at the WHOI DSL is the SeaBED vehicle (http://www.whoi.edu/DSL/hanu/seabed/index.html), this represents an alternative approach to AUV imaging. It is a readily available operationally simple AUV designed to rapidly test imaging methods and docking methodologies with the aim of pursuing repeat surveys for change detection and quantification of features. SeaBED is a hover-capable vehicle that performs optical sensing with a 12 bit 1280x1024 monochrome CCD camera, combined with acoustic high resolution mapping systems.[16] The systems and protocols developed with SeaBED will be adopted by larger systems such as *Autosub* and ABE which will allow these new methods to be carried out in deeper and more remote environments.

AUV photography has a number of novel scientific applications beyond the work in remote environments discussed, these are predominantly in high resolution surveys over reasonably large areas. Survey work is the most important area of commercial AUV use,[17] with AUV survey already being explicitly commissioned in deepwater surveys for the oil and gas industry.[18] While this commercial survey work is principally acoustic, it is inevitable that, with imaging technology becoming available, that this survey will extend to imaging. In many respects these applications could be achieved by other, existing technology such as ROVs or towed camera platforms, however, in these cases, the use of AUVs will be justified in terms of time or financial savings. AUVs are particularly suited to high resolution survey over long distances which can be conducted without the need for human intervention. The AUV can be launched then left to carry out the scientific task while the mother ship is conducting other work elsewhere. This was proven in the *Autosub* Arctic field operations where the vehicle was deployed and two WASP stations were surveyed (56512#1 and 56513#1) while *Autosub* was carrying out a photography mission (mission 377). As well as this, the ship requirements of AUVs are potentially low, certainly without the expensive, dynamically-positioned support vessels needed for ROV operations.

One particular aspect of AUV operations, relevant to photography is the unique ability of AUVs to closely follow terrain and maintain a constant altitude. This can be a problem in towed camera studies where only coarse altitude control is possible and as a result, images vary in altitude depending on bathymetry and sea conditions (although typically ±2m), leading to many unusable images for analysis. Surveys carried out by a large class of imaging platforms, particularly operator driven ROVs and towed camera platforms, may typically contain large rotational and scale changes between successive images. AUVs, as a stable platform, will avoid these limitations, facilitating photomosaicking of reasonably wide areas of seafloor.[19] Much current work is going into the design of docking systems, for re-charging and data download, that will allow AUVs to operate for long periods without human intervention.[20] This will expand the scientific uses of AUVs allowing temporally replicated wide area, high resolution imaging without human intervention. AUV docking technology may allow high temporal resolution through increased access to deepwater environments and substantial savings in ship time.

CONCLUSIONS

The following summarise the key points that relate to this paper:

- AUVs have a unique role in science allowing the exploration of remote areas and adding value to research cruises, allowing multiple simultaneous operations.
- Photography has been very important in marine science and the integration of camera systems into AUVs opens a new range of possibilities for science.
- The *Autosub* vehicle represents an important development for scientific AUVs, its torpedo-shaped body houses a variety of instruments for measuring and sampling the marine environment, including a camera system, CTD, ADCP, multibeam bathymetry system and water sampler.
- There are a number of important limitations and requirements for effective underwater photography from an AUV including the optical properties of water, operating altitude and autonomous camera control, image storage and retrieval.
- The *Autosub* camera system overcomes these limitations through a low noise monochrome camera system with flash separation, accurate positioning and terrain tracking as well as onboard computer control of imaging and storage with short range wireless transfer of data.
- Field operations of the Autosub show its potential for deepwater imaging in remote areas. Its design is well suited to long range missions in remote environments without intervention.
- The images produced by *Autosub* are of broadly comparable scientific value to those obtained by traditional deepwater camera systems. The high resolution image produced enable highly satisfactory identification and quantification of biological and geological features.
- There are a number of improvements to the camera system possible within the limitations set by integration into AUVs, particularly data optimisation through increased resolution and image rate. These features will be incorporated into future developments.
- *Autosub* presents an alternative approach to AUV imaging to that taken by other vehicles such as the WHOI DSL ABE vehicle. ABE is designed for smaller scale higher resolution studies whereas *Autosub* represents a longer range alternative that can work in more remote environments.

Autonomous underwater vehicles represent an exciting new phase of marine science where a high resolution, multifaceted study of the marine environment can be conducted without the need for human intervention in the most remote environments on earth. The *Autosub* camera system allows a large number of high quality images, well suited for scientific study, to be obtained in these areas. Seabed imaging highlights pattern and structure in deepwater benthic systems, allowing visualisation of ecosystems, geological processes and formations, complementing other measurements taken concurrently by the vehicle. The approach taken by *Autosub* for imaging is well suited to its next task of investigating the biological, physical, chemical and geological processes under Antarctic ice.

POST-SCRIPT

An *Autosub* campaign to the Antarctic was undertaken on RRS *James Clark Ross* cruise 97. Mission 382 was successfully carried out under Fimbul ice shelf (70°00S 1°25W), penetrating 25km into the under ice cavity. This first mission was run with cautious off-seabed and off-ice ranges and so afforded no opportunities for photography. Unfortunately, on the following mission (383), *Autosub* suffered a failure that immobilised the vehicle some 17km under ice and therefore beyond recovery.

The *Autosub* project will continue with a rebuild of *Autosub3* and the development of a new deep-diving vehicle *Autosub6000*. We hope to continue the camera operation and development with the new vehicles.

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REFERENCES

1. Hersey JB. 1967. Deep-Sea Photography. Baltimore. John Hopkins Press. 310

2. Heezen BC and Hollister CD. 1971. The Face of the Deep. London. Oxford University Press. 659

3. Piepenburg D, Schmid, MK. 1997. *A photographic survey of the epibenthic megafauna of the Arctic Laptev Sea shelf: distribution, abundance and estimates of biomass and organic carbon demand*. Marine Ecology Progress Series **147**: 63-75

4. Starmans A, Gutt J and Arntz WE. 1999. *Mega-epibenthic communities in Arctic and Antarctic shelf areas*. Marine Biology **135**: 269-280

5. Stevenson P, Millard NW, McPhail SD, Riggs J, White D, Pebody M, Perrett JR and Webb AT. 2003. *Engineering an autonomous underwater vehicle for under ice operations*. OMAE 2003. 22nd International Conference on Offshore Mechanics and Arctic Engineering. Cancun, Mexico, 8-13th June.

6. Stansfield K, Smeed D, Gasparini G, McPhail SD, Millard N, Stevenson P, Webb A, Vetrano A and Rabe B. 2001. *Deep sea, high resolution, hydrography and current measurements using an AUV: The overflow from the Strait of Sicily*. Geophysical Research Letters **28**: 2645-2648

7. Brierley AS, Fernandes PG, Brandon MA, Armstrong F, Millard NW, McPhail SD, Stevenson P, Pebody M, Perrett J, Squires M, Bone DG and Griffiths G. 2002. *Antarctic krill under sea ice: elevated abundance in a narrow band just south of Ice Edge*. Science **295**: 1890-1892

8. Millard NW, McPhail SD, Stevenson P, Pebody M, Perrett JR, Webb AT, Squires M, Griffiths G, Thorpe SA, Collins MB, Statham P, German C, Burkill PH, Stansfield K and Smeed DA. 2003. *Multidisciplinary ocean science applications of an AUV: The Autosub science missions programme*. G Griffiths. The technology and applications of

autonomous underwater vehicles. London. Taylor and Francis. 139-159

9. McPhail SD and Pebody M. 1998. *Navigation and control of an autonomous underwater vehicle using a distributed, networked, control architecture*. Underwater Technology **23**: 31-42

10. Montaruli T. 2003. *ANTARES status report*. 28th International Cosmic Ray Conference (ICRC 2003). Tsukuba, Japan, July 31-August 7, 2003.

11. Wakefield WW and Genin A. 1987. *The use of a Canadian (perspective) grid in deep-sea photography*. Deep Sea Research **34**: 469-478

12. Grassle JP, Sanders RR, Hessler GT, Rowe GT and McLellan T. 1975. *Pattern and zonation: a study of the bathyal megafauna using the research submersible Alvin*. Deep-Sea Research **22**: 457-481

13. Wentworth CK. 1922. *A scale of grade and class terms for clastic sediments*. Journal of Geology **30**: 377-392

14. Nicholls KW, Makinson K and Robinson AV. 1991. *Ocean circulation beneath the Ronne Ice Shelf*. Nature **354**: 221-223

15. Yoerger DR, Bradley AM and Walden BB. 1992. *Autonomous benthic explorer*. Sea Technology **33**: 50-54

16. Singh H, Whitcomb L, Yoerger D and Pizarro O. 2000. *Microbathymetric mapping from underwater vehicles in the deep ocean*. Computer Vision and Image Understanding **79**: 143-161

17. Danson EFS. 2003. *AUV tasks in the offshore industry*. G Griffiths. Technology and applications of Autonomous Underwater Vehicles. London. Taylor and Francis. 127-138

18. Knott T. 2005. *Delving deeper*. Frontiers, the BP magazine of technology and innovation **11**: 11-15

19. Singh H, Howland J and Pizarro O. 2004. *Advances in large-area photomosaicking underwater*. IEEE Journal of Oceanic Engineering **29**: 872-886

20. Galletti di Cadilhac R and Brighenti A. 2003. *Docking systems*. G Griffiths. Technology and applications of autonomous underwater vehicles. London. Taylor and Francis. 93-108